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Preface

Widely regarded as second only to direct loss of natural habitats as a threat to native plants and animals throughout the world, the ecological roles and impacts of so-called alien species (often, ‘exotic species’) are a global concern in conservation. Their diversity and effects continue to increase and ramify throughout all major communities and ecosystems, and in a considerable variety of contexts. Many are related to human activities, and others are more natural or fortuitous as increasingly complex novel interactions occur between alien and native species with no history of previous co-occurrence. The outcome is a world that has been described as increasingly uniform with massive erosion of natural regional peculiarities to produce an environment that has been termed the ‘Homogenocene’ or ‘Anthropocene’, in which the extinction of evermore numerous localised and ecologically specialised life forms seems inevitable as biotic homogenisation progresses and adaptable ecological generalists spread and predominate as consequences of human activity and as environments change.

Amongst these, the roles of insects are very diverse – both as aggressors or putative aggressors when they reach new areas, and as the resident (native) victims or beneficiaries of a massive variety of alien insects, plants and other invaders. Both role categories occur in many parts of the world and in many different terrestrial and freshwater environments – essentially, wherever insects are found. Any species reaching a hitherto uninhabited area represents an addition to that area’s biota (some only temporary presences but many species establishing and spreading to become enduring, essentially permanent, additions) and may influence the receptor community strongly in positive or negative ways, or be entirely neutral with a little or no detectable impact.

The ecology and economic importance of alien invasive species has generated immense global and regional concerns, and their study and tailored countermeasures to redress undesirable impacts have led to a correspondingly vast and complex literature. The pioneering book by Elton (1958) was a major stimulus for interest – and some of the examples he discussed are still of major concern, and his influences displayed in the volume edited by Richardson (2011). Elton’s prescient comments on the Argentine ant, for example, were discussed there by Sanders and Suarez

(2011). Numerous other books since the appearance of Elton's volume have dealt with the theoretical, economic and ecological impacts of 'biological invasions' and 'alien species' (with other terms such as 'exotic', 'invasive', 'noxious' and others essentially synonyms unless otherwise specified, and many such species regarded broadly as 'pests') and are accompanied by burgeoning numbers of scientific papers examining both individual cases and wider fields from both practical and theoretical viewpoints. Some themes have come to the fore only well after Elton's book appeared – Richardson and Pysek (2008) noted propagule pressure, risk analysis, multi-scale studies and experimental approaches as examples flowing from more recent approaches to conservation biology and applied ecology in the intervening half century, together with progressive advances in technology and the availability of large data sets. Many more recent accounts display the legacy of the principles enunciated by Elton, and these are elaborated in more recent texts and essays such as those by Mooney and Drake (1986), Simberloff (1986) and Lockwood et al. (2007). Studies range from individual local situations involving single species to global scope for wide 'biodiversity', but each contributes progressively to sound understanding. Some appear in specialist journals (such as 'Biological Invasions'); others in a wide spectrum of broader conservation, ecology, entomology and plant and animal biology journals, symposium proceedings and government agency reports. Collectively, they span considerations of fundamental ecological changes from planned and less purposeful introductions, as well as numerous practical and economically vital aspects of crop and other commodity protection. They thus encompass aspects of pest management, suppression of threats to native biota and ecosystems, quarantine and 'biosecurity' (with accompanying regulation and legislation) to prevent arrivals and establishment, the subsequent spread and ecological impacts and prediction of those impacts in the future, in relation to changes such as climate modifications and changing availability of key resources such as susceptible crops. In short, alien species affect many aspects of human well-being, as well as the integrity of the receiving environments, and the survival of many of the species they contain. Not all those influences are harmful – many alien species confer massive benefits on humanity, and many others scarcely intrude on normal societal consciousness. However, in comparison to the massive concerns over impacts of alien vertebrates and plants, many alien insects gain only a relatively low profile unless they are direct pests or control agents of concern for human welfare – this trend is clear in two recent compendia on invasive species in Australia (Prins and Gordon 2014, with no chapter on insects) and eradication of alien species from islands (Veitch and Clout 2002, with only two insect-focused essays amongst more than 50 case studies outlined). Whilst such biases reflect the predominant major concerns arising from mammals and weeds, in particular, the ecological insights from parallel studies on insects and other invertebrates add enormously to understanding.

In this overview, I bring together some of the massive amount of information available (up to late 2015) on the roles of alien species in insect conservation and drawing on the themes noted above, to illustrate both the concerns that arise from their presence and interactions with native species, and the balances between the benefits and threats they confer. The substantial economic and sociological implications of alien species sometimes result in intense debate – as in some classical biological control programmes against arthropod or weed pests. Collectively, they affect almost all terrestrial and freshwater communities and ecological processes. Members of many plant and animal groups participate and, very broadly, an 'alien species' is simply one living beyond its natural range – often with the connotation of being 'invasive' in continuing to spread and thrive in this expanded distribution. These, and related terms, are often used loosely and are discussed further later in relation to ambiguity of definitions, categorisation and the numerous ecological processes through which such range expansions occur (Chaps. 1, 2, and 3). The major concerns for conservationists relate to impacts of these arrivals on native biota (Chap. 4), with my emphasis here on the fates of native insects. A wide array of direct impacts and intricate cascade effects are involved and are exemplified especially well amongst (1) the interactions between insects and plants; (2) interactions between predators or parasitoids and prey or hosts; and (3) mutualistic associations, in all of which either one or other participating taxon is alien, or both are alien in a new, expanded range beyond their historical arenas. They are exemplified for a variety of taxa and contexts in Chaps. 5, 6, 7, and 8, and the need for each chapter to be self-contained necessitates some minor overlaps of themes. The principles displayed have much wider applications in understanding changes in natural communities and advancing appreciation of the complex roles of alien species in novel environments as a key, and increasing, concern for insect conservation for which increasingly novel management will be needed (Chaps. 9 and 10). This book complements parallel treatments of two other major aspects of 'threat' in insect conservation, with similar ambiguities and varied opinions of balances between harm and conservation opportunity. Those others dealt with the roles of 'fire' (New 2014) and 'urbanisation' (New 2015) to summarise some of the recent increases in knowledge and understanding that contribute to effective environmental management for the maturing science of insect conservation, and appreciation of need for the discipline to continue to develop and contribute to safeguarding this most diverse animal component of non-marine biodiversity. I hope that the roles of invasive species and their effects on native insects, many of them locally endemic and highly vulnerable – so of fundamental conservation interest in addition to their ecological intricacies, may thus become understood increasingly by biologists and others on whom their fates depend.

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Chapter 1
The Significance of Alien Species to Insect Conservation

1.1 Introduction: Alien Species in Insect Conservation

The pursuit of insect conservation is founded in informed management of species, assemblages and their functional environments to sustain them in the face of increasing variety of imposed changes, stresses and threats. Anthropogenic changes to natural environments are perhaps most severe in intensive processes related to the large areas subsumed by urbanisation and related industrialisation, agriculture and commercial forestry, in all of which land cover is changed fundamentally from its original condition. Those changes continue to expand and to progressively inflict dramatic alterations on natural areas, notably of native vegetation, wetlands and freshwater bodies. Many sensitive ecological communities, many of them unique or highly restricted in extent, have been lost, together with the plants and animals they previously harboured.

Direct destruction of natural and semi-natural areas, broadly 'habitat loss', is the most universal of a panoply of threatening processes associated with losses of biodiversity, with impacts that span the entire variety of Earth's biological heritage. Many factors contribute to increased endangerment of insect species – and, in most contexts in which the habitat or biotope is not clearly lost, the relative importance and impacts of these factors remain largely conjectural. Linked intricately with habitat changes, and major contributors to changes in native biodiversity, the advent and impacts of alien species – newcomers to their receptor environments – are also universal, with potential to markedly confound other habitat changes through imposing a range of novel ecological stresses and interactions. They are thus major concerns in conservation management, with the taxa of concern spanning all major taxonomic groups. Most alien species considered are plants, arthropods or vertebrates, but Wagner and Van Driesche (2010) also included invasive pathogens and detritivores in their review of impacts and drawing largely from North American contexts.

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Together, habitat despoliation and alien species dominate much conservation concern, as the twin ‘core threats’ on which others become superimposed, and their impacts enhanced. More broadly, invasive aliens are one of five major ‘drivers’ of population declines and species losses, together with habitat degradation (as above), climate change, pollution and overexploitation, each of which interacts with others and also with the biological idiosyncrasies of species, and of the ecosystems in which they occur. Insects may respond especially rapidly to changes in these drivers and Comont et al. (2014, following other workers) noted the need to elucidate alien species impacts within this broader array of ‘threats’ and to examine impacts and losses at the population level (as extirpations) rather than just more widely (as extinctions). Conservation concerns associated with alien species fall broadly into two intergrading categories, which are recurrent themes in this book: (1) the direct and indirect impacts of alien species themselves when they encounter a new environment and biota and necessarily form novel ecological associations which may ramify widely in the receiving environment, and (2) the impacts of measures imposed to suppress or eradicate alien species that are deemed undesirable. Paradoxically, those measures may involve deliberate introductions of further alien species (such as by being classical biological control agents, p. 135), and fears for their impacts on native biota have been prominent in some recent conservation discussions. Concerns for impacts of alien species on native insects span all accessible terrestrial and freshwater environments. However, those impacts occur at several measurable levels. Reviewed by Parker et al. (1999), those levels are (1) effects on individuals, such as growth rate, dispersal and mortality; (2) genetic effects, including hybridisation; (3) population dynamics impacts; (4) community impacts, such as on diversity and trophic relationships; and (5) impacts on ecosystem processes. Historically, impacts on populations have been most studied, with extinctions of native species the extreme outcome of conservation concern and related directly to regarding alien species as ‘threats’. Synergistic impacts may occur from multiple invasive species in the same environments, and are often difficult to separate, or to allocate to each individual contributor. In South Africa, Argentine ants (*Linepithema humile*) benefitted from the presence of alien trees (pines or eucalypts) because the tree cover led to less extreme hot or cold conditions at different times of the year (Schoeman and Samways 2013). A parallel effect was that the same canopy also gave more constant conditions over the year, so that *Linepithema* could maintain its abundance. Significant effects on native ants varied greatly across species and seasons, but ‘naturalness’ of the sites was important for sustaining native ant species richness.

Particular concerns may arise if so-called ‘foundation species’ are affected, as occurs frequently from invasive insect impacts. These are those ‘key’ species that create and stabilise the local conditions and processes that define the structure of local native communities; they can include, for example, the predominant tree species that characterise regional forests in which highly characteristic arthropod communities occur. One such example is Eastern hemlock (*Tsuga canadensis*) in eastern North American forests and highly vulnerable to attack by the Hemlock woolly aphid (*Adelges tsugae*, Adelgidae), introduced from Asia (Adkins and Rieske 2013).

The aphid can potentially lead to massive changes in forest structure, resulting from extensive mortality of *T. canadensis* and its elimination from local landscapes, with changes also in biogeochemical recycling and ecosystem functions. Adkins and Rieske, endorsed through studies cited by them, demonstrated serious consequences for insects and other taxa associated with the hemlock, and that shifts in forest structure from *Tsuga*-dominated to deciduous-dominated led to changed balance amongst selected arthropod groups over their 2-year study. Assessed only at the family level, greater representation of millipedes, isopods, Staphylinidae and Formicidae in the deciduous-dominated stands indicated that they might benefit from the transformation.

Very broadly, environmental damage caused by alien invasive species manifests through species extinctions and reduction of biological diversity, with changes in composition of resident assemblages through losses of, especially, ecologically specialised native taxa and leading to changes in ecosystem functions. This arises because the alien species (1) in some way reduces and/or displaces populations of native species; (2) modifies the food webs (trophic structure) within the receiving community; or (3) induces other disturbances that decrease ecosystem integrity or 'health', perhaps predisposing it to further vulnerability. Most such impacts have been reported as changes in distribution, abundance and reproduction of affected native species, in addition to more dramatic extirpations. Some impacts are highly localised, and landscape heterogeneity may help to counter some invasive species impacts by imposing a mosaic of resilience to invasion. Ant communities can thus differ markedly amongst neighbouring areas based on vegetation structure, and such a comparison in southern California implied that locally increased species richness and unique ant assemblages on fragments might be associated with ability of the Argentine ant (p. 159) to colonise (Staubus et al. 2015). Correlations suggested that this alien ant had only limited capability to colonise non-native grassland and sage scrub, leading to recommendations that sustaining a mosaic of these may be valuable in conserving native ant biodiversity. Inland sage scrub fragments (with lower Argentine ant invasibility) supported higher ant richness than more heavily invaded fragments in coastal areas. It was also clear that non-native grasslands, especially in areas where no native grassland remained, were significant for conservation.

Although relatively rarely considered, novel interactions can also influence the evolution of the native taxa by selective pressures from aliens (Strauss et al. 2006), and facilitate adaptation of the natives to alien presence. Adaptive changes may lessen harmful impacts of invasive species and foster coexistence, so that consideration of any such outcomes contributes to understanding long-term impacts of alien species. Reviewing the complex themes involved, Strauss et al. showed that characteristics of both the invader and the affected native species may determine any evolutionary responses, as in Fig. 1.1. A significant evolutionary response may be expected, for example, if the invader has strong ecological impacts that affect native genotypes differently, and when the native species' population size is large enough to withstand impacts and contains sufficient genetic variability for selection to act upon. More usually documented, if the invader's impact is strong but does not

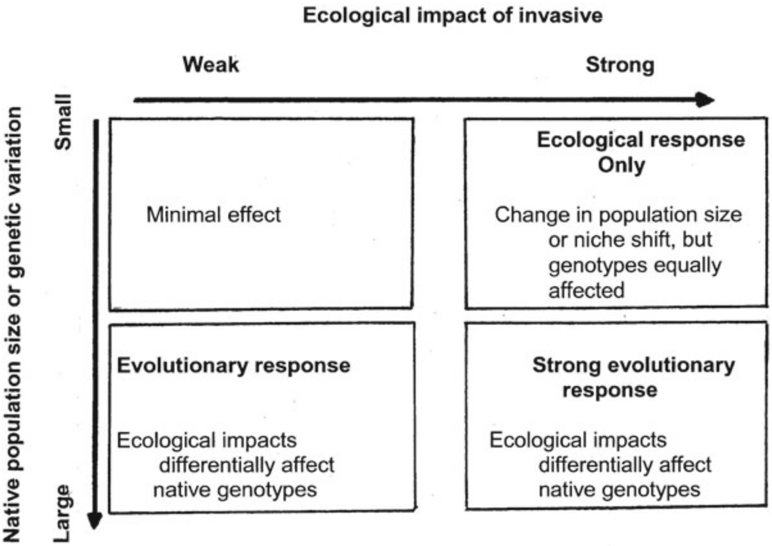

Fig. 1.1 The influences of characteristics of the invasive species and the affected native species on the likelihood of an evolutionary response. The invasive species' impact ranges from weak to strong, and the genetic variation or population size of the native species ranges from small to large. If an invader has strong ecological effects, genotypes of the native species may be affected differentially and, if the native species has a sufficiently large population to withstand those ecological impacts, an evolutionary response may occur (Strauss et al. 2006)

differentially affect native species' genotypes, the native may respond by declines of flexibility in habitat or resource use, but have no such evolutionary responses.

Allocation of species as either native or alien can be difficult and, as Carlton (1996) emphasised, the common default position is to classify species with no clear record of introduction as natives, in some cases regarded as cosmopolitan because of their broad distributions. Many species, however, cannot be allocated reliably to one or other category, and Carlton advanced the term 'cryptogenic species' for those that are not demonstrably native or introduced. In the marine environments he exemplified, many such species occur and, as they may by far outnumber currently recognised alien species, true outcomes of analyses of invasive species richness may be more difficult than supposed from unambiguous cases. Listing of invasive alien species is highly uncertain (McGeoch et al. 2012), and has been approached most reliably in Europe (where, in general, the biota have been explored and documented more thoroughly than in most other parts of the world), through the DAISIE (Delivering Alien Invasive Species Inventories for Europe) project, for which outcomes for arthropods are discussed by Roques et al. (2010). The rationale of that project consolidated contributions from 15 countries to produce an integrated inventory of all alien species as a continuing project to 'describe patterns and evaluate trends in biological invasions in Europe, identify priority species and assess their ecological, economic and health risks and impacts' (Hulme and Roy 2010). A key

Table 1.1 The categories of error that can occur in listing invasive alien species, as identified from published information by McGeoch et al. (2012)

Error	Explanation
Human error	Misidentifications; errors in data entry
Incomplete information searches	Incomplete evaluations
Species identification	Misidentifications from taxonomic uncertainty, including undescribed species
Survey information on presence, extent, population dynamics outside indigenous range	Failure to recognise invasive species due to lack of information on establishment or spread
Resolution of data and scaling of 'alien range'	Overestimate from coarse resolution of distribution maps and related documents; extralimital species (introduced outside the natural range) may not be recognised as invasive, so are not considered
Data and knowledge not documented	Not available in publications or organised databases; existing documentation outdated – eradicated/extirpated species may remain from earlier listing
Documented data and knowledge not readily or widely accessible	Much 'grey literature' not accessible; language barriers may exist; collation problems common
Baseline information on indigenous range	Inadequate information may lead to subjective interpretation
Research on biodiversity impact	Limited information on biodiversity impacts can lead to incorrect listing decisions
Species designation as 'invasive'	Wide spread of definitions lead to differences; different approaches to designations

component of DAISIE is the European Alien Species database, a major factor in Europe becoming the continent with the most complete information on its alien biota, initially summarised in a handbook by DAISIE (2009).

Elsewhere, in particular, many lists of alien invasive species – in themselves the foundation for concerns, and setting priorities for policy and management of biological invasions – almost inevitably contain numerous errors or are highly incomplete. Ten forms of error were identified by McGeoch et al. (2012) (Table 1.1) and the magnitude of many of these is itself very difficult to infer. Many of the errors flow from inadequate knowledge – for insects and other invertebrates, the highly incomplete taxonomic and distributional information for many taxa is a major component of uncertainty over much of the world. Each category in Table 1.1 reflects such limitations, and such errors are easily perpetuated. Taxonomic uncertainty is, perhaps, amongst the most important parameters for many insects, and eight of the ten error categories relate to basic knowledge and how it is acquired, with insufficient data on identity, distribution and impacts of invasive species especially important. Differing opinions by specialists in any taxonomic group ('expert judgements') can be highly influential in constructing inventories. McGeoch et al. (2012) found inter-specialist differences of 30–60 % for specific taxon-country contributions.

Table 1.2 The key tactics available to reduce uncertainty in listings of alien invasive species, each addressing a range of the ten error categories listed in Table 1.1 (After McGeoch et al. 2012)

1. Continuing and expanding (especially geographically) investment in invasive alien species research and monitoring – especially taxonomy, abundance, distribution, impact
2. Support for regional and global efforts to improve accessibility of information through inventory and collation of information on invasive alien species, and making these available electronically
3. Adoption of measures to improve transparency, repeatability and communication of listing methods, with standardised use of terms and concepts
4. Greater attention to understanding the location, nature and extent of linguistic uncertainty on the invasive alien species listing process

They suggested several key tactics towards improving accurate listings of invasive alien species by reducing the effects of these errors (Table 1.2), not least that of greater attention to what they termed 'linguistic uncertainty' (below) – the variations and inconsistencies in terms, definitions and coverage across different regions and recording systems.

However records may be accumulated and interpreted, and however their included species may be categorised (Chap. 2), inventory surveys in highly altered environments can reveal unexpectedly high diversity of purportedly alien species, and their richness in many more remote and supposedly more natural ecosystems is often also high. At both these environmental extremes, their presence and influences may not be evident through species richness estimates alone. Relatively little change in the overall number of species may be found, and this does not reveal that many endemic resident species have been lost and replaced by aliens, in some cases from the direct effects of those alien species. Many of the most invasive alien species have become almost cosmopolitan, so have near-global impacts. Others have caused concerns in single or otherwise restricted areas, notably on small islands or in otherwise localised but vulnerable ecosystems. Alien species, especially when invasive, represent 'a significant component of global environmental change' (Vitousek et al. 1997) in both island and continental environments. Biotic homogenisation, in essence the loss of regional species distinctiveness, is a broadly predominant component of that change.

Enhanced rates of extinctions of local endemic species and losses of genetically distinct populations are among the most difficult impacts to counter or predict. The severity and diversity of such problems are recognised widely, and continue to be addressed by ecologists and managers. However, formidable challenges arise in seeking how best to sustain highly vulnerable ecologically specialised species and wider entities as the variety of invasive alien species and their impacts continues to burgeon. Much emphasis in invasion biology thus continues to be on predicting the outcomes of invasions, by seeking generalities amongst invading species to discover attributes they may share in influencing their establishment and subsequent rates and extent of spread. However, predicting the fate of any particular invasion remains highly uncertain. Despite some unifying features by which particular invasive species may be regarded as universally severe, characteristics of the receiving environment and native assemblages there may be highly influential. Mosaic disturbance habitats, exemplified well by urban and agricultural matrices, provide a considerable variety of environmental conditions, with the changes from primarily more natural conditions often facilitating adventive species. Those changes have most commonly been assessed along some form of environmental gradient – urban-rural gradients, for example, purportedly display changes in assemblages from highly disturbed (urban) through moderately disturbed (suburban) to most natural outermost (rural) sites (New 1915, for examples) and, in the wider context of alien invasive species have provided examples of their facilitation by some level of intermediate disturbance. Thus, in San Francisco (California) the highest ant abundance in seminatural habitats usually included only two species, the invasive Argentine ant (*Linepithema humile*, 81 % of the overall 19,450 worker ants trapped at baits during survey) and the native Winter ant (*Prenolepis imparis*) (Vonshak and Gordon 2015). One interpretation of this was that the invasive ant competed successfully with native species, and did not encounter the more diverse competition with other alien species in more urban environments. Three of the four ant species regarded there as 'urban exploiters' were alien species.

The wide array of ecological consequences from biological invaders occur through an equally wide range of mechanisms and spatial and temporal scales. As Ehrenfeld (2010) emphasised, no single mechanism or pathway can account for all observed ecological changes. The same invasive species may have very different impacts in different places and contexts. In short, some impacts of alien invasive species are often initially obvious, but both ecological and economic outcomes can be difficult to quantify or anticipate. Much investigation of impacts is retrospective, occurring only after the alien is evident – as a pest, nuisance, benefit, or simple curiosity. Most attention, not surprisingly, has devolved on species that are important in agriculture and forestry, or medical and veterinary fields, with appraisals of wider impacts very secondary to direct economic or health effects on human or industrial welfare. For many of these species and contexts, predictive modeling of impacts can draw on an increasingly documented information base. But, as Canyon et al. (2011) noted for invertebrate invasions in Australia, local impacts may be easier to obtain but 'broader effects are confounded by too many factors to enable a reasonable level of certainty in any conclusion'. They asked, for example, how the damage done to the environment by insecticide spraying over mangrove swamps to eliminate invasive disease vector mosquitos breeding there – a practice long of concern to conservationists in the region – might be properly assessed. Invasive mosquitoes are, indeed, one of very few groups of aquatic insects for which invasions have become a concern. Most information on invasive insects has been on terrestrial species and de Moor (1992) noted that 'aquatic insects are seldom regarded as invasive species', with many of the major aquatic insect groups (other than Odonata) regarded as poor colonisers and unlikely to be moved by people, other than by accident.

Impacts of alien plants (in the contexts discussed by Groves 2011) in natural ecosystems vary far more to people's perceptions than do alien plants in agricultural systems. There, aliens are usually identified more accurately and their costs established more reliably. Similar contrast applies to insect invaders, many of which do not come to human notice other than in applied contexts. However, and again emphasised for plants in Australia, many widespread alien species occur in both natural and agricultural systems, with their relative impacts dynamic.

Many of the themes noted in this brief perspective are discussed more fully in later chapters. Some of the problems of assessing impacts of alien species on insects and their critical resources also draw on many aspects of 'classical ecology' to elucidate their importance in conservation.

1.2 Semantics and Understanding

Understanding the various processes associated with alien species arrivals and establishment as residents in novel areas is hampered by imprecise definitions that may lead to a variety of interpretations. In their observation that 'terminological confusions are common in and between research, management and public policy publications and discussions regarding invasive species', Reymanek and Randall (2004) also emphasised that those differences have considerable potential for poor communication and inappropriate management and policy decisions that determine whether, and how, to respond to the species concerned. Thus, it is central that alien species can have 'impacts' on the receiving environments, as discussed above, but the term is often not defined and clear interpretation is hampered. Jeschke et al. (2014) urged the need to remedy this, and devised a series of key questions to help address the needs. These were allocated amongst four categories (Table 1.3) and derived from published examples. 'Directionality' reflects that many studies focus only on potential for harmful impacts, whilst the complexity of ecological systems may induce a mix of both harmful and beneficial outcomes. 'Classification and Measurement' is also subject to value judgements, with different stakeholder groups

Table 1.3 The four suites of key questions that can help to define impacts of non-native species (After Fig.1.1 of Jeschke et al. 2014)

Category	Question
Directionality	Are only unidirectional changes considered or are bidirectional changes considered?
Classification and measurement	Is the definition as neutral as possible or are human values explicitly included?
	Is the term 'impact' only used if the change caused by a non-native species exceeds a certain threshold, or is it used for any change?
Ecological or socioeconomic change	Are ecological or socioeconomic changes considered, or both?
Scale	Which spatio-temporal scale is considered?
	Which taxonomic or functional group and levels of organisation are considered?
	Consideration of per capita change, population density, and range?

Table 1.4 Six key features that affect the incidence and magnitude of alien pest impacts on forest ecosystems, as exemplified by Lovett et al. (2006)

Pest
Mode of attack – e.g. defoliators, sap-suckers, borers
Host specificity – e.g. specific to single tree species/genus, or polyphagous; particular age or size class of the tree population
Virulence – e.g. widespread host mortality; if so, rapid or more general decline over many years; resistance of tree or stress susceptibility
Tree
Importance – is the host tree a dominant component of the forest?
Uniqueness – does the host tree have any unique/unusual properties in the ecosystem, such as nitrogen fixation, large seed crops, rapid regeneration after disturbance (etc.)?
Phytosociology – does the host tree tend to grow in pure stands or with other species that do not suffer attack? What is its place in successional dynamics of the forest? How effectively does it regenerate after mature trees damaged or killed?

valuing an alien species' effects in different ways – for example, of an introduced pollinator being valued positively by crop growers, but feared by conservationists for its wider competitive impacts on native species. Threshold levels of change (or of alien abundance) are a related concern. 'Ecological or socio-economic changes' are not always considered together and, whilst appearing commonly to be correlated, may not be so: Jeschke et al. used the example that a strong ecological impact (such as a species extinction) need not necessarily correlate with a strong socio-economic impact. The final category, 'Scale', emphasises the variety from local to broad-scale impacts, short or long-term effects, and from specific to more general changes. The third term in this category reflects the complexity discussed by Kumschick et al. (2015) (p. 91).

The variety of ecosystem-scale impacts, as the most difficult to study and circumscribe, are illustrated by some key alien insect pests in North American forests, used by Lovett et al. (2006) to devise a conceptual framework for potentially assessing those effects. They distinguished short-term impacts (such as defoliation leading to tree death) and long-term effects (culminating in changes to forest structure and productivity, leading to widespread alterations in nutrient and water cycles, litter quality, and other parameters affecting habitat suitability for numerous insects and other animals). Six key factors influence the extent of those changes (Table 1.4), with knowledge of these enabling ecologists to make initial predictions of the likely type and magnitude of impacts. The two insect examples they discussed (Gypsy moth, *Lymantria dispar*; Hemlock woolly aphid, *Adelges tsugae*) are amongst the most significant and most intensively studied forest pests, and much of the focus has been on short-term impact, much of it on the most important tree species in native forests. The six categories of factors vary independently, and numerous combinations are possible. However, the kind of predictive generality devised by Lovett et al. is exemplified by 'the most severe long-term impacts would be expected from a virulent, host-specific pest attacking a dominant and unique tree species that grows in nearly pure stands'. Such trends accompanied their belief that species shifts from impacts of alien pest and pathogens may become predominant drivers of ecosystem change, leading Lovett et al. to urge conservation efforts to eliminate transfers of known pest and disease species.

Even more broadly, adjectives such as ‘alien’, ‘non-native’, ‘exotic’ or ‘invasive’ are amongst the many ecological descriptors that are often used loosely and ambiguously to denote known adventive species, often subjectively (Colautti and Richardson 2009), and leading to inconsistencies in interpretation and some difficulties in comparing different accounts. They are major contributors to the ‘linguistic uncertainty’ component of evaluation error in listing or enumerating species of concern. Colautti and MacIsaac (2004) showed that development of a ‘neutral terminology’ based on the stages of the invasion process might help to overcome this by providing a more useful operational framework that unifies ecological understanding and management processes. They exemplified the problem by listing a series of published definitions of ‘invasive’, namely (1) a synonym for non-indigenous; (2) an adjective describing a native or non-indigenous species that has colonised natural areas; (3) describing a non-indigenous species established in cultivated areas (where non-invasive) to distinguish it from such species established in natural habitats; (4) descriptive of widely distributed non-indigenous species; and (5) widespread non-indigenous species that have adverse effects on the invaded habitat. The last of these is adopted widely in conservation protocols, but has also been criticised heavily for overlooking earlier phases of the process. A consensus amongst such diverse interpretations has clear value in reducing confusion and gaining consistency in use and understanding (Colautti and MacIsaac 2004). Such uniformity seems unlikely to occur in the near future, but these authors also emphasised need for workers to provide clear objective designations of such terms to managers and others to whom the tasks of practical conservation may fall. Functional designations may have considerable value – thus, for plants, Ballard et al. (2013) designated ‘non-native species’ as ‘species introduced from areas outside of local food webs’ and replacing native vegetation. The central stages of arrival, establishment and invasion are discussed in Chap. 3, but a major reality – that the process of becoming invasive is a culmination of a sequence from establishment and local spread, followed by increased abundance – is noted here for clarity. Many alien species are not invasive.

In a further attempt to clarify the confusing nomenclature related to invasions and to seek generality, Davis and Thompson (2000) devised a scheme based on coloniser features, and including three hierarchical dichotomies. First, the dispersal or movement distance may be ‘short’ or ‘long’, this being scale-dependent but short implying movement between adjacent or nearby environments and long implying crossing some form of barrier to a more distant environment. Second, a coloniser may be ‘common’ or ‘novel’, reflecting whether the coloniser is native to the region or a new arrival extending its range. These terms need definition in the context of any individual study, to include features such as successional changes and progressive colonisations. Third, the coloniser’s impact on the new environment led to separation of those that had a small impression from those with a large impression. Summarised in Fig. 1.2, this scheme presents distinctions between eight different

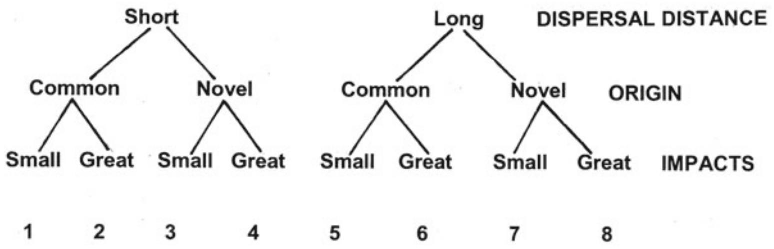

Fig. 1.2 The eight categories of 'coloniser' (1–8) resulting from a classification scheme based on dispersal distance, origin of the colonising species, and impacts in the new environment (Davis and Thompson 2000)

Table 1.5 The eight categories of colonisers differentiated by Davis and Thompson (2000) by the features of dispersal distance (Short *Sh*, Long *L*), origin in the region (Already present *C*, Newcomer or novel *N*), and pressures or impact on the environment (Small *Sm*, Great: *G*)

Type	Characteristics	Comment
1	Sh, C, Sm	Diffusion coloniser with negligible environmental impact
2	Sh, C, G	Diffusion coloniser with large environmental impact
3	Sh, N, Sm	Diffusion coloniser, newly arrived and with negligible environmental impact
4	Sh, N, G	Diffusion coloniser, newly arrived and with large environmental impact
5	L, C, Sm	Long distance disperser already within range, with negligible environmental impact
6	L, C, G	Long distance disperser already within range, with large environmental impact
7	L, N, Sm	Long distance disperser novel to region, with negligible environmental impact
8	L, N, G	Long distance disperser novel to region, with large environmental impact

categories of coloniser. Type 1 are short distance colonisers, not undergoing range expansion and typified by species moving into a local site following disturbance. At the other extreme, Type 8 comprises long distance dispersers colonising a new range, where they have substantial impacts. They include what Davis and Thompson called the 'quintessential invaders' that spread rapidly in their new environments and often have major consequences for native biota and human welfare. Features of the eight types are summarised in Table 1.5. Four (1, 2, 5, 6) are principally colonisers during successions, two (3, 7) expand ranges without serious impacts, and the remaining two (4, 8) are those best assessed as invaders. From the perspective generated by this scheme, Davis and Thompson (2000) regarded 'invasion' as fundamentally a special form of the wider process of 'colonisation'. Any species, however, may fall into different categories in different circumstances, with its opportunities and impacts not always predictable. Very commonly, 'invasive' has connotations of causing harm and, indeed, is sometimes defined with that emphasis; according to

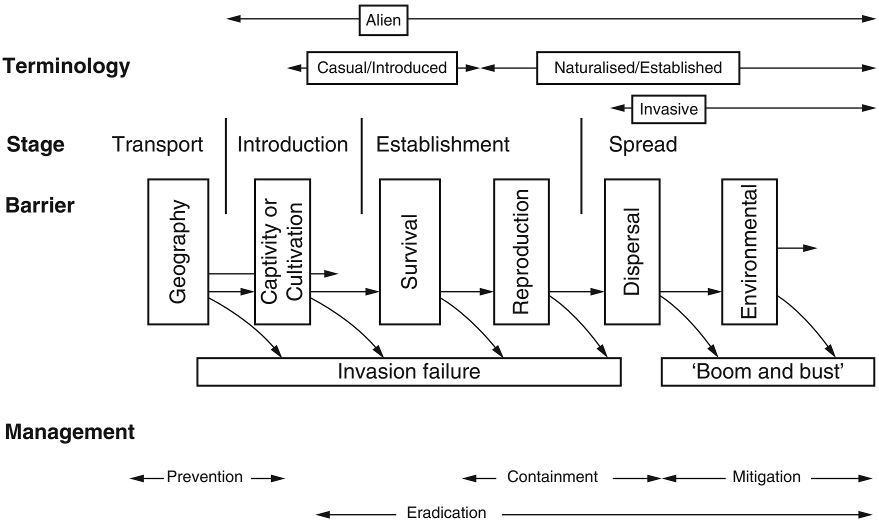

Fig. 1.3 A suggested unified framework for biological invasions, recognising that the process constitutes a series of stages, each imposing a barrier that must be overcome in order for the species to move to the next stage, and indicating generalised terminology used to categorise stages and describe species (Based on Blackburn et al. 2011)

Chornesky et al. (2005), an invasive species is 'a species that is not native to an ecosystem and whose introduction does or is likely to cause economic or environmental harm or harm to human health'.

An important approach towards a unifying framework to describe the sequence of the invasion process acknowledged that the different frameworks adopted by various workers have led to 'a confusing range of concepts, terms and definitions' (Blackburn et al. 2011). Their approach helped to characterise populations at different stages of the invasion process, recognising that barriers at each stage must be overcome by the invader. That scheme (Fig. 1.3) marks a major advance in understanding and describing the process. In various slightly modified forms this scheme has been anticipated or repeated elsewhere.

Many studies on invasive species report differences in native species richness and abundance, and of assemblage composition, between invaded and uninvaded areas and attribute differences to the impacts of the invader(s). Many are also single 'snapshot' comparisons based on limited periods of survey or observation. Moller (1996) noted that such studies may not reveal whether the invasive species cause such differences, or such differences occur beforehand and are those features that enable the potential invaders to invade. Longer-term perspective from repeated (interval) surveys to elucidate the dynamics involved give information that cannot be gleaned from single occasion samples. Studies of the same areas before and after invasion are needed, to provide inventory and characterise the environments on which impacts may ensue.

Table 1.6 The continuum of six 'trophic effects' that can help to assess the impact of an introduced natural enemy on a rare or endangered species (Ehler 2000)

Stage	Trophic effect
1	Feeding (parasitising, infecting), but no development of progeny
2	As in '1', but incomplete development of progeny
3	As in '1', but with development from egg to fecund adult
4	As in '3', leading to reduction in population density
5	As in '4', but leading to local extinction
6	As in '5', but leading to global extinction

One such study involved surveying distribution of the alien Big-headed ant, *Pheidole megacephala*, in Australia's Northern Territory 9 years after an initial survey, re-surveying the same area and including a site not infested on the first occasion (Hoffman and Parr 2008, following Hoffman et al. 1999). Over that period, *P. megacephala* had increased its range from about 25 to 45 ha, predominantly in shaded moist areas along drainage lines. Its biomass in infested sites was up to 18 times greater than that of native ants in uninfested areas, with some sites showing more than 20-fold increase since 1996. The native epigaeic fauna had almost completely disappeared, with no native ants found on the earliest infested sites – a major contrast with the first survey and reflecting a period over which the invader had exerted major competitive advantage over the native fauna, leading to an overall decline in macro-invertebrate abundance.

Impacts of alien species on individual rare or threatened native species can be categorised along a gradient of increasing severity and concern, as suggested by Ehler (2000). His six 'trophic effects' (Table 1.6) comprise the first three demonstrating increasing capability to use the species of concern, and a second trio showing increasing scale of impact. The wider focus of this book is on interactions between alien species and native insects, and the conservation implications of those interactions, but the study of alien invasive species has much wider importance. Significant insights into fundamental ecological and evolutionary processes may flow from studies of invasions (Sax et al. 2007), and the key needs in assessing conservation impacts are understanding the processes by which alien invasives arrive, establish and spread, and those by which they interact in novel environments and influence the native species and biotopes they encounter. The most serious concerns arise from invasives that have moved into natural environments, many such species straying from the anthropogenic milieux in which they were present initially – some as deliberate introductions for human benefit, but many others unplanned arrivals. Nevertheless, as Sax et al. noted, the crucial impacts from species invasions have 'fundamentally informed our views on many issues based on the changes that result'.

Interactions between native and alien invasive species are most commonly assessed as 'direct' – through the key interactive processes of herbivory, predation, parasitisation, competition or mutualism – or ‘indirect’, such as by modifications to habitat or by interactions affecting resource supply and leading to changes in the population biology of the native species (Sakai et al. 2001). Many such interactions are rather simplistic, but all have potential to cause concern. The interactions are sometimes viewed as coming from two ‘directions’, with the relative importance of ‘bottom–up’ (impacts of plants on herbivores and higher consumers) and ‘top-down’ (impacts of predators, parasitoids and herbivores on the food species) often difficult to assess. The most frequently cited conservation concern, the impacts of alien plants or alien predators and parasitoids on native insect herbivores, needs sound interpretation of broader community level processes to facilitate understanding (Harvey et al. 2010). Thus, alien plants might (1) have less harmful impact on predators or parasitoids than on their prey or hosts, or (2) be more attractive to natural enemies of potential herbivores than are native plants. Such possibilities led Harvey et al. to nominate four areas of research as priorities to enhance knowledge: (1) effects of plant quality (based on chemistry) in native plants and related invasive plants on the qualities of both native herbivores and their natural enemies; (2) field studies to explore roles of herbivores and natural enemies on plant defence traits, competitive interactions with neighbouring plants, and plant ‘fitness’, through comparisons of herbivores and natural enemy assemblages on native plants and related invasive species; (3) comparisons of total food webs associated with native and related alien plants, indicating extents and rates of change within native invertebrate communities as they adapt to new plants; and (4) comparisons of regional effects of communities associated with plant roots in native and alien plants on the behaviour and performance of herbivores and their natural enemies. Multitrophic interactions are central to penetrating the mechanisms by which alien invasive species affect native biota, with roles of plant volatile chemicals a key element of this (Harvey and Fortuna 2012). These can be attractant or repellent and some may be produced directly in response to herbivore larvae feeding, so presence of such consumers can be instrumental in attracting natural enemies and affecting their foraging behaviour. Such intricacies are widespread amongst co-evolved species in native communities, and clearly subject to disruption by invasive taxa.

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Chapter 2
The Diversity and Impacts of Alien Species

2.1 Introduction: The Diversity of Alien Species

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

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

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

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

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

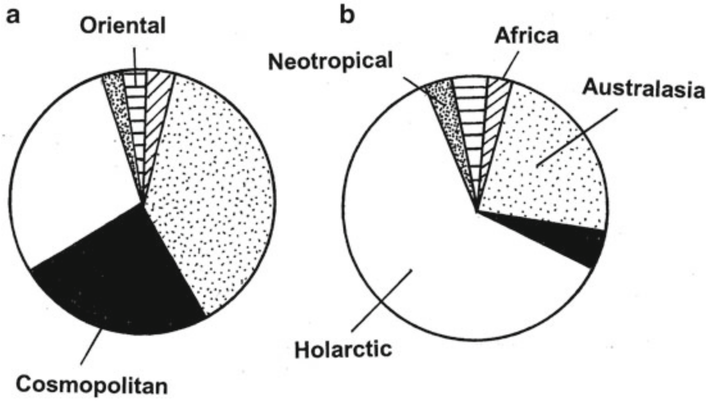

Fig. 2.1 The origins of alien species of Hymenoptera established in New Zealand, indicating differences between (**a**) unintentional introductions and (**b**) intentionally released species (Ward and Edney-Browne 2015)

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

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

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

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

No other order has any entry above 4 %

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

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

2.2 Alien Species in Invaded Ecosystems

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

Predominance and functional dominance of alien insects in feeding guilds on remote islands is exemplified by the parasitoid wasp fauna in Hawai'ian ecosystems (Lockwood et al. 2001). Peck et al. (2008) used Malaise traps in native wet forests at three elevations to monitor parasitoid richness and abundance over 17 months. Aliens dominated the 18,996 individual Ichneumonoidea collected, comprising 44 of the 58 species. Most species were captured in very low numbers, with the bottom collective 34 species making up <1 % of the total. Ichneumonidae was more diverse than Braconidae (69 % of species, 67.5 % of individuals), but a single alien braconid (*Meteorus laphygmae*) was the most abundant wasp, as 28.3 % of the total catch. Collectively, alien species accounted for 75.9 % of individuals. Their incidence was greatest on lowland areas, and declined from 98.8 % there to 64 % at the highest elevations sampled. Their impact on native Lepidoptera, the predominant host group for the great majority of parasitoids obtained (many of them with broad host ranges within that order), appeared severe. As many earlier workers had noted, a broad host range was considered advantageous for species introduced during early biological control programmes on the archipelago. Their legacy has been strong implication in the reduction and extinctions of many native endemic hosts. Thus, *M. laphygmae* has been reported from hosts in six families of Lepidoptera, and whilst difficult to ascribe the dramatic losses of Hawai'ian Lepidoptera unambiguously to any single cause, increased parasitisation rates associated with proliferation of alien species have been widely considered the predominant single contributor (Gagné and Howarth 1985). Other factors involved include loss of native host plants, and predation by invasive ants and social wasps (notably *Vespula pensylvanica*).

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

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

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

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

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

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

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

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

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

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

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

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

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

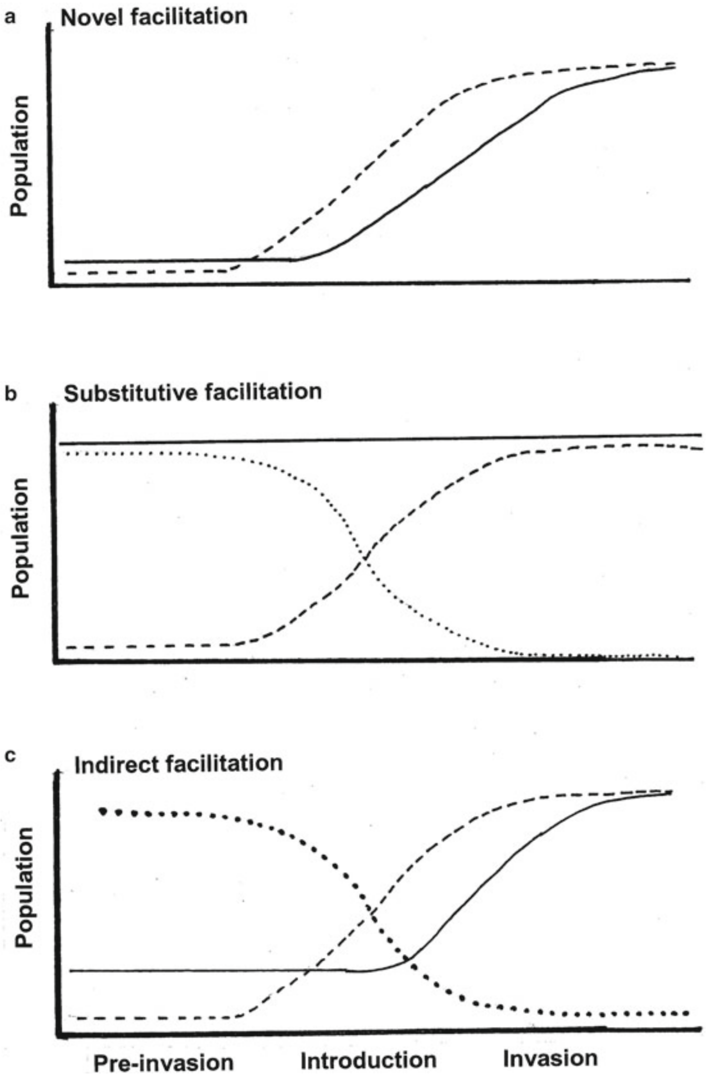

Fig. 2.2 Three conceptual models of different scenarios that define why invasive species can facilitate native species, shown along the timeline of successive invasion events. The scenarios are (**a**) novel facilitation, when no native facilitator existed; (**b**) substitutive facilitation, when an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

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

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

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

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

The invasive social wasp *Vespula pensylvanica* (p. 22) is both a predator and a nectar feeder in Hawai'i, adding considerable complex and unanticipated malfunctions in invaded communities. These include changing intricate plant-pollinator mutualisms. Experimental reduction of wasp populations in large plots containing the insect-pollinated endemic tree *Metrosideros polymorpha* led to significantly increased visitation rates by bee pollinators (Hanna et al. 2013). As a further complexity, the alien *Apis mellifera*, itself preyed upon strongly by *Vespula*, also became a significant pollinator of *Metrosideros* once wasps had been removed. This case thereby involved management of one key invasive species, which had caused decreased fruit production of an endemic tree by disrupting pollination, enabling a different introduced species to facilitate that mutualism and increase fruit production. This positive attribute for *A. mellifera* (introduced to the archipelago in 1857) must be weighed in the context of its broader community impacts, considered widely to be harmful.

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

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

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

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

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Chapter 3
The Stages of Invasion

3.1 Introduction: Becoming an Invasive Alien Species

Concern over alien species by conservationists is not a recent phenomenon, but wider recognition of the extent of ecological impacts and changes with which they may be linked has drawn increased attention to both recently established species and also to those whose presence is now taken for granted. Many, indeed, are not included in conventional appreciation of 'aliens' – numerous animals and plants originating elsewhere are now parts of the contemporary landscapes and treated as natural after decades to centuries of assimilation into their expanded ranges. Most foundation agricultural crops, for example, originate far from where they have become staple foods, and many pests and other species associated with agricultural and forest industries founded on imported species, likewise, are long-term and well–established residents. Many are termed 'naturalised', reflecting often that their historical origins and modes of arrival are undocumented and that they are accepted as permanent residents, many occurring in natural environments and known to feed on native species, but others more clearly restricted to anthropogenic arenas. A historical whimsical comment on a widespread pyralid moth associated with stored fruit products helped to draw attention to the latter situation during the nineteenth century. The following petition, unattributed to any more formal author (but almost certainly editorial by H.T. Stainton), appeared in the Entomologist's Weekly Intelligencer for May 10 1856:

> Ephestia Ficella petitions to be naturalized
>
> To the Right Honourable Corporation of the Entomologists of Great Britain
>
> The petition of Ephestia Ficella
>
> Humbly showeth –
>
> That having been for many years an inhabitant of Great Britain, and being fully determined never to depart, your petitioner humbly craveth to be naturalized. Nor should it be objected that your petitioner liveth in-doors, for so also doth V-flava; nor that he hath travelled hither within the memory of man, for so also have Pseudospretella and Cerealella; nor that he is a great nuisance, for so are many of his friends and relations.

T.R. New, *Alien Species and Insect Conservation*,
DOI 10.1007/978-3-319-38774-1_3

> Your petitioner therefore humbly craveth to have his name added to the British list.
> And your petitioner will ever prey – on figs
> (signed) Ephestia ficella

In order to become resident beyond its natural range a species must move (or be moved) to a new area, establish there through propagules (with, in many cases, only very small numbers needed for this to occur – a single gravid female insect may suffice), persist and increase in numbers and range. Many such species (including stored products pest such as *Ephestia* [now *Cadra*] *ficella*, above) are restricted to anthropogenic environments or to their sites of introduction. Those of greater conservation concern are invaders of more natural ecosystems where they are enforcedly brought into contact with native biota. They include numerous recently adventive 'pest' species, many of them initially affecting native or introduced crop or other commercially valuable plant species but expanding to less manipulated environments. These invaders are the typical 'aliens' of conservation biologists, and the novel interactions that result implicate many of them as threats in both continental and island environments. Early successional ecosystems are commonly more prone to invasion than the more complex and mature later successional stages. Likewise, invasions on isolated islands are commonly more severe than those on continental land masses, and frequency and intensity of human impacts can also be linked with high invasive impacts – with, in the worst cases, cascading impacts producing fundamental changes to the invaded systems and to numerous 'interaction webs' (Memmott et al. 2007). The stages of the invasion process, and the characteristics of potential and actual invasive species have been discussed repeatedly, and a valuable overview of relevant themes, based on invasive plants and plant pests in the United States (Mack et al. 2002) included discussion of many insect examples.

Globally, plants are the most numerous invaders (Vitousek et al. 1997), and are linked inevitably with vast numbers of phytophagous insects, the most diverse and predominant guild of animal consumers and in many cases accompanying their host plants from areas of origin. Invasive plants and insects participate in many intricate novel interactions, with each other and with native and naturalised biota. These include interactions and associations that are immensely challenging to interpret accurately and to manage effectively.

As noted, invaders are not a new phenomenon, but their vastly increased rates and opportunities related to human mobility and trade represent a massive change in scale over recent decades. Vitousek et al. (1997) contrasted the historical and current Hawai'ian insect faunas – with the entire endemic fauna established from a colonisation (and subsequent radiation) every 50,000–100,000 years now augmented by 15–20 species being introduced, and establishing, each year (Beardsley 1979). The impacts of many of these, as with numerous invaders elsewhere, are often very poorly understood and this lack of information renders setting priorities to counter or oppose their continuing spread very difficult (Simberloff et al. 2013).

Whenever a known potentially harmful invasive species is detected in a new area, a key need is for information on its likely rate of spread, as a component of inferring impacts. Writing on alien plants in Britain, but perhaps of much wider relevance, Williamson (2011) suggested that one reason why aliens appear to be more narrowly distributed than native species could be simply that they are still spreading and have not yet attained their full accomplishable range – so that the current range for any such species may be very misleading in indicating capability. A time lag may occur before spread occurs, but many insects then parallel plants in spreading rapidly and effectively in their new environments. In many cases, perhaps especially for insect herbivores, some information on extent and rate of spread can flow from knowledge of host plant range and availability of known host plants in the new areas. The small Australian native moth known as the Gum leaf-skeletoniser (*Uraba lugens*, Nolidae) was first recorded in New Zealand in 1996, when it was successfully eradicated from a localised occurrence. More recently, it was discovered near Auckland in 2001 and has since spread substantially, leading to incentive to control it before the moth reaches plantation areas of Myrtaceae where the extensive larval defoliation could become a significant economic threat. Individual moths may fly for only a kilometre or so, but wind transport (as for many insects) may be over much longer distances. Potential spread, with likely range in New Zealand evaluated though climate matching based on Australian data, was refined by surveys for adult moths in Tasmania using a synthetic pheromone (Kriticos et al. 2007). In this example, the potential systematic use of such lures as a monitoring tool appeared useful in predicting range expansion. Potential range of *U. lugens* in New Zealand includes much of the cooler wetter regions of the central North Island and also much of the South Island. However, and again as a potentially wider generalisation, such trials represent realised distributions and cannot heed constraints from biological processes such as competition and impacts of natural enemies.

Many workers consider the process of invasion to comprise three main sequential phases, namely arrival, establishment and spread (Engelkes and Mills 2011), that collectively have generated many ideas to ‘explain’ the fate of alien species as they actually or potentially exploit new environments. Thus, 29 major hypotheses were discussed by Catford et al. (2009), based on invasion ecology of plants. In seeking a more general unifying scheme, they compared six wide ‘stages’ of invasion – transport, introduction (arrival), colonisation (survival), naturalisation (formation of self-sustaining populations), spread (dispersal) and impact (effects on ecology/economy) and how these may be structured by propagule pressure (size and frequency of introductions), abiotic characters (‘invasibility’ of the receiving environment) and biotic characters (of the invader, the recipient community, and their interactions), together with influences of people on all three of these. All three main parameters are involved in successful invasion but their relative strength and importance clearly vary, and Catford et al. noted a series of five potential invasion pathways that increase in complexity as the factors interact in different ways. As summarised in Fig. 3.1, this interpretation suggests that a unifying approach to examining biological invasions might be to determine the validity of these pathways for a species, progressing from ‘1’ to ‘5’. Pathway 1, for example, reflects human-mediated dispersal and propagule pressure alone, without other environmental influences. Contrast with the most complex case (Pathway 5) shows the latter to

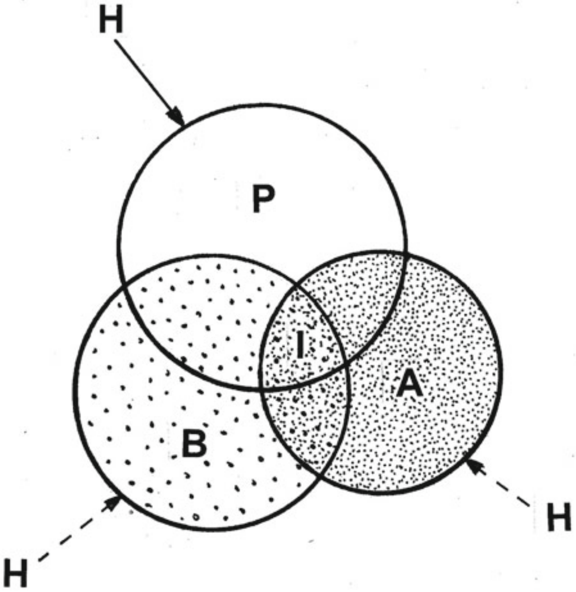

Fig. 3.1 Propagule pressure. Schematic diagram to illustrate how propagule pressure (*P*), abiotic characteristics (*A*) and biotic characteristics (*B*) interact to drive invasion (*I*, which occurs when the above three interact), and how humans may modify each factor (*H*). The strength and extent of influence from each factor can vary, as can be shown by different size of *circles*, with intensity differentiated by shading: in this example, darker shading of '*A*' indicates that *A* drives invasion, followed by *B*, then *P*, whilst '*P*' has greatest extent (time and space) so limits the invasion least; '*H*' is shown as more likely (*solid line*) for *P*, and less likely for others (*dotted line*) (After Catford et al. 2009)

incorporate all the influencing factors, and the interactions between all components.

The four sequential stages of any invasion (namely, arrival, establishment [often, colonisation], dispersal, and range expansion [implying use of resources, as a possible precursor to invasion]) recognised by many commentators are often presumed to follow a rapidly diminishing trajectory – far more species 'arrive' than 'establish', many arrivals do not 'disperse', and so on, and species or populations at any stage of the sequence may respond very differently to local conditions and environmental impediments (Blackburn et al. 2011, see Chap. 1). The four phases have been studied rather unevenly, with much less attention to arrival and establishment than the later phases (Memmott et al. 2005). Figure 3.2 (from Hulme 2008) shows the parallel predominant management responses along this sequence, with earlier actions generally being the most cost-effective and emphasising the importance of early detection. This dictates that increased understanding and knowledge of the invasion process transfers to support effective management. However, Hulme identified three factors that currently represent those linkages, all relevant in insect examples. They are (1) much current research effort is directed to quantifying scales

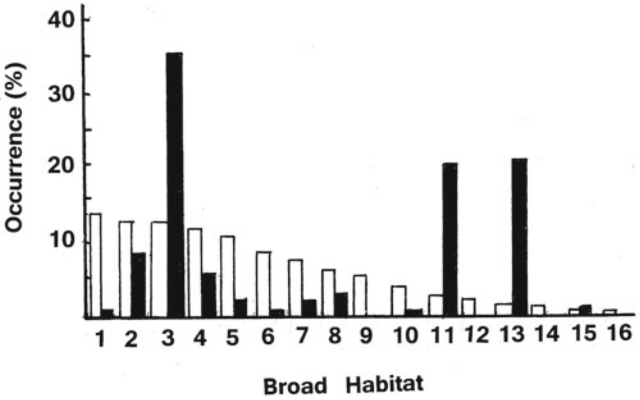

Fig. 3.2 Habitat distributions of alien (*black bars*) and native (*open bars*) plant species across the broad habitat types found in five study regions in England. The regions, each of 3600 Km^2, encompassed northern, southern, eastern, western and central areas, and data are based on the New Atlas of the British and Irish Flora. 'Broad habitat' categories are (1) fen, marsh and swamp, (2) broadleaved wood, (3) boundary, (4) inland rock, (5) calcareous grassland, (6) neutral grassland, (7) standing water, (8) rivers, (9) acid grassland, (10) dwarf shrub heath, (11) arable, (12) bog, (13) built up areas, (14) conifer wood, (15) improved grassland, (16) bracken (Hulme 2008)

and scope of the problems rather than toward robust management solutions; (2) even when the research is applied in nature, it has usually not addressed all stages of the invasion process, especially initial dispersal (as above), so limiting management available for rapid response; and (3) most studies focus on individual species, with relatively few extending to incorporate a wider ecosystem approach that integrates interactions between an invasive alien species and others, in addition to wider context of landscape structure and human impacts. Vermeij (1996) used the term 'integration' for the processes by which the invader and the species encountered respond to each other, both ecologically and evolutionarily.

Invasive taxa are thus a subset of those that have arrived and become naturalised, a reality that emphasises that many alien species are not invasive and may require little management or further attention in their new ranges. However, the sequence leading to invasion also confirms that three fundamental objectives for invasive species management ensue. As listed for invasive weeds (Reymanek 2000), these are (1) prevention or exclusion; (2) early detection and rapid assessment; and (3) control, containment or eradication. Setting priorities amongst the species of concern draws on five major fields of invasion biology – again from Reymanek (2000), these are (1) stochastic (the roles of inoculum sizes and residence times); (2) taxon-specific knowledge of whether the taxon is invasive elsewhere; (3) extent of the biological characteristics that facilitate or are associated with invasiveness; (4) evaluation of habitat compatibility in the invasive area; and (5) experiments, to test predictions made on the basis of evaluating the first four approaches – in practice, usually a very limited contribution to the overall scenario. Some intuitive principles are involved – thus, the reality of invasion chances increasing with initial population

Table 3.1 The invasion process and the factors influencing each phase for invasion by the mealybug *Maconellicocus hirsutus* (From Culik et al. 2013)

Invasion phase	Ecological process	Influential factors
Arrival	Immigration	Quarantine measures
Establishment	Reproduction	Suitable host plants
Integration	Population growth	Favourable climatic regime
	Dispersal (short distance)	Wind
	Mortality	Natural enemies
Spread	Dispersal (long distance)	Travel. Commerce (movements of seedlings and produce)

size, invasion frequency and time of residence is sensible but, as Reymanek commented, is 'admittedly trivial'. Likewise, past history of invasiveness elsewhere may be a strong indicator of future trends, and lead to cautions over any deliberate introductions, but such guidelines do not automatically preclude further investigations in what may prove to be very different receiving environments.

For any species, key factors may influence the various stages of the invasion sequence: Table 3.1 indicates these for the Pink hibiscus mealybug (*Maconellicoccus hirsutus*, Pseudococcidae), currently expanding its range in northern South America but believed native to southern Asia or Australia (Culik et al. 2013). For this pest, quarantine is relevant because eggs and early stages are commonly attached to imported plant material, after which suitable host plants are needed in the new environment. Wind facilitates dispersal of the crawlers (first instar larvae), as a major distribution mechanism. Such biological knowledge of any individual species can indicate both need and approaches to suppression – for this mealybug, early detection, before high reproduction and extensive dispersal occurs, may determine whether economically viable eradication can occur. Once it has spread, any containment increases markedly in difficulty.

The importance of understanding invasion pathways is underlined by 'Aichi Target 9' of the Convention on Biological Diversity's strategic plan to reduce the rate of biodiversity loss by 2020 (CBD 2014), which proposes 'By 2020, invasive alien species and pathways are identified and prioritised, priority species are controlled or eradicated, and means are in place to manage pathways to prevent their introduction and establishment'. Discussed by Hulme (2015), the challenges raised by this target include that a species may travel through several different pathways of the six broad categories distinguished (see also Hulme et al. 2008 for these groupings) as deliberate release, escape, parasite and pathogen contaminants, stowaways, navigation corridors, and unaided spread across borders. Incorporating these realistically into policy will depend on effective communication and engagement between scientists and those who translate that science into effective management and policy.

3.2 The Invasion Sequence

The key sequence of processes, and the concerns they engender, are outlined below. Each may be viewed as a 'transition' that must be overcome successively as (1) success in transportation and introduction; (2) success in establishment; and (3) success in spread and invasion (Kolar and Lodge 2001).

3.2.1 Arrival

A comment that 'The study of the arrival phase is the study of opportunity' (Vermeij 1996) remains wholly apt, with opportunities continuing to diversify and provide increasingly rapid and effective modes of transport and pathways for ingress of alien species.

Passive transport of organisms is very widespread and immensely difficult to prevent or control (Chap. 9). Even when quarantine inspections can be reasonably thorough, as for small volumes of goods and few people traveling to remote or ecologically sensitive areas, 'stowaways' occur, some represented by cryptic early stages that are inherently difficult to detect and recognise. Timber freighted to Antarctica (with a climate in which most imported organisms are highly unlikely to survive) has yielded timber beetles (Cerambycidae). Two species, both alive when found and one represented by both larval and adult stages, were reported by Osyczka et al. (2012), together with a number of fungi, in timber sent to one Antarctic station. Shipping is a major avenue for accidental introductions of insects. In some cases this might have been the primary route for species that were also released intentionally as biological control agents (p. 135): Day et al. (1994) suggested that this could be so for the ladybirds *Coccinella septempunctata* and *Harmonia axyridis* in North America, because both species initially became established near shipping ports. Cargo holds of aircraft also harbour insects, but may test their temperature and starvation tolerances more. The Glassy-winged sharpshooter (*Homalodisca vitripennis*, Cicadellidae) is a serious biosecurity risk as a vector of a widely damaging plant pathogen, the bacterial *Xyella fastidiosa*. A study of its temperature and starvation tolerances followed observations that the sharpshooter entered aircraft holds and yellow-painted cabin areas in Tahiti (Rathe et al. 2015). For various combinations of age, food and temperature the proportion of insects surviving for 24 h was quite high (21–93 %), with food increasing survival. The lowest mean number of hours survived (seven) was easily long enough to survive flights within the western Pacific region, including from Tahiti to Australia or New Zealand, suggesting that such transport could provide viable inocula of this polyphagous pest – as for many other insects, single females could be sufficient to establish an alien population. Rathe et al. noted a record of a single sharpshooter female laying 967 eggs over her lifetime, and many of the insects that survived their initial temperature treatments survived for a further 50 days or more. Stowaways on aircraft are common, many of them attracted by lights to enter whilst aircraft are on the ground for cleaning, loading or refueling, and perhaps especially at airports in less industrialised areas of the tropics.

For some insect groups, the most likely entry modes may be suggested with reasonable confidence – alien wood-boring beetles, for example, are most likely to be transported in timber or wooden packaging such as crates or pallets at international shipping ports (Rassati et al. 2015). Surveys at 15 Italian ports and in nearby forests, using a generic multi-lure baiting system known to attract a wide variety of wood-boring beetles and with baits hung at 2 m above the ground, yielded 14 alien species (11 Scolytinae, 3 Cerambycidae). Five of these were previously unrecorded from Italy. Altogether, 81 beetle species were collected – so 67 native species were also found. Beetle richness at any port was related to the amount of imported commodities. Eight alien species were regarded as already established: two were found in this survey only within ports, two exclusively in forest traps, and four in both arenas (Rassati et al. 2015). Extensive monitoring is vital to increase probability of detecting new arrivals, for which one inevitable consequence is movement of imported wood (perhaps especially in packing material destined for inland locations), with many opportunities for beetles to emerge in new and widely separated environments. Surveys such as this one have implications far beyond detecting invaders. The numerous native species trapped in ports confirm the presence of a considerable pool of potential stowaways that could exploit wood at point-of-export, and themselves be conveyed elsewhere. Opportunities for stowaways are clearly numerous, and often difficult to detect as the primary mode of entry. The scale of timber movements can be substantial. Importation of coniferous logs to Belgium from Russia and the Baltic area reached more than a million cubic metres of wood by 2004, and represent a pathway for alien beetles that could become important forest pests (Piel et al. 2008), with further information needed to assess their significance.

The Yellow-legged hornet (*Vespa velutina*) spread rapidly across southwestern France and adjacent parts of Europe following its initial detection there in 2004/2005, to achieve a range of around 360,000 Km^2 by 2012 (Arca et al. 2015). It is suspected to have been imported from China in horticultural pots, and was first detected in France by a bonsai producer who imported such pots regularly. Genetic analysis of *V. velutina* populations in France and Korea (where it also become invasive) showed only very low levels of variation, suggesting that each invasion occurred through a single founder event. All French hornet samples examined were probably derived from a single female (Arca et al. 2015). Such genetic bottlenecks have been reported for other social Hymenoptera, such as the bumblebee *Bombus terrestris* in Tasmania (Schmid-Hempel et al. 2007). Perhaps only two female bees, from the New Zealand population (where the bee was introduced from Europe for Red clover pollination in 1885) established the now widespread Tasmanian population. The mode of arrival is uncertain – earlier interceptions in aircraft had occurred, and some form of stowaway passage is likely, although suggestions of deliberate introduction have also been made.

Regarded as a ‘paradox’ by Benvenuto et al. (2012), the common observation that invasive alien species populations founded from few individuals, and so with presumed low genetic diversity, can achieve long-term invasion success and sometimes outperform locally adapted taxa, has provoked investigations of impacts of the severe genetic bottlenecks associated with such small founder populations. Intraspecific hybridisation can enhance genetic diversity and, in turn, possibly increase adaptability of invaders – but such generalisations may be overly simple, and are difficult to test. The wasp parasitoid *Psyttalia lounsburyi* (Braconidae) is a classical biological control agent deployed against the Olive fruit fly (*Bactrocera oleae*, Tephritidae). Two source wasp populations, from Kenya and South Africa (and determined to be genetically distinct) were tested to determine whether hybrids differed in 'performance' from the parental populations, using female fecundity (potential and realised) and male ability to produce daughters as measures of fitness of the two sexes separately (Benvenuto et al. 2012). The sexes differed in relative fitness. South African females produced more offspring than Kenyan females, whilst Kenyan males sired more daughters than South African males. However, no hybrid superiority was detected in the laboratory crosses undertaken, and Benvenuto et al. noted that the tempting scenario of hybridisation proffering advantage in invasions might well be over-simplistic, and that further analysis of any post-release populations is necessary to interpret evolutionary changes following hybridisation.

Imported plants, including bonsai as above, may commonly carry associated insects either on/in themselves or their containers. The trade in 'Lucky bamboo' (*Dracaena* spp.) from China was associated with introductions of the mosquito *Aedes albopictus* (p. 191), because the plants are imported in standing water in shipping containers (Eritja et al. 2005).

More locally, and emphasising the variety of scales over which such vectors may operate – for example across contiguous countries or states, local use of firewood may be an important contributor to spread of some taxa. The Gypsy moth (*Lymantria dispar*, Lymantriidae) has spread widely in North America since it was introduced in 1869, and has become one of the region's most important forestry pests. However, it still occupies only about a quarter of its possibly susceptible range there (Bigsby et al. 2011). The serious economic losses from this polyphagous pest dictate the need for greater effectiveness and understanding of how this range expansion occurs and might be slowed. Bigsby et al. noted that both short range 'diffusive spread' and long range movements occur, and found positive association between household use of wood for heating and probability of *L. dispar* invasion. Egg masses, the usual stage for such transport, are laid on wood and persist for about 8 months. Wood transported to homes and campgrounds occurs and, although individual transport of firewood is regulated, and movement from quarantine areas needs inspection and certification, those regulations are often unrecognised and are easy to circumvent. As the range of *L. dispar* expands, it overlaps increasingly with forests that have been invaded by non-native plants, to facilitate a potential additional suite of interactions. Modes of arrival and subsequent spread can thus be similar, with parallel measures needed to prevent them from occurring.

Modes of arrival of many naturalised or long-resident insect species can never be clarified fully. The Monarch butterfly *(Danaus plexippus*, Nymphalidae), native to North America, is well known for its spectacular and long migratory flights that are an integral feature of its annual life cycle pattern. It underwent major range expansions in the late nineteenth century, and has been present in Australia since 1870/1871; it is now common there. As with its colonisation of Hawai'i, this arrival has been attributed widely to continued 'island hopping' across the Pacific Ocean, engendered by its strong flight capability, but it is uncertain whether Australian populations were founded by natural arrivals, human-aided movements or a combination of these. Before 1870, the nearest confirmed *D. plexippus* populations to Australia were in Vanuatu and New Caledonia and the approximately 1500 Km from the latter to Queensland is considerably less than the distance travelled nowadays by individual butterflies moving from North America to their Mexican overwintering sites. Clarke and Zalucki (2004) hypothesised that, rather than such slow diffusive natural arrivals, large numbers of butterflies were carried to Australia by cyclonic winds. Three cyclones hit the Queensland coast in early 1870 and, whilst it cannot be confirmed that one or more of these tracked over Vanuatu and/or New Caledonia, cyclone records indicated a strong likelihood that this occurred, and could have deposited butterflies at two of the Australian sites from which they were first reported. A larval food plant, *Asclepias curassavica*, had by then been introduced by the Acclimatisation Society, and the suggestion that the Monarch arrived as eggs on imported milkweed plants was regarded as unlikely because of the time involved (Clarke and Zalucki 2004). Future genetic comparisons of monarchs from different parts of the current range may help to ascertain the origin of Australian stocks.

Hurricanes in the Caribbean area may have contributed to dispersal of the cactus moth, *Cactoblastis cactorum* (Pyralidae), initially introduced deliberately to the region for biological control of *Opuntia* cacti in 1957 and more recently invading parts of North America. Surveys of genetic diversity (using CO1 DNA sequences) showed a pattern that reflected possible movements paralleling paths of recent Caribbean hurricanes (Andraca-Gomez et al. 2015) and suggested a role for hurricanes in the moth's invasion of Florida, in particular.

Wind-assisted movements of insects in the 'aerial plankton' may be an effective means of transport, and has frequently been implicated in pest movements, for example. The Island sugarcane planthopper (*Eumetopina flavipes*, Delphacidae) is one suggested beneficiary of wind in reaching northern Australia from Papua New Guinea via islands in Torres Strait (Anderson et al. 2010). This species is a high risk quarantine threat as the only known vector of an important disease of sugarcane (Ramu stunt virus) present in Papua New Guinea but not yet in Australia. Simulations of weather patterns suggested numerous opportunities for this invasive pathway, with arrivals of many other insects similarly facilitated. Many Australian insects reported from New Zealand have apparently arrived there on weather systems, many of them repeatedly and some now well established residents.

Determining or inferring entry routes for significant species or larger groups of invasive aliens is a key component of setting priority policy and scope for increased biosecurity. For some taxa, surveys can be sufficiently comprehensive to infer the more important modes of arrival, as demonstrated for some European arthropods. Nentwig (2015) summarised information on 184 alien species of spiders in Europe

Table 3.2 Alien arthropod species in Europe: numbers (percentages) of species entering by different pathways (From Rabitsch 2010). Summing is irregular because some species are entered more than once, for different pathways

Pathway	Number of species (%)
Intentional	218 (14)
Released	175 (11)
Unintentional	1341 (86)
Animal husbandry	42 (2.6)
Greenhouse escapees	204 (13)
Crops	70 (4.3)
Forestry	90 (5.6)
Horticultural/ornamental	468 (29)
Leisure	13 (0.8)
Stored products	201 (12)
Stowaways	95 (5.9)
Unknown	431 (27)

to clarify that most introductions occurred through one of three routes. The most frequent route was in shipments of fruits, followed by shipments of potted plants. Together, these comprised 88 % of detected cases, with 26 leading to establishment. The third avenue was in packing or containers – the remaining 12 %, with nine of these establishing successfully. Species in the first two were categorised as 'contaminants' and the third as 'stowaways'. All indicate the needs for enhanced quarantine and biosecurity inspections (Chap. 10), but it is unlikely that such events will ever be prevented fully. The pathways of arrival of alien terrestrial arthropods reaching Europe, examined by Rabitsch (2010), demonstrated that most species (1341, or 86 %) were introduced unintentionally, with the remainder (218 species) almost all imported deliberately for biological control purposes (Chap. 6). The various pathways summarise terminology, as in Table 3.2, but the pathway is unknown for more than a quarter of the species involved (431 species, 27 %). Identifying these is an important basis for any strategy to prevent further such occurrences and setting priorities to reduce propagule pressure (p. 54). Thus, recognition that trading operations are a major pathway for invasion by particular groups can dictate some practices to reduce propagule pressure during introduction. For potential pest bark beetles introduced in imported timber, modelling exercises (Skarpaas and Okland 2009) suggested a range of effective strategies to reduce introduction risks (Table 3.3) with differing but complementary effects, and following the principle that investment in such preemptive measures may be more cost-effective than the measures needed against already established beetle pests.

Deliberate introductions of insects are also very difficult to detect, and to control, not least because small numbers of resilient living insects (as either adults or more cryptic early stages) can easily be hidden or transported. Deliberate smuggling of desirable species, such as queen bees to improve domestic honey bee stocks continue to test ingenuity of border staff, leading to countermeasures such as specially trained sniffer dogs to help detect transgressors. Escape of alien 'pet insects' and other arthropods (such as giant centipedes, *Scolopendra* spp. and some millipedes:

Table 3.3 Management actions needed to reduce risks of introducing alien forest pests from timber imports, and their bases (Skarpass and Okland 2009)

Management action	Effect
Import less timber	Less import volume with forest pests
Process timber sooner	Less time for pests to develop during storage
Irrigate timber	Reduce survival of pests in stored timber
De-bark timber at source	Fewer pest individuals and species imported
Import timber later	Less time for storage population to exploit timber
Store timber far from forest	Fewer pest individuals arrive in forest
Store timber in building	Fewer pest individuals escape storage

Roques 2011) is a very minor, usually overlooked, consequence of introductions, but there is clear potential for some escapes and discards of surplus animals to establish. Some published codes of behaviour for insect conservation counsel against such casual releases of both alien species, and of native species beyond their natal or natural range areas. Again, well-organised circumvention for commercial gain may not be unusual. Many releases, in any case, are not in any way illegal and cause no official concerns. Three contexts that have caused recent conservation-related comment are alien ants imported into Europe as pets (Buschinger 2004), the importations of living beetles into Japan (Kameoka and Kiyono 2004), and releases of butterflies at weddings and other ceremonies. They raise rather different issues, but any such trade in living insects can lead to inadvertent introductions. Likewise, casual releases or escapes of reared Lepidoptera from hobbyists have occasionally caused comment, and attention is drawn to this practice in several 'codes of conduct' for that readership. Especially in the past, many deliberate and unauthorised/unpublicised introductions of larger Lepidoptera to Britain were made by hobbyists and others seeking to enhance local biodiversity and with no consideration of any wider consequences (Oates and Warren 1990) – those activities were paralleled by well-intentioned organisations such as Acclimatisation Societies importing and releasing (non-insect) 'species from home', some with lasting detrimental consequences, in many parts of the world.

Some ants are amongst the most potent and harmful insect invaders (p. 156), and releases/escapes of a single gravid queen ant may be sufficient to found a colony, most likely without detection for, perhaps, several generations and extended distribution from the point of release. Taxonomy of many ant groups is incomplete and some taxa advertised for sale on web sites are imprecisely or inaccurately named, so that their relationships or novelty to any receiving fauna are both undocumented and may never be known. Polygynous species tend to be favoured in the pet trade (Buschinger 2004). Hybridisation between introduced and resident populations could lead to loss of distinctive local populations and hamper evolutionary interpretations. Buschinger also noted risks of ant parasites (listing tapeworms, gregarines and fungi as candidates) being introduced by imported species and transmitted to native ants. Such risks are not likely to be appreciated fully by people simply seeking an unusual imported pet and, in the absence of regulation or readily available advice, seem unlikely to be diminished. In addition, ‘novelty’ species restricted to a region may be attractive to hobbyists seeking rare or unusual charges. New (2005) noted the availability of endemic Australian bull-ants (*Myrmecia* spp., but with imprecise species identification) in Europe, for example.

The extent of importations of living beetles, notably rhinoceros beetles (Scarabaeidae) and stag beetles (Lucanidae), into Japan for the pet trade is very difficult to estimate, but is clearly substantial. Figures quoted by Kameoka and Kiyono (2004) for 2001 implied that during that year alone >680,000 beetles from 25 countries were imported, and far higher figures have also been quoted. The twin conservation concerns are the risks of escapes and their consequences, and possible impacts on the habitats of source populations of the rarest species – for which high prices are powerful incentive to overcollect and obtain beetles by whatever means are possible, irrespective of local conservation regulations and needs to destroy their dead wood resources. Both deliberate discards and casual escapes of beetles occur, and rearing of complexes of regional species (especially of the very variable *Dorcus curvidens*) with distinct local populations has led to losses of regional characteristics through hybridisation (Goka and Kojima 2004; Goka et al. 2004).

Butterfly releases at ceremonies (weddings, in particular) have two conservation implications – the introductions of regionally widespread taxa into previously non-range areas, and mixing of distinctive genetic stocks within an occupied range. Much discussion has related to large, showy and colourful species, notably *Danaus plexippus* (p. 82) which is a very popular subject for such releases. In North America, the activity has potential for genetic mixing between the behaviourally distinctive western and eastern populations (Pyle 2010), with concerns over possible disruption of their migratory behaviour that could lead to large scale mortality through failure to overwinter properly in their traditional areas of California and Mexico, respectively.

Providing commercially-reared butterflies for ceremonies and celebrations is a specialised activity, and many proponents are well aware of undesirable impacts – some, for example, will supply only males to avoid any novel post-release oviposition, and pre-release sterilisation is also possible.

3.2.2 Establishment and Spread

Transient colonisations, without establishment, are widespread. For alien ants in New Zealand, Lester (2005) noted such ephemeral establishment in six species – including tramp ants (p. 158) found nesting close to ports. Those species occur widely in the Pacific area and several had been intercepted regularly in New Zealand over the previous 40 years, leading Lester to suggest that they would be likely to have already become established if they were able to do so. At least one (*Anoplolepis gracilipes*) was probably restricted by the climate being too cold for it to thrive. Many other alien species do not normally extend beyond the anthropogenic environments to or near which they were initially introduced – more than 65 % of European

Table 3.4 Numbers of alien arthropod species and selected orders of insects in Europe that occupy each of a series of broad key habitats (Figures from Lopez-Vaamonde et al. 2010a, b; Rasplus et al. 2010; Skuhrava et al. 2010)

	Number of species of			
Habitat	Alien arthropods	Lepidoptera	Hymenoptera	Diptera
Coastal habitats	25	2	0	6
Wetlands, riparian habitats	20	0	3	4
Mire, bog, fen habitats	10	0	2	4
Grassland, tall forb habitats	86	3	12	6
Heathland, scrub, tundra habitats	99	13	9	4
Woodlands, forests	291	19	122	12
Inland without vegetation	19	2	4	1
Agricultural, horticultural lands	472	25	221	18
Parks, gardens	500	51	27	17
Buildings, houses	493	33	37	25
Greenhouses	251	16	65	6

alien arthropod species, for example, fall into this category (Lopez-Vaamonde et al. 2010a), with many of them found in several different habitats. Table 3.4 summarises numbers of alien species of some insect groups across a variety of European biotopes, with the last four categories the most human-influenced of the standardised European Nature Information System habitat categories. Reasons for this restriction are varied but broadly reflect that the species lack ability or need to move elsewhere and become more broadly invasive, or have that capability but have not had sufficient time to do so. Lopez-Vaamonde et al. suggested that disturbed urban/semiurban areas may have low resilience to alien insects, such as by reduced impacts of potential natural enemies or that some species frequent (and prefer) anthropogenic habitats within their natural range – such as herbivorous insects associated with cultivated plants used increasingly as ornamental or amenity plantings. Many urban and periurban areas altered extensively by people for amenity use, for example, contain numerous alien plants that are, in turn, susceptible to alien insect herbivores, should they arrive (Chap. 5).

Spread of a species to become invasive can clearly combine a variety of processes, with local diffusion and local colonisations following more punctuated long-distance movements that may be either or both of natural or human-aided. Predicting the spread of any species is thus difficult and, in practice, is most commonly attempted by examining distribution extent and changes in relation to time, with the assumption that the foundation information is accurate, reasonably complete and, where relevant, can be related to incidence of any specific invasive host plant or other critical resource. The Horse chestnut leaf-miner moth (*Cameraria ohridella*, Gracillariidae) has invaded much of central and western Europe in the two decades following its initial discovery in Macedonia (in 1985), with a typical pattern of initial observation in highly populated areas and subsequent spread into local country-side (Gilbert et al. 2004). Modelling studies suggested that long-distance dispersal is an essential component of the moth's invasion dynamics, but with the additional parameter of short-scale dispersal leading to spread of about 3 Km in each generation. Gilbert et al. considered it unlikely that this was achieved by active adult flight but, rather, was likely to reflect wind-blown dispersal. Discussion of the uncertainties of establishing any firm details of the processes, with human transport also a confounding influence, emphasised difficulties of constructing any reliable predictive model. Predicting the spread of invasive insects is increasingly attempted by simulation models that incorporate all available reliable biological information. Most successful attempts focus on economic pests that have been studied extensively; one such case is of the North American Western corn rootworm (*Diabrotica virgifera virgifera*; Coleoptera: Chrysomelidae) in Europe, where long-distance dispersal events were aided by human transport networks (Carrasco et al. 2010) and accompanied by natural short-range dispersal.

Rates and distance of dispersal by invading species are clear elements of colonisation success and speed, and the most appropriate dispersal essentially determines their success, as discussed for classical biological control agents by Heimpel and Asplen (2011). Exploring implications of rate of spread, they noted that low rates of dispersal may lead to features such as only very localised influence and associated potential for inbreeding depression and extinction and, in practice, create needs for multiple release sites or augmented dispersal through human-aided redistribution. The converse, of over-dispersal, may mean reduced chances of mate-finding as density declines, especially at the edges of the introduced range, hampering chances of establishment and reducing control impacts. Disadvantages could thereby be postulated for both excessively low and excessively high dispersal rates, leading Heimpel and Asplen to suggest that greatest chances of establishment may occur at some intermediate dispersal rate level – a circumstance they regarded as an example of the 'Goldilocks principle', that an optimal outcome avoids the extremes of the possible range of options.

Modelling patterns of spread of most species necessarily involves assumptions to compensate for lack of precise knowledge – even for many well-known pests. Thus, models to anticipate spread of the Asian longhorned beetle (*Anoplophora glabripennis*, Cerambycidae) combined two contrasting 'rules' for beetle dispersal as (1) 'strict', where beetles do not leave their natal tree until it is heavily utilised and (2) 'relaxed', in which it was assumed that all infested trees can be sources for dispersing beetles. At present (Trotter and Hull-Saunders 2015) it is unclear which of these might be biologically more appropriate, and – as in many similar modelling examples – the need is for practical investigations, such as by mark-release-recapture or radio tracking to clarify such anomalies.

At the time of establishment, it is often difficult – especially for species for which no prior parallel experience is available – to predict whether the arrival will spread and, if so, at what rate and extent. Discussed by Parry et al. (2013), several factors have been designated as important in tentatively estimating such spread, with some key considerations (FAO 2006) given there, for pests, as (1) suitability of the receiving environment, whether natural or managed, for natural spread; (2) movement within commodities or conveyances; (3) intended use of the commodity, if attacked by a pest; (4) potential vectors of such a pest in the area; and (5) potential natural enemies of the pest. In considering needs for monitoring spread, Parry et al. concluded that the vast diversity of ecological and landscape contexts, temporal and spatial scales of release, possible techniques and of policy applications, collectively precluded any 'single recipe'.

Difficulties of identifying any specific mechanisms that determine whether an invasive organism is 'successful' may dictate a more integrative approach than has occurred commonly in the past, leading Saul et al. (2013) to suggest the importance of what they termed 'eco-evolutionary experience'. This is the legacy of accumulated evolutionary adaptations of a species to biotic interactions in its native environment, and which can be complemented by an individual's life-experience – and collectively determines the species' (or individual's) capability to survive and thrive within a new ecological context. The resident taxa encountered by an invader also have the novel experience of encountering a previously unmet newcomer, so that their own experiences become relevant in reacting to the new situation. Saul et al. proposed a series of five hypothetical scenarios, based on type of ecological interaction, which may represent the influences of this experience in both the alien and the native species (Fig. 3.3). A major practical lesson from this exercise is to emphasise the roles of the receiving environment, and to consider both invading and invaded species, with the environment influencing which of several possible ecological roles an invader may adopt in its new milieu.

A more common focus is exemplified in the two widespread views on why species become invasive (Colautti et al. 2014), as (1) intrinsic factors making some species naturally good invaders and (2) species becoming invasive as a consequence of novel ecological and/or evolutionary interactions, such as natural enemy release (p. 117).

One novel approach to identifying potential high-risk invasive insect pests is predicated on the hypothesis that global insect pest assemblages are non-random groupings, irrespective of whether they occur through anthropogenic means – and, if this is so, can be subject to some form of predictive analysis (Worner and Gevrey 2006). Ranking of species for their potential for establishment can be based on the 'strength' of their association with a particular regional species assemblage, so aiding assessment of their relative priority. Using plant-feeding pest species, Worner and Gevrey suggested that geographical areas with similar pest assemblages share similar conditions that allow or enable those species to invade the area – so that the particular regional pest assemblage integrates the complex biological (plant presence) and abiotic (such as effectiveness of biosecurity) factors and interactions. The approach used self-organising maps, as an artificial neural network algorithm to show that geographical areas with similar pest assemblages became mapped neighbours and, in the example of 844 species employed, allowed for comparative assessment of the strength of association of each species with each assemblage as a 'distribution of risk'.

Predicting the fate of a biological invasion thus remains a highly uncertain process, despite information from an ever-proliferating array of examples of both suc-

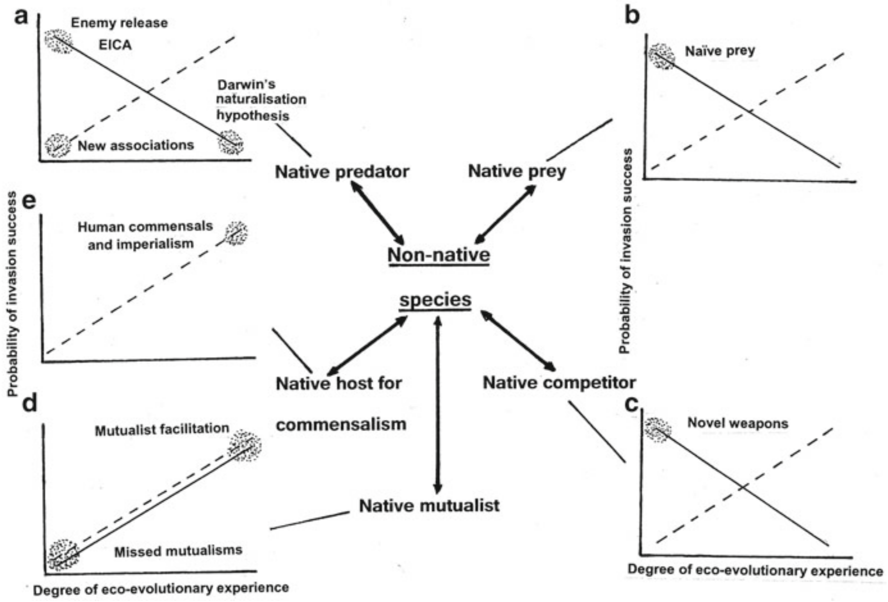

Fig. 3.3 Five hypothetical scenarios on the influences of eco-evolutionary experience in non-native (*dashed line*) and native species (*solid line*) on probability of invasion success, according to the kind of ecological interaction. Interactions are: (**a**, **b**) predator-prey; (**c**) competition; (**d**) mutualism; (**e**) commensalism; the general trends are that lower native experience (except in mutualisms) and higher non-native experience may give advantage in invasion success; shaded areas indicate parts of framework covered by major hypotheses in invasion ecology that implicitly include references to importance of an evolutionary legacy (After Saul et al. 2013)

cesses and failures derived from both natural and manipulated introductions. Whether planned introductions (such as classical biological control agents), major pests such as tramp ants, or the host of more innocuous taxa that have received attention, generalities and predictions are still largely elusive. Continuous tracing of spread and impacts over time has only infrequently been based on long-term systematic survey data from the time of arrival in the context of the novel environment, and trends are more often based on more infrequent or limited observations commenced at some more indefinite time after arrival. The recent informative example in Britain, of the arrival and spread of the Harlequin ladybird beetle (*Harmonia axyridis*, Coccinellidae) (Roy and Brown 2015), traced the invasion trajectory in the decade since an earlier review (Majerus et al. 2006). *Harmonia* was first recorded in the United Kingdom in 2004, and the UK Ladybird Survey was established in 2005 to encourage and enable citizen scientists to record it and so track its spread. Majerus et al. (2006) noted its potential impacts, with those projections discussed in the later overview (Table 3.5) with assessment of the evidence for each. Rapid spread reflected both natural dispersal ability and human-aided transport. *H. axyridis*' establishment and predominance within native aphidophagous insect guilds reflected its generalist feeding habits and developmental plasticity, together with

Table 3.5 The alien ladybird *Harmonia axyridis* in Britain: predictions of its fate after arrival, with overall conclusions on each of these after the first decade (2006–2015), to indicate which factors might be involved in successful invasion (Roy and Brown 2015; following Majerus et al. 2006)

Prediction	Comment and outcome
Eurytopic nature contributes to rapid spread	Important contribution to success
Climatic adaptability confers competitive advantage over some specialised native species	Climate is important factor in determining spread, but only together with other interacting factors
Maritime climate allows breeding throughout summer, without summer diapause	Multivoltinism is important contribution to rapid population growth and spread
Phenotypic plasticity extends breeding season though autumn	Some local adaptations may accelerate spread
Will spread across entire British mainland by 2008	High dispersal ability over most of England and Wales; limited distribution and breeding in Scotland
Spread may be beneficial to crop systems by restricting aphid populations	Further work needed to clarify this
Likely to have negative effects on other aphidophages through resource competition, interspecific competition and intraguild predation	Considerable evidence of intraguild predation; strong correlation between presence of *H. axyridis* and declines of some native ladybirds
Efficient chemical defence and large size give significant reproductive advantage over many native species	Requires further investigation
Will become a nuisance to humans	Some evidence of negative impacts, through large aggregations in buildings constituting nuisance

high resistance to natural enemies encountered after invasion, and its high reproductive capacity. Its establishment in Britain also correlated with declines of seven species of native ladybirds (of the eight species evaluated).

The ladybird's range expansion in Asia may result from transportation on trains, following earlier reports that *H. axyridis* can enter vehicles as potential overwintering sites (noted by Orlova-Bienkowskaja et al. 2015), and with its high fecundity ensuring that even a few females may provide effective colonisation.

Establishments occur over varying periods, over which any range spread involves one or both of two processes. Range increase through gradual diffusion or incremental spread from range edges differs from more discontinuous spread through more distant movements of 'nucleated' introductions, in that the range remains continuous. *Bombus terrestris* in Tasmania shows this pattern well (Fig. 3.4: Schmid-Hempel et al. 2007), with dated estimates clearly showing progressive colonisation of the island. As examined by Schonrogge et al. (2012), this gradual process allows the progressive invaders to be followed by any natural enemies they may have acquired since establishment. The parallel processes of continued range expansion and continued accumulation of natural enemies were examined through eight related alien oak gall-wasps in Britain surveyed in 2004–2005. Of these, four species of

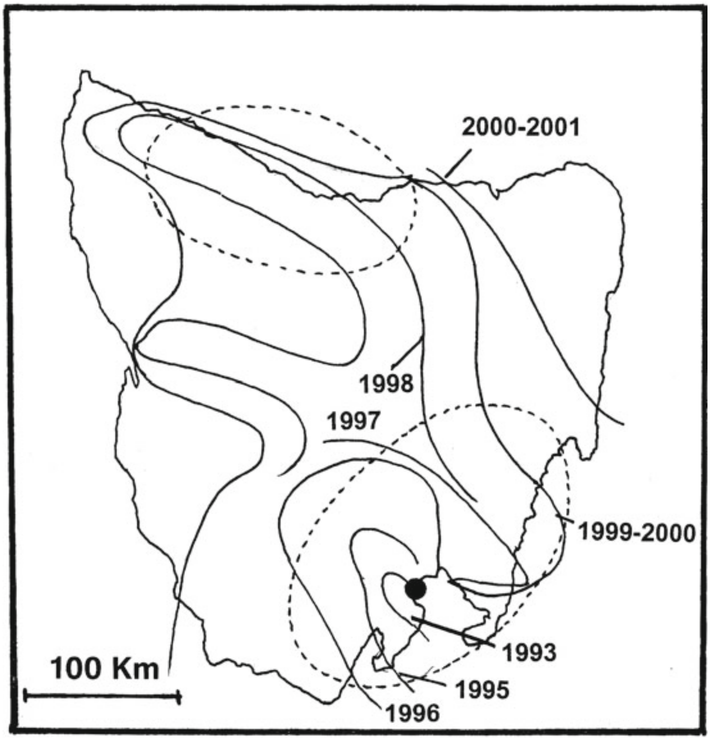

Fig. 3.4 Outline map of Tasmania to indicate range expansion of the bumble bee *Bombus terrestris*, plotted from historical records from its arrival (first sighting in Hobart 1992, site shown by *black spot*) to summer 2000–2001. Different *year numbers* indicate records in new areas for time indicated; *lines* indicate approximate invasion fronts (After Schmid-Hempel et al. 2007)

Andricus (Cynipidae) had reached Britain from Europe by 1990, and three had expanded their range from southern England as far as northern Scotland. One of these is a long-term coloniser first recorded in 1834 (*A. kollari*), and the other three were recorded first in 1961 (*A. quercuscalicis*) and 1974 (*A. lignicola*, *A. corruptrix*, this last being the only univoltine species of the four). The four other invasives (three species of *Andricus*, *Aphelonyx cerricola*) reached Britain between 1992 and 2000. All these wasps had recruited natural enemies, and Schonrogge et al. found no evidence of continental European parasitoids or inquilines accompanying the colonisers, and these appear not to have invaded. The wasps depended collectively on the same two species of oaks, so share the same functional environment. The four recent arrivals have continued to spread, but at different rates, with *A. cerricola* (wholly dependent on *Quercus cerris* and the only univoltine species of this set) expanding only little. By 2004–2005, the parasitoid assemblages of the early arriving species had changed little since a previous survey in 1994–1995, whereas the assemblages associated with the recent arrivals had developed rapidly, reaching 9–15 parasitoid and inquiline species from each. Many of these are known to be natives through previous records from other cynipoids in Britain. This survey of recent novel associations thus indicated that the invasive gall wasp/parasitoid/inquiline associations in Britain continue to assemble as reflections of the local species pools rather than historical inheritance.

The fate of any novel species in a new range is affected by numerous factors – the number of propagules (linking with so-called ‘Allee effects’, referring to the reality that some minimum number of individuals is needed to sustain a viable population, and that subsequent decreased population growth may be related to low abundance), reproductive mode (such as parthenogenesis, which may facilitate establishment of many Homoptera, such as aphids and scale insects, and some beetles, in particular), the levels of human or other disturbance to the receiving environment, the tolerances of the alien to physical and climatic features of the new site, and the availability of critical resources as an aspect of interactions with and within the receiving community. The last, the most frequently cited of these, can contribute ‘biotic resistance’, a term due to Chapman (1931) and emphasised extensively since then, with the premise that a community of native species with numerous interactions may resist invasion, and the corollary that species-rich communities should be more stable and more resistant to invasions than species-poor communities. The concept is attractive, but still needs further investigation. Most examples of biotic resistance involve competition amongst terrestrial plants or sedentary marine fauna. Biotic resistance should, in theory, be strong where generalists or omnivores are abundant (Crawley 1986). The belief that biotic resistance determines success or failure of invasions into native communities has considerable notoriety, but alternatives are also possible (Simberloff and Von Holle 1999). They include introduced species interacting with each other. Positive interactions between invading species could enhance probability of survival, and affect population size, to facilitate their establishment and subsequent wellbeing.

Conversely, competitive effects between invasive species may influence their establishment and also may become apparent only after a considerable time. Interference competition between classical biological control agents (p. 135), for example, has been discussed extensively within the venerable debate over optimising introduction procedures and whether to introduce single or multiple agents and if the latter, whether to opt for taxa with different attack patterns or that affect different stages of the target pest. Other contexts occur. The Hemlock woolly aphid (p. 63) is one of two major invasive insects affecting Eastern hemlock (*Tsuga canadensis*) in eastern North America, the other being the Elongate hemlock scale, *Fiorinia externa* (Diaspididae). As a possible determinant of community level impacts that flow from high insect densities, investigation of the interactions between these insects included study of the influences of sequence of settlement (Miller-Pierce and Preisser 2012). The influences of insect herbivores on co-occurring species through host plant effects (such as induced changes in plant chemistry or resource levels) are widely known and sometimes dramatic, so that the first-arriving species might gain competitive advantage simply through priority in reaching the host. If that first invader decreases host plant quality or leads to increased plant defences by its feeding, subsequent colonisers might experience diminished 'performance', so that understanding any such priority effect may aid understanding of the subsequent trajectory of establishment and abundance. Series of experiments involving initial introduction of one or other scale insect, followed by the other species 2 years later, and accompanied by a second series of trials in which the two species were introduced together, revealed an asymmetrical outcome. Two years of *F. externa* herbivory altered host quality sufficiently to affect *A. tsugae* settlement, but the converse did not occur – with 2 years of previous occupancy by *A. tsugae* not affecting *F. externa* significantly. Miller-Pierce and Preisser (2012) suggested that this outcome was through exploitative resource competition and/or induction of plant defences. *A. tsugae* crawlers require high quality foliage on which to feed, and survival rates on lower quality foliage are very low.

Species replacement of one invasive by another has been reported repeatedly amongst predators. Replacement of *Coccinella septempunctata* by *Harmonia axyridis* in North America (p. 168, Alyokhin and Sewell 2004) and displacement of the earlier invading German wasp (*Vespula germanica*) in native New Zealand forests by *Vespula vulgaris* (Beggs 2001) are amongst the classic examples, with exploitative competition a common inference, even if it is difficult to prove. The mechanisms involved may be complex. Beggs (1991) noted that *V. germanica* was attracted to fermenting honeydew in New Zealand forest, with their intoxication rendering their foraging efficiency relatively less than that of *V. vulgaris*, which remains sober!

'Species replacement' induced by alien species and the changes they incur is thus a complex process, with equally complex consequences. In the Azores (Borges et al. 2005), replacement of resident specialised forest-dwelling endemic arthropods by endemic generalist arthropods could increase homogenisation amongst the endemic fauna as conditions change, because the latter taxa are able to survive in disturbed marginal sites that may contain alien species. The richest endemic assemblages (forest endemics) thus became susceptible to invasion through facilitation by aliens. In this example, Borges et al. suggested that most endemic taxa involved are widely distributed and have only low conservation value. Assessing only the very basic feature of 'endemic species richness' as a measure of response could underestimate the contributions of rare endemics. The rates of invasion of high elevation natural vegetation fragments remain uncertain.

Releases of insects as classical biological control agents (Chap. 6) are commonly accompanied by the hope, even expectation, that the intentionally introduced agents will remain in their release area, a presumption that has commonly not proved true and has led to serious concerns as such agents move into more natural environments. As noted earlier, such spread encompasses the two general categories of overcoming geographical barriers and crossing political boundaries. Numerous examples of insects undergoing such range extensions have been reported amongst species introduced for weed control (as herbivores) or arthropod pest control (as predators or parasitoids), with a variety of undesirable non-target impacts (Parry 2009). Pratt and Center (2012) pondered whether <u>any</u> geographical barriers remain that can realistically restrict spread of introduced natural enemies, especially due to the increased impacts of globalisation and human-facilitated transport systems. Investigations on insects released as classical biological control agents suggest that release size, the number of potential propagules, may influence establishment – but trials with the European psyllid *Arytainella spartiophylla* released to control broom (*Cytisus scoparius*) in New Zealand found this to be important only for the first year after psyllid release (Memmott et al. 2005). Although they were less likely to establish, some releases of only two or four psyllids persisted for 5 years and larger releases (of up to 270 psyllids with 1:1 sex ratio) that survived the first year were almost certain to persist as long as the release sites were not destroyed.

A similar outcome occurred for leaf beetles (Chrysomelidae) in New York State (Grevstad 1999). Two related species (*Galerucella calmariensis*, *G. pusilla*), imported to potentially control the European Purple loosestrife (*Lythrum salicaria*, Lythraceae), were released at different batch sizes of adult beetles, namely 20, 60, 180, and 540 individuals/site. Each of the 36 sites (separated by a minimum of 10 Km) was inspected over the next 3 years. In parallel, a set of 20 releases (10 of each species) of single gravid females was made at additional sites. At the end of the survey period, after three full generations of the beetles, population sizes ranged from 2–876 (*G. calmariensis*) to 1–7083 (*G. pusilla*), amongst the 12 and 21 populations persisting from the initial 36 of each species. Of those populations lost, 28 of the 39 went extinct without completing a generation, but all extinctions of the smallest release size occurred within the first year. Increasing release sizes correlated with delayed extinctions. For the single specimen founders, only one population survived over 3 years. Establishment is clearly possible from single propagules, as reported in several other classical biological control cases and likely to be reflected in natural arrivals for which suitable resources are immediately available. One implication of this, however (and described as ‘frightening’ by Grevstad 1999), is that even single insects not detected by quarantine officers may found invading populations. In nature, repeated arrivals of small numbers of insects may be more likely than single large invasions. As examples, one or two individual herbivores carried on wind may be far less conspicuous than a mass migratory arrival, or their presence on imported plants may easily evade detection.

The term ‘propagule pressure’, a key theme in evaluating reasons for success or failure of an invading species to establish, is yet another for which definitions may become confused. Lockwood et al. (2005, 2009) discussed the need for more precise use, noting that ‘propagule pressure’ has been given at least three distinct definitions, as (1) most commonly, the total number of individuals arriving at a given location, either all together or in staggered arrivals or introductions by separate events; (2) the latter leading to separate consideration of the number of arrival or introduction events (‘propagule number’) and the number of individuals in each (‘propagule size’), with the product of number and size then being propagule pressure; and (3) the extent to which the established individuals of an invader add offspring to the receiving environment, defined by Lockwood et al. as ‘propagule rain’, and applied most commonly to plants. A wider community-based concept defines propagule pressure as the number of alien species in a particular place, defined by Lockwood et al. as ‘colonisation pressure’ to distinguish it from the other primarily population-level categories above. More recently, Ricciardi et al. (2011) incorporated a combination of colonisation pressure and genetic variation among propa-

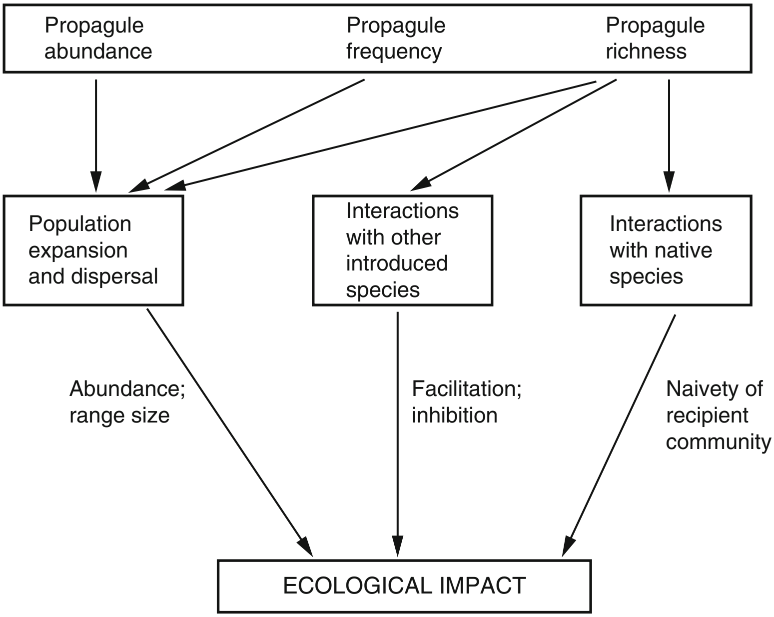

Fig. 3.5 The interactions between three components of propagule pressure (propagule abundance, frequency and richness) and the population-level and community-level processes that mediate impacts of introduced species. Major processes are blocked in the centre row and some specific mediating factors or important processes are indicated (After Ricciardi et al. 2011)

gules into a unified definition of propagule pressure, noting that the more familiar components of abundance, frequency and richness interact (Fig. 3.5) in creating ecological impacts, defined as some form of measurable change in the receiving community.

High propagule pressure allows some invasive species to overcome stochastic factors but, as Mikheyev et al. (2008) pointed out, it is one of the least understood components of biological invasions. Establishment of the Little fire ant (*Wasmannia auropunctata*) in a Gabonese oilfield was related to propagule pressure, but later spread was largely independent of this, so that study of other features (such as site characteristics and likelihood of competition from resident taxa) is needed to interpret the process.

Ways to monitor spread of invasive insects, derived largely from needs to track economically important taxa, can capitalise on any characteristic or unusual behaviour by which the species may be detected or concentrated – and methods are otherwise limited only by the ingenuity of the proponents and the performance and costs of the methods themselves. The extensive literature on insect sampling methods (Southwood and Henderson 2000; Samways et al. 2010) demonstrates numerous candidate possibilities as a foundation for modification or use in any individual context. Early detection is a key need for assessing invasive species, and the following two examples simply introduce the varied possibilities for achieving this.

The fruit fly *Bactrocera dorsalis* (Tephritidae), a major pest of commercial fruit crops, is native to Asia but was reported from Africa (Kenya) early this century, since when surveys using methyl eugenol attractant baits have recorded its rapid spread, leading to establishment (in 2006) of a national South Africa surveillance programme for this and other alien fruit flies (Manrakhan et al. 2015). Suppresion of the fly when found, and eradication of any isolated *B. dorsalis* populations, is advised – but risks of re-invasion are high and thought likely to occur in many fruit-producing regions. An integrated control programme will almost certainly be necessary. Many insects respond to chemical baits, and numerous taxa can also be monitored through use of pheromone analogues.

The Emerald ash-borer beetle (*Agrilus planipennis*, Buprestidae), an Asian native species that now causes severe mortality to North American ash trees (*Fraxinus* spp.), in contrast, also responds visually to conspecifics as a mate-seeking mechanism, and a combination of visual attractants with volatile chemicals from bark extracts of the host trees has been tested as a detection method. The novel use of 3-D printed plastic beetle decoy models deployed on sticky traps has been explored in Pennsylvania and shows potential as a cheap tool for monitoring the beetle (Domingue et al. 2015). For the same beetle, monitoring of the contents of predatory wasp (*Cerceris fumipennis*, the Smoky-winged beetle bandit, Crabronidae) nests led to its first detection in Connecticut (Rutledge et al. 2013), but such approaches are too laborious for routine uses, although valuable as wider inventory survey tools. *C. fumipennis* provisions underground nests with adult buprestid beetles, and the wasps can be intercepted with prey as they return to the nests. The Connecticut capture followed earlier detection of *A. planipennis* in Canada by this method, as well as records from several of the United States from where it was already known (Careless and Marshall 2010), leading to a more extensive programme of use in 'biosurveillance' for the beetles (Careless et al. 2014). *C. fumipennis* is the only eastern North American representative of the eight *Cerceris* species that hunt buprestids, and its use in surveillance for *A. planipennis* and several other actual and possible future invasive congeners may be facilitated by its broad distribution, use of a wide range of buprestid species, capability to detect these at low density when they are unlikely to be retrieved by other methods, and continuing to forage if prey is removed. However, Ryall (2015) noted that the wasp's relatively short flight season may limit its use. Parallels have been assessed in western North America: *Cerceris californica* in Washington state was considered only marginally suitable as a reliable monitoring device, because colonies are generally not large or common (Looney et al. 2014), but may have value in more general buprestid surveys.

The Emerald ash-borer has elsewhere been implicated as facilitating the range increase of another pest buprestid, *Agrilus convexicollis*, in Russia (Orlova-Bienkowskaja and Volkowitsch 2015). Almost all recent records of the latter were from declining *Fraxinus pennsylvanica* (itself an introduced North American tree) in regions invaded by *A. planipennis* and in which mass weakening and death of the trees had occurred. The locally increased amount of larval food for *A. convexicollis* may have led to its increase and spread.

Understanding and documenting the processes by which an alien species arrives and progressively becomes invasive links with considerations of ecological and economic outcomes and possible harmful impacts on biota and environments with which they come into contact.

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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

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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 conditions, 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 aphis (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. fenestrale* (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 compatability, 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

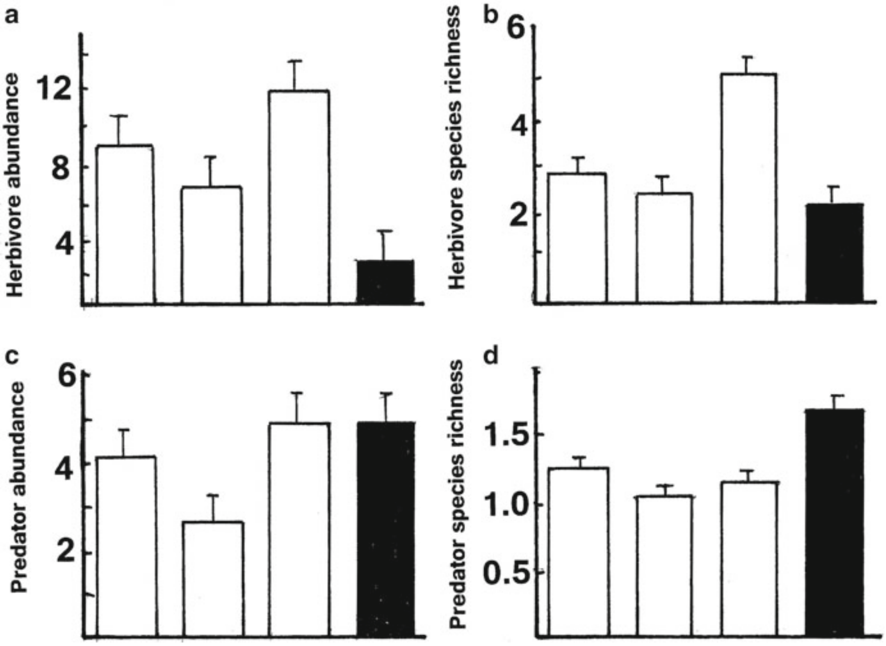

Fig. 4.1 Abundance and species richness of arthropod herbivores and predators, shown as average numbers of individuals and species collected/plot/sampling event, from four focal tree species in Texas: three native tree species (*open bars*, from *left to right* Silver maple [*Acer saccharinum*], Sycamore [*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 'compatability', 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	*Muehlenbeckia astonii*
Larval duration	*Rumex flexuosus*
Pupal mass	*M. astonii*
Adult mass	*Fagopyron esculentum*[b]
Eggs on emergence[a]	*F. esculentum*[b]
Survival	*Muehlenbeckia australis*

[a] No significant effect of plant species

[b] 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 posess 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 kurstacki*, (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

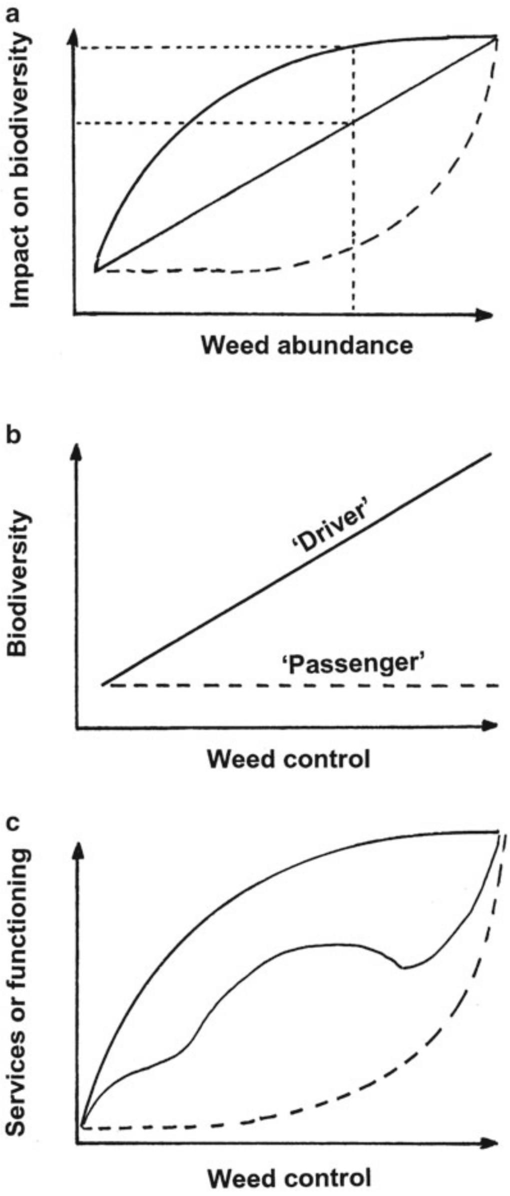

Fig. 4.2 Three aspects of the benefits of biological control for an environmental weed: (**a**) impact of the weed on biodiversity can be saturating, be more-or-less in relation to its abundance, or be negligible until weed abundance becomes high, so that quantitatively different benefits for biodiversity 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-

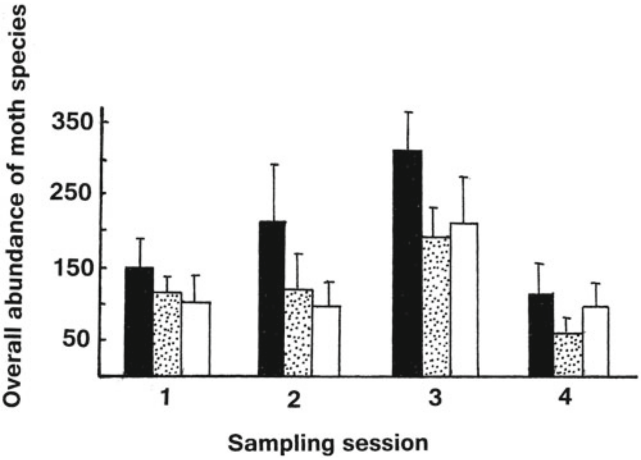

Fig. 4.3 Overall abundance of moth species across four light-trapping seasons and three categories of site history (undisturbed controls [*black*], defoliated [*dotted*], *B. thuringiensis* treated [*open*]) in Shenandoah National Park, in relation to *Bacillus thuringiensis* controls for Gypsy moth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

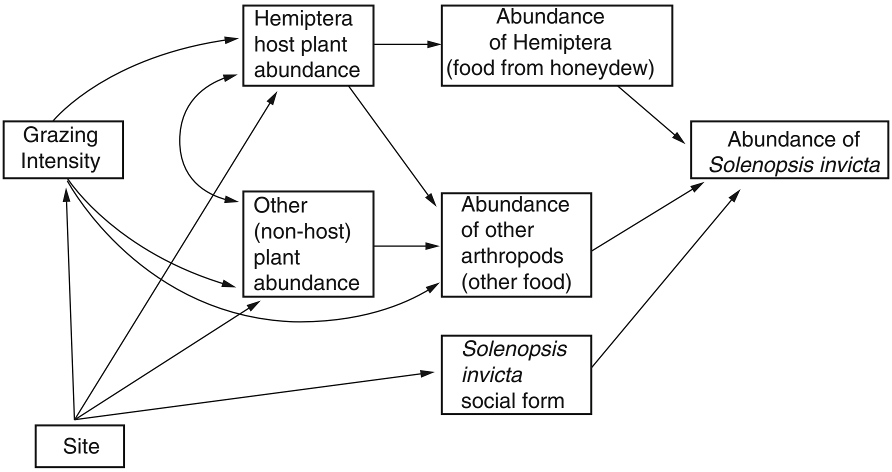

Fig. 4.4 Possible factors affecting the abundance of the invasive Red imported fire ant (*Solenopsis invicta*) in grazing pastures in Texas. The factors were hypothesised and tested for their importance, with the presumed relationship between grazing intensity and 'abundance of other arthropods' reflecting 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 (*Phylica 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 nonlethal 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 at 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*, Hesperiidae) 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 praevenosa*) 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. praevenosa* 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 behaviour 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

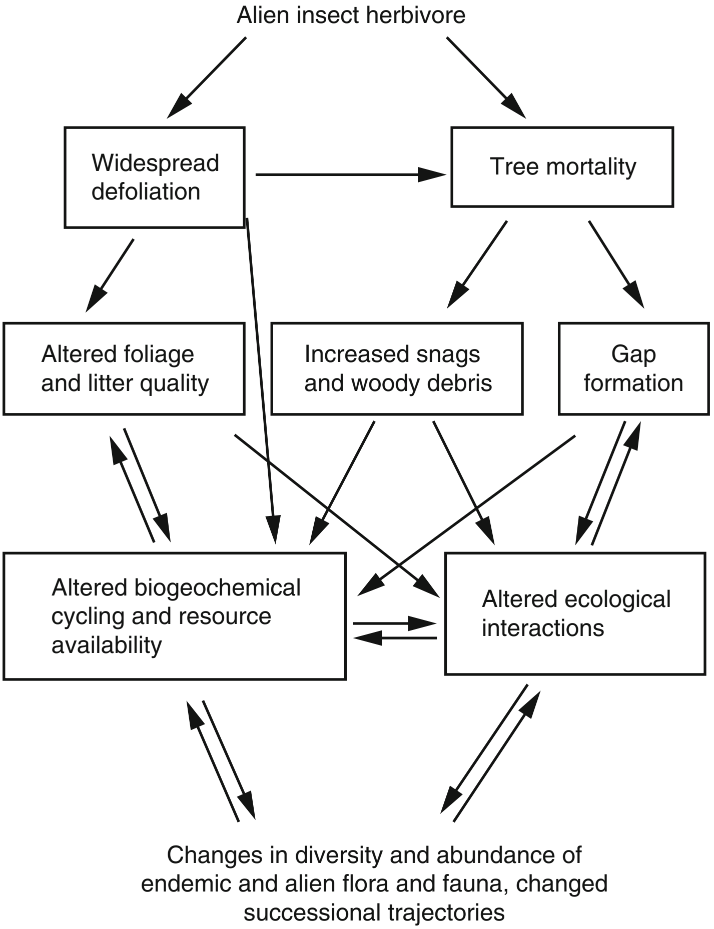

Fig. 4.5 A generalised conceptual model that shows cascading direct and indirect effects of alien insect herbivores on ecological processes and interactions that ultimately affect community composition and successional trajectories in eastern North American forests (after Gandhi and Herms 2010)

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

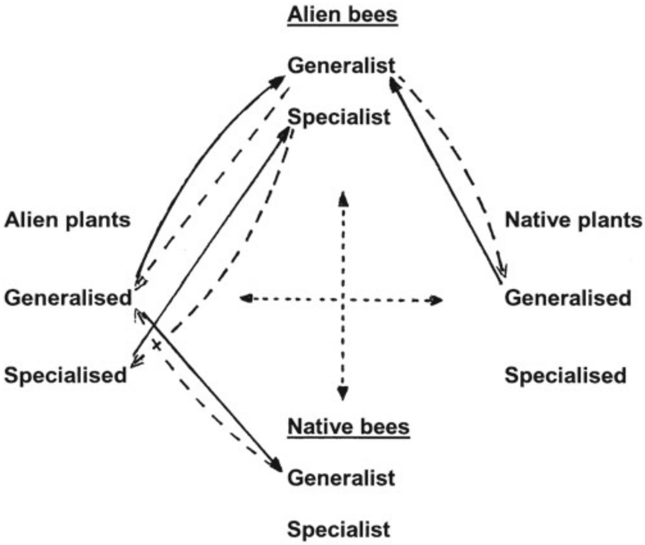

Fig. 4.6 Scheme of potential interactions between native and alien plants and bees in invaded ecosystems. Note that native specialist bees and specialised plants do not benefit from alien invasion, whilst alien generalist bees and generalist plants benefit the most. *Solid black lines* indicate direct 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

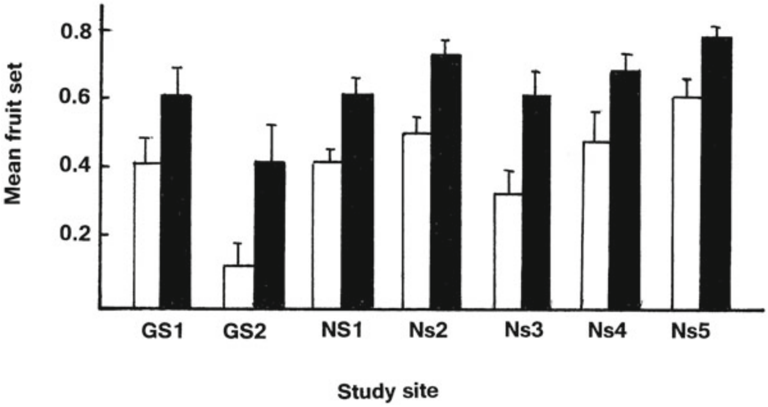

Fig. 4.7 Comparison of mean (with standard errors shown) fruit set for control (*open bars*) and artificial pollen supplement (*black bars*) treatments on *Byrsonima lucida* (at least three plants each site) at two garden sites (G) and five natural pine sites (N) in Florida (see text, p. 87). Reduction 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 socioeconomic 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)

Environmental impacts	Competiton	Transmission of disease
	Predation	Herbivory
	Hybridisation	Ecosystem
Socioeconomic impacts	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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Chapter 5
Alien Plants and Insect Conservation

5.1 Introduction

Alien plants are amongst the most universal invaders, and are globally important agents of ecological changes, with far-reaching implications for the native animals and plants in invaded vegetation communities, and for the structure and functions of those communities. Many points of detail remain unclear in understanding the mechanisms of many of the observed impacts, but changes to the central ecological roles of insects and their relatives are a key concern in understanding conservation need (Litt et al. 2014). Because many insects depend on particular plant species or structures for food and/or reproduction, losses of those plants, or structural or compositional changes to the vegetation communities in which they can thrive may be highly damaging. Accompanying changes to litter and soil may also occur, with impacts on decomposer organisms. All functional groups of insects can respond to changes in vegetation; historically, most attention in conservation has been paid to declines of specialist herbivores with direct links to particular host plants, overall richness of herbivore assemblages, and pollinators, with flow-on effects to associated parasitoids and predators included only more rarely. Competitive effects between alien and native plants for flower-visiting pollen vectors exemplify this complexity. Most such reported cases involve single species, with the wider community impacts studied relatively rarely.

As Lopezaraiza-Michel et al. (2007) noted, the impacts of a single alien plant can ‘potentially ripple through the whole plant-pollinator network’ exposed to the alien species. Their study of the strongly invasive Indian balsam (*Impatiens glandulifera*, Balsamaceae) in Britain involved comparisons of flower visitors (collected directly during standard transect walks) in series of paired plots with flowers of the balsam removed from one of each pair. Insect samples were compared for identities, richness and abundance, and characterisation of pollen removed from each individual. Collectively, the 173 species of insect visitors were collected from 27 of the 38 flowering plant species present, and in each plot *Impatiens* was within a complex

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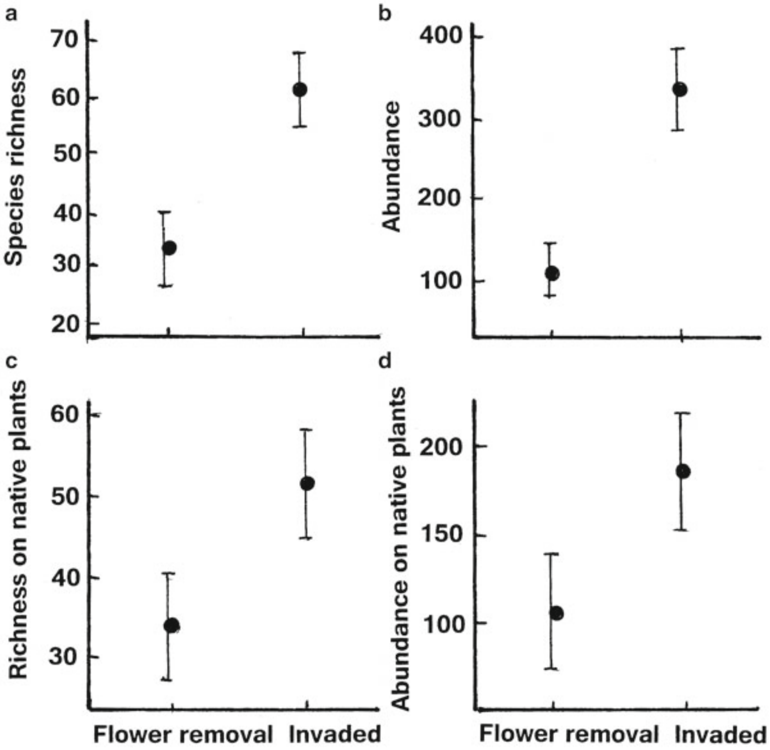

Fig. 5.1 Flower visitor diversity and abundance at experimental plots involving invasion and removal of flowers of the invasive *Impatiens glandulifera* in southern England. (**a**) overall species richness of flower visitors; (**b**) overall abundance of flower visitors; (**c**) species richness of flower visitors to native plants; (**d**) overall abundance of visitors to native plants. Standard errors shown (Lopezaraiza-Michel et al. 2007)

network of plant-pollinator interactions. Both overall visitor richness and abundance and richness and abundance on native plants were considerably higher in invaded plots (Fig. 5.1), in which the most abundant insect taxa visited *I. glandulifera*. However, rather than competing with native plants, facilitation for visits to native plants occurred. Such predominant visitation of alien plants by generalist native potential pollinators is not unusual, but it is not yet clear whether facilitation (as in this case) is widespread. Many alien plants attract native pollinators, which then participate in the invaded communities, with a variety of ecological impacts. Gibson et al. (2013) exemplified these by listing changes in seed set by native plants, pollen deposition, pollinator density and abundance, pollinator visitation rates, and composition of the pollinator fauna. Whilst many of these long-term effects have not yet been thoroughly explored, effective management of alien plants may clearly have impacts with ramifications far beyond the most obvious threats or changes. The simple abundance of ornamental alien flowering plants in amenity areas such as gardens and parks is often viewed positively as a resource for foraging insects, but those plants vary greatly in their attractiveness, leading Garbuzov et al. (2015) to recommend that gardeners and park managers can help insect wellbeing at little cost, simply by planting attractive varieties (species or cultivars) rather than unattractive plants. Similar principles apply to 'butterfly gardening' and related activities in which alien plants are often selected over native species.

Changes to pollination regimes caused by alien plants can become complex. In Thailand, selected logging of a forest tree (*Shorea siamensis*, Dipterocarpaceae) was associated with abundant understory flowering plant cover dominated by the invasive alien *Chromolaema odorata*. This led to increased butterfly activity close to the ground, and reduced butterfly pollination of the tree *Dipterocarpus obtusifolius*. Butterfly activity decreased most in more intensively logged areas (Ghazoul 2004), but increased pollination by birds or moths apparently compensated for reduced butterfly pollination.

Effects of plant invasions on arthropod communities can be severe, but rather few have been studied in detail. Some trends may be relatively obvious – the direct association of arthropod richness decline with loss of plant species richness, for example, may be a direct result of invasion (van Hengstrum et al. 2014) – whilst others are more complex. Increasing presence of alien plants, if these indeed support only lower arthropod richness than the native plants they replace, may change food web structures. Comparisons of arthropods on the two plant groups in Delaware (across six ruderal focal plant species each of natives and aliens) showed species richness on native plants to be about three times that on aliens; 83 insect species were found only on natives, but only eight were limited to aliens (Ballard et al. 2013). When analysed separately, both herbivores and predators/parasitoids showed this bias. Increasing presence of non-native plants here was anticipated to lead to an overall decrease in biomass, abundance and diversity of insect herbivores, in particular.

Individual accounts on alien plant impacts differ enormously in primary focus, scope and scale across the vast suite of biological features of the different species studied. Conservation benefits from invasive plants do not necessarily involve direct biological associations. The Australian *Eucalyptus globulus* (Myrtaceae), grown widely as a timber and amenity crop in many parts of the world, can become invasive and is then often targeted for eradication. In southern California, it became a significant roosting site for overwintering Monarch butterflies (*Danaus plexippus*, Nymphalidae), and more so as the dense groves of traditionally used native trees declined. Lane (1993) advocated local retention of *E. globulus* in those places where they were utilised by large numbers of butterflies – but also that they can be gradually phased out as they are replaced by other trees to assure continuity of suitable overwintering resources. Many invasive plants have both undesirable impacts and benefits, with the balance between these both often subjective and locally variable. The popularity of *Buddleia davidii* as the 'butterfly bush' in gardens (p. 89), for example, is offset by its spread as an aggressive riparian weed – in Britain, Williamson (2011) noted that it was replacing food plants of the Scarlet tiger moth, *Callimorpha dominula* (Erebidae, Arctiinae), for example.

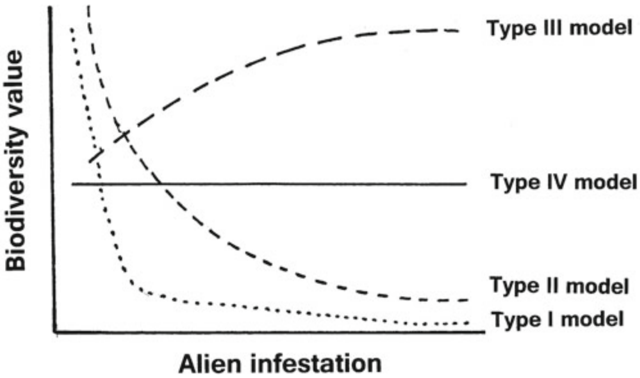

Fig. 5.2 Four hypothetical models that demonstrate some of the relationships possible between 'biodiversity value' (such as the number of native plant species) and alien infestation (here, weed density) (see text) (Groves 2011, After Adair and Groves 1998)

Hypothetical models described by Adair and Groves (1998, discussed further by Groves 2011) illustrated some of the possible relationships between 'biodiversity value' (taken as the number of native plant species) and alien infestation (weed density). The four models (Fig. 5.2) emphasise the diversity of responses, from negative (rapid, Type I; more gradual Type II), positive (where the weed provides resources or living space for native biota, Type III) or with no apparent effect (Type IV). However, depending on the parameter of 'biodiversity value' assessed, the same alien weed may be interpreted with different types of response: Groves (2011) discussed several Australian examples, with some woody weeds changing floristic composition of ground vegetation, reducing numbers of reptiles and most birds (and, although not stated, in all likelihood many insects) (Negative), but with some insectivorous birds increasing (Positive) and no apparent effect on granivorous bird abundance (Neutral). The two models of decline (Types I, II) differ in that Type I has a clear inflection point, marking the point at which management activities in relation to that threshold for any given measured biological parameter should be directed. The parameter measured, and the variety that could be measured, means that several different models within this range may apply to a single species. Predicting any single, general, response from an alien species is thus commonly over-simplistic unless a context is specified clearly.

Development of an overall 'Invasive Species Impact Rank' for invasive plants incorporated responses to questions dealing with ecological impact, current distribution and abundance, projected trends of distribution and abundance, and management difficulty (Randall et al. 2008). The first category is based on the premise that the most severe problems are generated by species with the most severe ecological impacts, with later categories augmenting this by more abundant and widespread species with high potential for expansion and so becoming the most important species to address. The last category recognises that ease of control, accessibility of invaded sites, and likelihood that collateral damage to native species will flow from control measures – with the premise that the most difficult species to manage are less likely to be controlled and, consequently, be most likely to persist.

In their new range, alien plants may help to generate new communities in which native consumers participate. This trend may be most likely when the alien plants are related closely to natives and thus have chemical characteristics to which native consumers are broadly attuned. Pierid butterflies on Brassicaceae (p. 81) are one such group. As discussed by Fortuna et al. (2013), *Pieris brassicae* oviposited on the alien Turkish rocket (*Bunias orientalis*) and benefited from this alien host in late summer when other (native) crucifers were scarce. The rocket is becoming more abundant in parts of Europe, and the above trend may lead to positive selection for this host, allowing the different butterfly generations to develop on the same host species, enforcing 'preference-performance' context in concert with an abundant food supply. Impacts of the parasitoid *Cotesia glomerata* are also influential: Fortuna et al. noted the likelihood of the wasp learning to exploit the more beneficial host plants, increasing parasitisation rate on *Pieris* larvae there. The general outcome could thereby be release of the alien plants from local herbivores in the invaded environment.

Replacement of native plants by aliens is likely to have especially marked impacts on phytophagous insects, commonly including those of greatest individual conservation concern or economic importance. A likely more functional change could result if alien plants affected insect biomass, in conjunction with community structure. In a native laurel forest in the Azores, a series of 35 food webs were used to assess impacts of alien flora through changing representation of plants, insect herbivores and their parasitoids (Heleno et al. 2008). Species richness of plants and insects decreased with increased level of plant invasions. In contrast, insect abundance was not affected significantly – but slight decrease in insect biomass was sufficient to cause about 33 % decrease in insect productivity if the study site was taken over completely by alien plants. Herbivores reared from alien-dominated plots were less specialised than those from native plots, a widespread trend across many such comparative studies on herbivores, but a concerning prediction from the Azores study was that if invasions of alien plants in the laurel forests cannot be stopped, insect productivity there could fall by more than 67 %.

Although they are often overlooked in favour of more individual, isolated or recent introductions, large scale historical and continuing movements of crop plants for agriculture and alien trees for forestry and amenity uses also take over large areas of land. They have been major transforming features of landscapes throughout the world, with grasslands and shrublands especially vulnerable, but native forests also succumbing – the seemingly insatiable needs for plantations of oil palms in south east Asia at the expense of complex tropical forests are a dramatic modern example which, with others, directly destroys the habitats of enormous numbers of native insects and other taxa – with the real extent of losses never to be documented. Many forestry plants, and alien weeds associated with agricultural crops, have invaded natural areas, with impacts on native biota. Richardson (1998) noted that at least 19 species of *Pinus* trees have become invasive in the southern hemisphere, where some species cause major environmental problems. Thus, impacts of

Monterey pine (*Pinus radiata*) introduced into Australia as the now predominant softwood crop are severe and varied, as shown by several studies on changes in insect assemblages. Comparative surveys of epigaeic beetles in *P. radiata* plantations and native forest in Victoria showed that both support high species richness (Gunther and New 2003), endorsing earlier contention (Neumann 1979) that the alien pine forest environments can provide suitable habitats for a wide range of native insects. In marked contrast, pine plantations in the same region support very few ant species, these being an ecologically impoverished subset of those found in adjacent eucalypt forests – with the implications that the plantations directly reduce native epigaeic ant assemblages, and that recolonisation from nearby either does not occur or is ineffective (Sinclair and New 2004). Similar trends in South Africa (Donnelly and Giliomee 1985) support suggestions that native forest remnant refuges are important conservation needs for forest ant diversity in such modified areas. Clearing of native Kanuka (*Kunzea ericoides*) forest in the South Island of New Zealand, and its replacement by *P. radiata* plantations, was associated with declines of the endangered endemic ground beetle *Holcaspis brevicula*, but pitfall trapping surveys in pine forests and native forest remnants suggested that (1) the pine plantations may, at least partially, help to sustain the beetle whilst (2) the native forest remnants may be too small to sustain viable populations (Brockerhoff et al. 2005).

Associated with the monocultures represented by tree plantations and agricultural crops, and devised largely for pest contexts, the 'diversity-resistance hypothesis' states that more diverse plant communities are less prone to insect herbivore damage. Two major features have been proposed to support this. Discussed by Dulaurente et al. (2012), these are (1) diverse plant assemblages may provide natural enemies with appropriate resources and refuges, increasing their potential to control invasive herbivores, and (2) mixtures of plants may hamper polyphagous insects seeking hosts because suitable hosts may be hidden or scarce amongst non-host plants. The most conspicuous host plants are likely to be the most susceptible to attack, as long implied (Root 1973) within the 'resource concentration' hypothesis of host plant selection – easy detection facilitates attack, so that host plants exposed along forest edges and similar conspicuous areas may suffer increased herbivory.

Invasion of temperate grasslands by invasive alien conifers is a major environmental concern (Pawson et al. 2010) that can lead to declines and losses of native biota, including native plants and their consumers. In New Zealand, insect groups characteristic of grassland ecosystems (Hemiptera, Orthoptera – the latter including notable endemic and threatened species) declined significantly as conifer invasion proceeded to reach high density levels in which increasing canopy cover became influential.

In the 'other direction' Australian eucalypts exported as rapidly growing crops for polewood and wood chips, as well as shelter belts and roadside amenity plantings, also cause severe concerns – for both *Eucalyptus* and *Pinus*, as the two globally predominant widespread alien tree genera, insect attack (by alien or native species) may lead to biological control measures involving use of further alien species. The major impetus for alien tree uses are very varied. They include strong economic incentives but also include societal benefits extending well beyond immediate economic use for timber. Insect conservation implications are, simplistically, twofold, reflecting (1) associated pest problems from species infesting the trees, their spread in tracking food hosts into wider environments, and measures taken to suppress them, and (2) the impacts of the alien trees on native taxa, whether harmful or beneficial, direct or indirect.

Changes to physical environments from invasive vegetation can often lead to conservation concerns, with impacts greater than initially evident, and with the major management step needed being removal of that vegetation. Alien invasive trees (mainly the Australian *Acacia mearnsii*, Mimosaceae) comprising riparian vegetation in South Africa are associated with declines in native odonatan assemblages (Samways 2007) by reducing structural diversity and creating more intensively shaded regimes: they are 'by far the most important threat' to some endemic Odonata there (Samways and Taylor 2004), essentially because of the shading canopies they create. Impacts of trout (p. 184) are almost certainly synergistic with those of alien trees. Samways and Taylor implicated alien trees as major threats to all of the 12 globally threatened Odonata in South Africa. Comparison of Odonata in study sites along five rivers and in three vegetation regimes (namely, native indigenous riparian vegetation, invasive alien trees, cleared with these alien trees removed) revealed considerable differences in assemblages. Mean dragonfly abundance and richness was greatest on the cleared sites (Samways and Sharratt 2010). Natural sites supported many abundant endemic species, whilst the somewhat greater representation of taxa in cleared sites included almost equal abundance of endemic and widespread species. Densely-vegetated alien sites yielded far lower abundance, but species richness was highest in less dense alien sites where sunlight and understorey plants were still present. The major implication is that removal of invasive alien riparian trees benefited odonate abundance and richness, to the extent that those in cleared and natural sites were very similar. Densely shaded environments were associated with losses of many sun-seeking species that reappeared and became more abundant when conditions were changed. Widespread species were the major initial beneficiaries of this treatment, with reappearance of local endemics following later, in association with more natural plant establishment. The key restoration need was to rehabilitate natural vegetation through removal of invasive trees and protecting further areas from invasions, so preventing fragmentation and isolation of Odonata populations, and providing for the continuing needs of both local endemics and more generalist taxa. Those trends may be more widespread, as invasion of riparian zones by alien trees is sometimes associated with wider homogenisation of aquatic habitats and associated macroinvertebrate communities (Magoba and Samways 2010). Those communities recovered rapidly if the shading aliens were removed, to more resemble those of more natural sites with the higher richness communities there reflecting richness of aquatic plants and greater substrate heterogeneity.

Alien grasses can markedly change the physical structure of native grassland remnants, through changes in sward height, amount of bare ground and other factors that can affect native insect herbivore behaviour, reproduction and fitness, irrespective of their values as foods relative to native grasses. Their management, such as by changed burning regimes on North American prairies, may also have unforeseen conservation impacts (New 2014). Progressive invasion of short-grass prairie remnants by Tall oat grass (*Arrhenatherum elatius*), which is two to three times the height of the dominant native grass, is one such example. The endangered Fender's blue butterfly (*Icaricia icarioides fenderi*, Lycaenidae) depends on the primary larval food plant on remnant prairie grassland, which becomes 'shaded' by oat grass (Severns 2008). Natural food plants may be obscured by vigorous invasive grasses, as noted by Weiss (1999) when sites occupied by the checkerspot butterfly *Euphydryas editha bayensis* (Nymphalidae) were invaded by alien grasses and herbs which induced losses both of native host plants, and of butterfly populations. Experiments with clipping *A. elatius* to native grass sward height markedly increased the numbers of butterfly eggs laid on the then detectable larval food plant, Kincaid's lupin (*Lupinus sulphureus kincaidii*). Elsewhere, dominance by oat grass diminished host plant detection by the butterflies, leading to increased chances of emigration and decreased colonisation. Severns also noted that the few conspicuous lupins in patches of shorter grass surrounded by oat grass may become 'overloaded' with eggs, possibly leading to larval mortality and population decline, with the broader implications of the invasion including this ineffective oviposition, as well as changed thermoregulation, and habitat selection or detection. Even more broadly, general habitat quality loss through comparable alien grass invasions altering sward height could reflect a widespread process toward degrading butterfly communities associated with open ground.

5.2 Environmental Weeds

The very wide impacts of some alien plants resulting from their status as environmental weeds and intrinsically self-evident through their predominance in invaded ecosystems, can commonly only be couched in such embracing terms rather than of specific impacts on individual native species. Examples are common – in northern Australia, the Rubber vine (*Cryptostegia grandiflora*, Asclepiadaceae), native to Madagascar, is an aggressive invader of dry rainforest ecosystems, smothering and killing trees and shading out ground cover, and can form substantial barriers of riparian vegetation along water courses. An early summary (Mackey et al. 1996) noted that it 'has the potential to completely destroy many unique ecosystems', and has had massive direct costs to the grazing industry. Introduced to Australia as an ornamental about 1875, *Cryptostegia* spread rapidly to become naturalised, since when its invasions of native forests have been implicated in declines of native mammals and birds. There can be little doubt that many localised insects across the up to 2 million hectares of infested country have been affected as a component of the wider environmental impacts as the vine produces increasingly monoculture-like appearance of previously diverse ecosystems. Continuing suppression efforts involve mechanical, chemical and biological approaches.

The most serious effects of environmental weeds thus alter major ecological features of landscapes (such as choking or full surface cover of water bodies by aquatic weeds) or essentially replacing diverse native vegetation. The entomological consequences of many cases have been assessed only very inadequately, but some clearly have widespread and dramatic impacts on native fauna. The woody *Rosa rugosa* has completely displaced original vegetation on many northern European sand dunes – in the example studied in Denmark by Elleriis et al. (2015) the change from marram grass-covered dunes by the rose was described as change from ‘a dune grassland poor in flowering plants to a low monospecific shrubbery rich in large flowers’. Comparisons, using pitfall traps, of arthropods in *R. rugosa* plots and nearby native vegetation at each of 20 dune study sites in the National Park Thy both supported several prior predictions and revealed changes that were not (and, perhaps could not be) specifically predicted. Predictions supported included that established (probably 10–25 years old) rose patches supported arthropod communities very different from those on nearby dune vegetation, and that the differences were driven by change in the relative abundance of different functional groups. Thus, flower-visiting insects (Hymenoptera, Diptera), generalist herbivores (Lepidoptera larvae) and some detritivores (Diptera familes) increased in abundance, and one predatory group (spiders) showed lower richness through reduction in diurnal xerothermic species. Non-predicted outcomes included reductions of spiders and Staphylinidae (predators) and leafhoppers (herbivores) in rose vegetation. It appeared likely that numerous xerothermic dune specialists would decline further if *Rosa* invasion continues (Elleriis et al. 2015).

Simple ‘occupation of space’ by invasive plants such as the above can impose severe impacts on native plants and associated food webs and, as Gerber et al. (2008) emphasised, studies that transcend trophic levels can provide useful insights into ecological impacts of those invaders. Their example, of alien Knotweeds (*Fallopia* spp., Polygonaceae) from eastern Asia invading riparian habitats in Europe, demonstrated a probable link between replacing native plant species and reduced invertebrate abundance and morphospecies richness. Large-scale *Fallopia* invasion might thereby seriously affect quality of riparian systems for numerous ‘insectivorous’ vertebrates. Pitfall and window trap samples in *Fallopia*-invaded areas and native (grassland and brush-dominated) vegetation showed considerable differences in each of numbers of individuals and morphospecies, and in overall biomass, with herbivores the most consistently different guild (Fig. 5.3) and linked with knotweed sites having the lowest plant richness. Reducing *Fallopia* density might help to partially redress this trend of reduced diversity and productivity.

Many less-noticed invasive plant weeds may spread unobtrusively to affect native plant community composition and attendant insects. The invasive lupin *Lupinus polyphyllus* in Finland has spread rapidly along road verges and in other disturbed habitats, and has become a threat to native low-growing plants adapted to nutrient-poor conditions (Valtonen et al. 2006). That spread is associated with declining abundance of butterflies, mostly meadow-frequenting species. The lupin

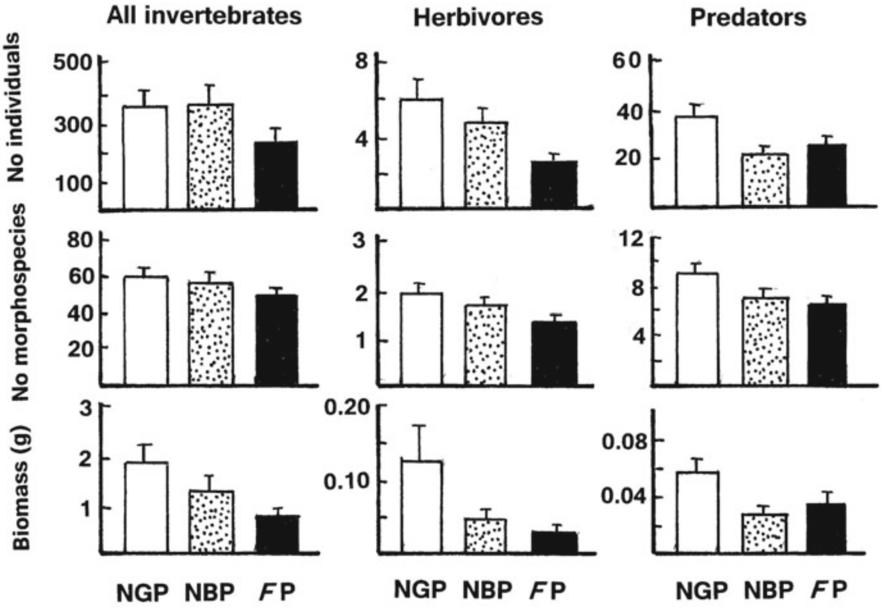

Fig. 5.3 Invertebrates in pitfall traps in three different vegetation types (in sequence from *left* to *right* in each figure native grassland plots (NGP), native bush plots (NBP), *Fallopia* plots (*F*P), showing numbers (*top*), morphospecies richness (*centre*) and biomass (*bottom*) of all invertebrates and selected key guilds (Gerber et al. 2008)

does not provide food for Lepidoptera but decreases cover and species richness of potential larval food plants and nectar supplies for adult insects.

Associations between introduced trees and native insects vary enormously, with the most extensive impacts rivalling the extent of pest concerns from introduced insects attacking native trees. Some native European insects thrive on, and cause major damage to, tree species introduced from North America, whilst other trees from the same areas suffer little if any significant damage. Phylogenetic relationships between alien and native tree hosts may sometimes predispose aliens to attack, with increased relatedness increasing susceptibility to oligophagous or polyphagous herbivores; there is widespread belief that polyphagous insects preferentially select alien trees that are related closely to their ancestral hosts. However, Bertheau et al. (2010) emphasised that 'fitness' (indicating ability to produce numerous viable and fertile offspring) may be a better indicator of probable host shifts than relationships alone. They reviewed 346 comparative studies of forest insect 'fitness' on alien and native host tree species, excluding studies that also correlated impacts of natural enemies. Their comparisons incorporated both (1) alien trees attacked by native insects and (2) native trees attacked by alien insects. Fitness was expressed by different measures across studies, and included evaluation of fertility, fecundity or number of surviving progeny, or correlated characters such as progeny or adult body size, weight or feeding efficiency. Collectively, those comparisons embraced

93 tree species and 224 forest insect species of several different feeding guilds. Insect host tree specificity was a major correlate, with generalist feeders strongly represented amongst the successful invaders, and generalists also showing lower average losses of fitness than specialists. One wider implication, flowing from polyphagous insects being the more likely damaging 'pests' of novel hosts, was expectation that introduced tree species with no close relatives in the receiving area are likely to be those least affected by native insects, as above. Some conifers, such as *Pinus radiata* in New Zealand and Australia, regions with no native Pinaceae, are one example, but host-switching by native insect herbivore species with no previous association with such alien hosts can occur, to the extent that some become significant economic pests of commercially important softwood plantations (Britton and New 2004). A number of Australian moths, including representatives of several endemic lineages, now use *P. radiata* commonly as a host, but this may not obviate the reality that numerous less conspicuous native moths associated with native eucalypts and other vegetation lack this versatility, and have been displaced from sites converted for pine plantations.

5.3 Alien Plants as Hosts for Native Insect Herbivores

Alien plants may be threats to newly-encountered biota, and disrupt long-coevolved mutualisms between insects and native plants, but they also comprise novel resources for consumers to which they become exposed. Many are exploited readily as host shifts occur or host ranges expand, as a basis for accompanying native predators and parasitoids to also change their occupancy. Levels of herbivory on invasive plants have been suggested as a possible predictor of invasiveness (Cappuccino and Carpenter 2005), drawing on observations that although a small proportion of alien plants become highly aggressive invaders, most remain restricted and minor members of the invaded plant communities.. Highly invasive plants surveyed in eastern North America showed considerably lower foliage herbivory than non-invasive plants. However, Cappuccino and Carpenter emphasised the lack of any proven causative links between herbivory level and plant 'performance', and that the roles of phytochemicals and the taxonomic relationships between alien and native plants are both complex to interpret.

Adoption of a new host plant has the potential to influence the developmental pattern of a native insect herbivore, with flow-on effects including changing the season at which particular life stages may be exposed to seasonally active natural enemies. The Pine beauty moth, *Panolis flammea* (Noctuidae), normally feeds on the native Scots pine (*Pinus sylvestris*) in Britain, but after extensive plantings of the North American Lodgepole pine (*Pinus contorta*) in Scotland has become an important pest that undergoes periodic outbreaks on this alien host (Hicks et al. 2007). However, larval development is slower on *P. contorta*, reflecting poorer nutrition than that provided by Scots pine and, whilst this results in longer exposure time to parasitoids, larvae on *P. contorta* are actually less frequently attacked by wasps.

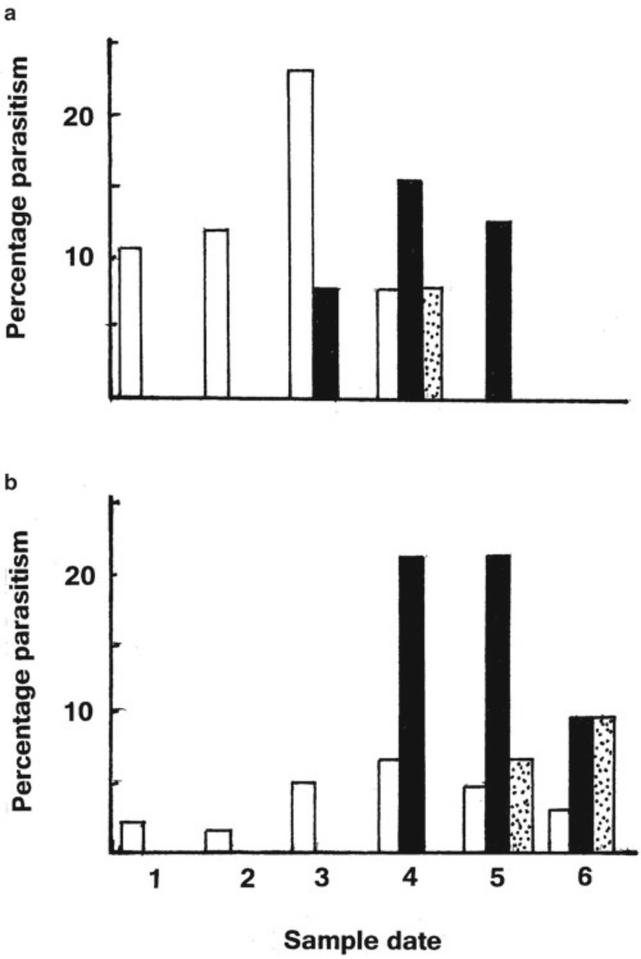

Fig. 5.4 The percentage parasitisation by three dominant parasitoids on larvae of the Pine beauty moth, (*Panolis flammea*) on (**a**) Scots pine and (**b**) Lodgepole pine in Scotland on successive sample dates (1-6); parasitoids are *Meteorus versicolor* (*open bars*), *Zele albiditarsus* (*black bars*), *Therion circumflexum* (dotted bars) (Hicks et al. 2007)

This leads to considerable differences in population structure induced by the different timing of the various larval instars; larvae hatch earlier on *P. sylvestris* and also leave the tree to pupate earlier than on *P. contorta*. The patterns of attack by the three major parasitoids (Fig. 5.4) show clear differences on the two hosts. Cohorts of preferred instars last for a shorter time on Scots pine but they occur as a greater proportion of the optimal host stages available, and so are more vulnerable to attack than larvae on Lodgepole pines.

'Spill-over' effects of insect herbivores are often believed most likely to occur on plant species related to normal hosts, so that testing for non-target impacts commonly involves giving priority to such related plants, and incorporating both 'no choice' and 'choice' tests to detect acceptability and preference. Thus *Uraba lugens* (p. 35) in New Zealand posed possible risks of both temporary spill-over, sometimes from the propensity of female moths to lay on a wide range of plants, and from the more serious establishment of more permanent populations (Withers et al. 2011). The latter was considered highly unlikely to occur in native forests, whilst temporary impacts may be most likely in urban areas where mixed species plantings involving both native and alien plants occur. For another Australian moth invader of New Zealand, the Painted apple moth (*Teia anartoides*, Lymantriidae), no-choice laboratory trials confirmed its polyphagy, with 42 % of the 79 native and alien plant species tested supporting development to adulthood (Suckling et al. 2014). Planning an eradication campaign against this moth required further evaluation of the 'true' host range in New Zealand – but laboratory testing alone was insufficient to achieve this: some native plants with field infestations were not predicted as hosts by those trials, but infestations were self-evidently robust, and counselled need for caution if conservation interests were involved. Self-sustaining populations of *T. anartoides* could develop on a variety of native hosts and could then impose pest pressures on some forest crops (Brockerhoff et al. 2010). Predicting the host range for any such invasive phytophagous insect as its invasion progresses remains a considerable challenge.

The process of predicting movements of native herbivores onto novel host plants may be improved by considering relationships of alien and native hosts, with many insect herbivores (1) having a taxonomically circumscribed suite of host plants, so that (2) non-native plants not related to native hosts often experience less damage from native herbivores than do more closely related alien plants (Pearse and Altermatt 2013). Using a matrix involving 1944 native plant species and 900 species of European native Lepidoptera to forecast use of 459 non-native plant species, modeling successfully predicted most novel interactions through extrapolating host use from the networks of native herbivores and food plants. Where related plants occur in the invaded area, shared phytochemicals may facilitate or encourage host transfers. Bezemer et al. (2014) also discussed the roles of 'associational effects' on native insects – the influences of neighbouring plants on the selection of hosts by those insects, so that invasive plants can either attract or deter herbivores, compete with native plants for nutrients and light, and alter chemical environments that affect the behaviour and performance of insect consumers. Predicting novel plant-herbivore interactions, whether from arrival of alien plant or alien insect (or both, if not associated previously), is a major concern for community ecologists, conservationists and pest managers alike. The variety of possible interactions and impacts renders this task extrordinarily difficult, but the central roles of insect herbivory in many communities represent the major links between primary production and higher trophic levels (Pearse et al. 2013). The successive steps of an insect herbivore exploiting a novel host plant (Fig. 5.5) are each a filter across which the traits of either or both species may prevent access to the next stage. The traits that mediate each step encompass many aspects of biology, involving factors such as diet breadth, plant defences and attractants, and inherent levels of specificity and specialisation

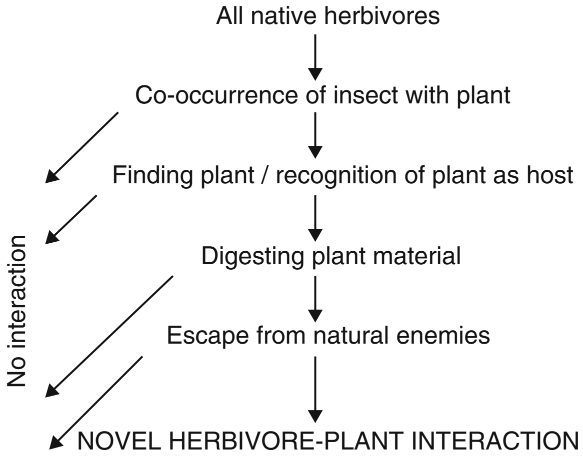

Fig. 5.5 The successive steps involved in developing a novel herbivore-plant interaction (Pearse et al. 2013)

of each partner. As such, in Pearse et al.'s words 'the ability of a herbivore to adopt a novel plant will invariably be determined by the match of a multitude of plant traits with herbivore habits and feeding mechanisms'. Plants that are accepted but are not digestible are probable ecological traps (p. 81) but, more universally, there may or may not be strong links between a herbivore's preference for a novel host and its performance on that host. The overall relative 'costs' of breeding on a native or alien plant host can be complex. In one classic study, some populations of the Baltimore checkerspot butterfly (*Euphydryas phaeton*, Nymphalidae) adopted the alien plantain (*Plantago lanceolata*, Plantaginaceae) rather than remaining with the native Turtlehead (*Chelone glabra*, Scrophulariaceae), with newly hatched larvae heavier on the alien host (Bowers et al. 1992). However, female butterflies preferred to lay on Turtlehead, whichever host they were reared on, but would accept plantain if the native host was not easily found. Consequences for the larvae also differed – when fed on *Plantago* they were palatable to birds (Blue jays) but on *Chelone* were unpalatable and caused the predators to vomit. This reflected rapid accumulation of iridoid glycosides from the normal host, but also suggested that butterfly populations on plantain may only be short-lived because of the increased predation.

The numerous reports of native insect herbivores adopting introduced plant hosts clearly demonstrate the potential for evolutionary changes linked directly to the presence of those aliens, with associated potential to 'reconfigure contemporary and future communities' (Carroll 2007), in some cases rapidly. However, for a novel plant to be important for selection by herbivores, it must often be abundant – so that some insects on crop or horticultural plants are amongst the most informative examples, with trials of insect feeding or oviposition on the newcomer key features of the process (Carroll 2007). The wide range of interactions between invasive plants and native insect herbivores was summarised also by Sunny et al. (2015), as in Fig. 5.6, and indicating the consequences for either the plant or the insect.

Unlike insect predators gaining immediate food reward by prey selection, insect herbivores selecting host plants for oviposition are essentially selecting the food

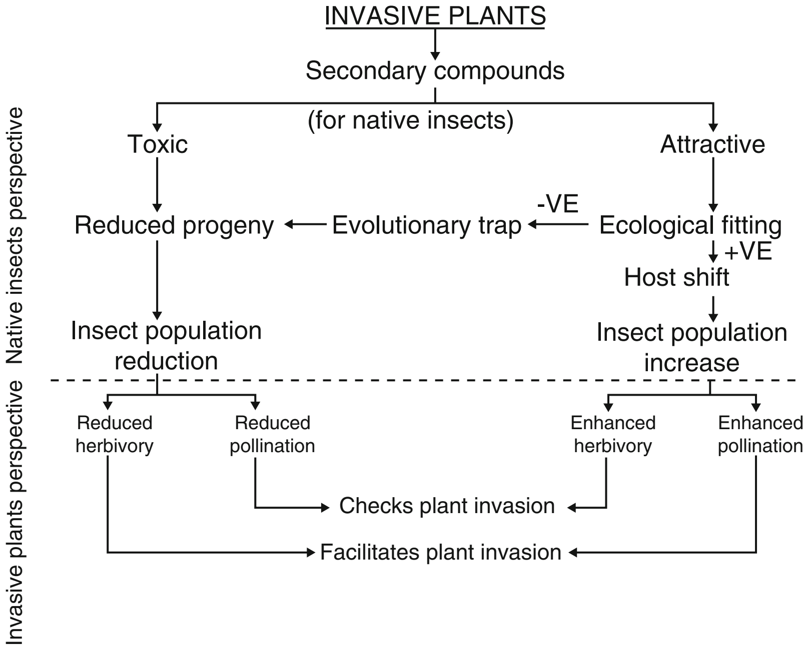

Fig. 5.6 The interactions between native insects and invasive alien plants, from the perspective of both native insects and invasive plants. '+VE' indicates positive performance; '−VE' indicates negative performance of native insects on invasive plants; the *dotted line* separates native insects perspective (*upper*) and invasive plants perspective (*lower*) to aid understanding (Sunny et al. 2015)

available for their offspring. In many cases, the plants selected may not be the 'best' for offspring development, and the best plants may be neglected – suggesting to Mayhew (2001) that some herbivores 'appear to be bad mothers', and emphasising the need for exploring the adaptations of host choice far more broadly.

The values and roles of alien plants as hosts for native herbivores are thus a major theme in understanding their impacts. Their status as hosts for native Lepidoptera in North America were surveyed through examining host records of larval feeding for all 1385 plant genera in parts of the United States (Tallamy and Shropshire 2009). Of these, 725 genera (511 natives, 214 aliens) hosted a pooled 2809 species of Lepidoptera. Native woody plants used as ornamentals supported 14-fold more Lepidoptera than introduced ornamental species (Fig. 5.7). Neglecting ornamental status, native plant genera supported threefold more Lepidoptera than introduced plant genera, and woody plants supported ten times as many species as herbaceous plants. The marked contrast between native and alien ornamentals demonstrated that introduced ornamentals (those species most commonly planted intentionally in managed landscapes) are not functional ecological equivalents of native ornamentals. Tallamy and Shropshire commented that, if Lepidoptera are realistic surrogates of all insect herbivores, the impacts of introduced ornamental plants in highly

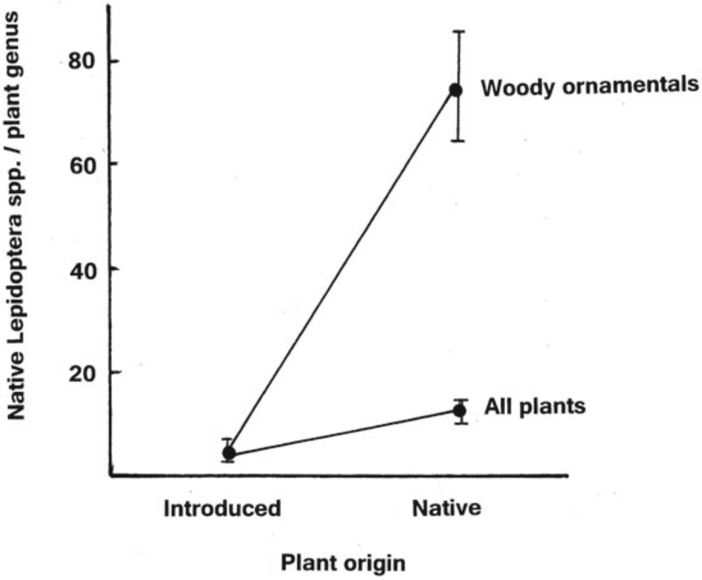

Fig. 5.7 The numbers of native Lepidoptera species recorded in the mid-Atlantic states of the United States on all plant genera and on native and introduced woody plant genera used as ornamentals (*bars* are standard errors) (Tallamy and Shropshire 2009)

managed urban areas and invaded natural areas must be substantial. The wide ecological importance of insect herbivores implies that continuing landscape creation without understanding how the constituent plants support insects – with, for example, a widespread tendency to select ornamental plants on the basis that they are relatively ‘pest-free’ – may lead to continuing declines of some native species.

Conversely, native herbivore species may benefit from alien plants. The native New Zealand pasture scarab beetle, *Costelytra zealandica*, has become invasive in pastures that comprise largely alien plants such as clover and ryegrass, to achieve pest status in those environments (Lefort et al. 2014). The initial hypothesis that this invasion may be due to host range expansion was later modified to the more likely one of host shifts (p. 120) initiated through host range increase and perhaps facilitated by native and alien hosts suitable for larval development occurring close together. Perhaps reflecting a more widespread scenario, the process has led to formation of distinct host races in *C. zealandica*, through progressive evolutionary changes in populations feeding on alien host plants.

Bezemer et al. (2014) observed that rates of herbivory are commonly higher in tropical than in temperate areas, to develop the idea that latitudinal variation in invasion success for invasive plant species may be influenced by the latitudinal variation in interaction intensity between native plants and their herbivores. The invasive species may not initially show any latitudinal gradient in palatability or defensive capa-

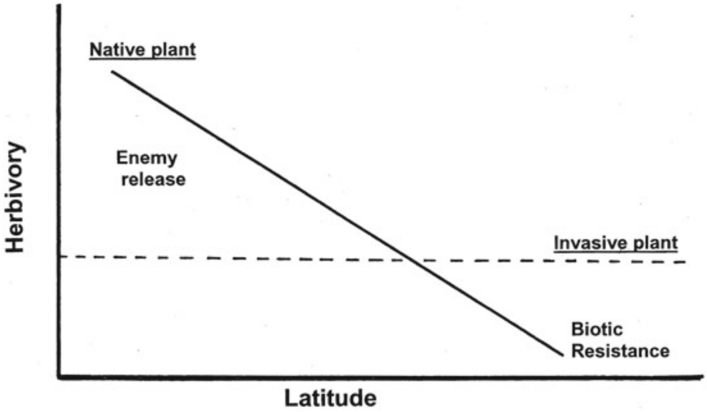

Fig. 5.8 The hypothetical relationship between latitude and herbivory for a native and an invasive plant species. The native species exhibits a latitudinal gradient in herbivory, but the invasive species does not; at lower latitudes, herbivory is much greater on native than on invasive plant species, supporting the enemy release hypothesis; at higher latitudes the greater herbivory on invasive species relative to native species suggests a case for biotic resistance; invasion success may thus be predicted to be greater at lower latitudes (Bezemer et al. 2014, with authors' permission)

bility, so that considerable differences in latitudinal responses may occur between native and invasive species. This idea is summarised in Fig. 5.8, and could help to explain why invasion success is higher in lower rather than in higher latitudes, and may also support the enemy release hypothesis (p. 116) by demonstrating herbivory to be greater on the native than on the alien plant. Conversely, at higher latitudes greater herbivory on the invasive species relative to the native species could support the case for biotic resistance.

Lepidoptera larval assemblages on two alien Neotropical *Piper* species (Piperaceae) forming woody trees in Papua New Guinea forests were compared with those on 69 species of native woody hosts, revealing that richness on each alien species exceeded the median richness across all native hosts examined (Novotny et al. 2003) and demonstrating that assemblages very similar in character can originate from the native species pool in lowland tropical rainforest in under 50 years. Most colonisers were polyphagous generalists, but many were not found on the native *Piper macropiper*, and this low overlap was unexpected. No species found feeding on the alien *Piper* hosts was otherwise restricted to *P. macropiper* (Fig. 5.9). The other anomaly from this study was the dominance of the assemblage on the alien *P. aduncum* by abundance of a single species which is neither a specialist on this host genus nor a wide generalist. This moth, the crambid *Herpetogramma* sp., was not found on the other alien *Piper* species (*P. umbellatum*) and, although Novotny et al. believed it to be native, they could not exclude the possibility that it was introduced to Papua New Guinea with its host.

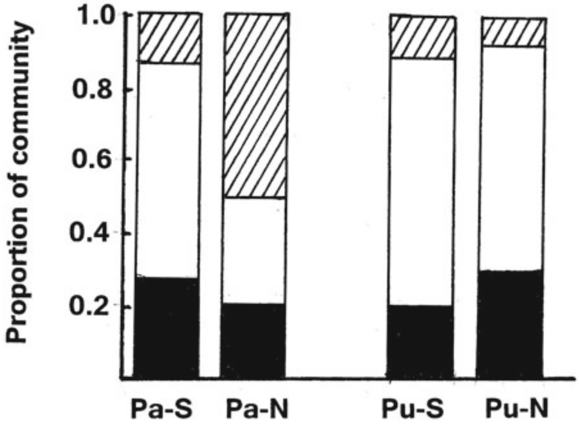

Fig. 5.9 Native hosts of species of Lepidoptera whose larvae feed on invasive species of *Piper* in Papua New Guinea. The proportion of species (S) and individuals (N) in assemblages from *P. aduncum* (Pa) and *P. umbellatum* (Pu) which were also found on any plants of other families (*black*), only plants from other families (*open*) or which were not found on any native plants (*hatched*). No species feeding on alien *Piper* hosts also fed only on *P. macropiper* (Novotny et al. 2003)

5.4 Enemy Release

Alien plants, whether crops, ornamentals or weeds, are frequently predicted to become less affected by insect herbivores in their expanded ranges than in their natural environments – the ‘enemy release hypothesis’ is invoked commonly, but also questioned frequently. The hypothesis has three major predictive components: (1) specialist natural enemies of the alien plant will be absent from the new region; (2) the specialist natural enemies of native plants, even those congeneric with the alien, will only rarely attack the new arrival – which they have not encountered previously; (3) generalists will have greater impact on the native competitors. These parameters, from Keane and Crawley (2002), have subsequently been explored by many other ecologists, with the outcomes of individual studies very varied, in supporting or refuting the hypothesis. In reviewing the hypothesis for plants and their herbivores, Liu and Stiling (2006) noted that the idea conveys intuitive sense in emphasising separation from co-evolved natural enemies, and is one of the most frequently advanced ‘explanations’ for the success of introduced invasive plant species in many parts of the world. Analysis of published literature tested three predictive themes across a wide array of studies in varied environments, and this important overview also demonstrated the major gaps in investigation and understanding. The tested predictions were:

1. The number of herbivore species should be lower on introduced invasive plants than on native plants. This was supported strongly, with the additional implication that escape from herbivores by invasive plants is biased towards specialists

and endophytic species, as well as insects feeding on reproductiuve parts of the plants. Nevertheless, alien plants can gain herbivores in invaded areas with such recruitment from the local native community partially countering the initial loss.
2. Herbivore damage levels are greater on native plants than on alien invasive congeneric hosts. This idea received some support.
3. Impact of herbivores on plant population wellbeing is reduced. This question was unresolved due to the complexity of the herbivore exclusion experiments needed to investigate it clearly, and remains so as a generality.

The major inference from that review was that it is often difficult to draw robust conclusions on the enemy release hypothesis, and the practical problems were discussed further by Liu et al. (2007). As Cogni (2010) remarked, how native herbivores respond to new plants has important implications for plant invasions, through either or both of 'enemy release' or 'new association', with these not mutually exclusive but influencing whether the plant can be exploited as edible.

The enemy release hypothesis itself embraces a variety of ecologically distinct forms. A review of published studies (Colautti et al. 2004) recognised two major categories based on scale of investigation. The wider 'biogeographical scale' embraced native and introduced populations of a given host, and 'community scale' compared native and alien species together in the same community. Both categories were represented by correlative studies and studies based more directly on field surveys or other practical approaches. Biogeographical studies broadly supported that species experience release from natural enemies, but community studies were more varied, with little consistent support for the enemy release hypothesis. Colautti et al. indicated two pathways whereby a host may be 'released' from effects of natural enemies, and that these have commonly not been distinguished clearly. They are (1) regulatory release, when a host species is strongly regulated by one or more enemy species to which it has low resistance – so that loss of those enemies from host invasion could lead to distinct changes in surviviorship, fecundity or other demographic features; and (2) compensatory release, in which loss of enemies against which a host is well defended may have little consequence for the host population but, if the defence involved costs to the host, loss of enemies may enable reallocation of those resources. This distinction is important for interpreting outcomes.

However, the widespread observation of reduced herbivore numbers on alien plants may be a more general trend (Proches et al. 2008), with a considerable number of studies supporting the enemy release hypothesis by demonstrating lower herbivory levels in a plant's introduced range than in its original range (Strong et al. 1984). Some comparisons of herbivore numbers across alien plants and native congenors or close relatives in the invaded area can help understanding. Insect abundance and species richness on invasive alien (Australian) plant species and resident South African native fynbos relatives within Mimosoideae (*Acacia*), Myrtaceae and Proteaceae (three predominantly southern hemisphere plant lineages) were compared in July and December, representing winter and summer trends (Proches et al. 2008). Outcomes varied but, in general, insect abundance was greater on the native

Table 5.1 Abundance and species richness of all insects and two major trophic feeding guilds on indigenous and alien plants across seasons (From Proches et al. 2008)

Taxon	Parameter	Interpretation
All	Richness	Indigenous plants have higher insect richness in summer, but in winter, indigenous and alien species do not differ significantly
	Abundance	Indigenous plants have higher insect abundance than alien plants, and abundance is higher in summer than in winter
Herbivores	Richness	Indigenous plants have much higher richness in both seasons: although lower in winter, this is not a significant effect
	Abundance	Indigenous plants have higher herbivore abundance than alien plants, and abundance is higher in summer than in winter
Predators/parasitoids		
	Richness	Indigenous plants have more clear seasonal patterns than alien plants
	Abundance	No clear differences between indigenous and alien plants

plants than on the aliens, although richness did not differ significantly. Some seasonal differences were found (Table 5.1), but the results were claimed to give some support for the enemy release hypothesis.

Kirichenko et al. (2013) emphasised the need for large-scale studies and showed, over a very large number of plant-herbivore systems examined in Switzerland and Russia (where pairs of congeneric woody plants, one native and one alien, were compared in arboreta and botanic gardens, and incidence of leaf-miners, gall-formers and free living consumers were assessed), a wide tendency for alien plants to partially escape from herbivorous insects. They also showed that different feeding guilds might react differently to adventive plants. Leaf-miners and gall-formers were richer and more abundant on native than related alien hosts, perhaps reflecting the 'intimacy' of coevolved endophytic associations. External feeders showed little difference in damage caused to alien and native plants. Kirichenko et al. thus raised the topic that the level of escape by alien plants from native natural enemies may depend on the feeding guild involved, in turn reflecting the level of specificity of the herbivores involved. Having 'escaped' from their native natural enemies, a successfully invading plant species should ideally then avoid attack from generalist herbivores in its new range (Joseph et al. 2009), and also escape from more oligophagous species that could potentially exploit newcomers. Some form of 'defensive novelty' may be a key to this – Joseph et al. noted that toxicity and related ecological traps are one such category of devices. Species-specific plant chemical defences against herbivores are widespread, so that trials comparing native and alien plants may give highly individualistic outcomes. Two such examples are variability amongst alien Asteraceae (nine species) and Brassicaceae (six species) against some generalist grasshoppers (*Schistocerca americana*, *Melanoplus femurrubrum*) in Canada (Jogesh et al. 2008) and amongst three invasive shrubs within the expanding range of Gypsy moth in North America (McEwen et al. 2009).

Experimental tests of the enemy release hypothesis on a range-wide scale are rare. The European Norway maple tree (*Acer platanoides*) has been planted widely in North America over the last 200 years and is a common invasive plant of woodlands, where its dense monospecific stands are implied to reflect it outcompeting native trees. This structure contrasts markedly with its European pattern of individual trees in multi-species stands. Extent of insect herbivory and fungal damage on populations of *A. platanoides* in Europe and North America was based on examination of freshly fallen leaves in two successive autumns. These were taken to represent the total lifetime damage to each leaf (Adams et al. 2009), by measuring percentages that were chewed, mined, skeletonised or galled (all insect herbivory), with fungal spot incidence assessed separately. Over both years, total foliage herbivory in European samples was more than 3.5 times higher than in North America. European sites also showed higher variability in total herbivory levels (<1–>50 %), whilst no North American sample exceeded 4 %, amidst generally very much lower defoliation levels. Results corresponded with predictions of the enemy release hypothesis, and might help to explain the invasion success of *A. platanoides* in North America.

One possible consequence of low herbivore pressures on invasive plants is rapid evolutionary changes through selection for reduced counter-herbivore defences, changing the plant's competitive ability through a 'shift' from defence to growth. This scenario, sometimes referred to as 'the EICA hypothesis' (for 'Evolution of Improved Competitive Ability', following Blossey and Notzold 1995), remains somewhat speculative, but was appraised through a study of Tansy ragwort (*Senecio jacobaea*, Asteraceae) that compared invasive populations in Australia, New Zealand and North America with its native Europe. Joshi and Vrieling (2005) noted the need to clearly differentiate specialist from generalist herbivores, to clarify that when plants are introduced into areas lacking the specialist herbivores but where generalists occur evolution might lead to increased defences against the latter (that is, 'cheap' qualitative defences) and decreased defences (namely, 'expensive' chemicals) against specialists. This trend could give the plant a net gain of resources that can increase growth and reproduction. For *S. jacobaea*, the general defence (concentration of of pyrrolizidine alkaloids) was indeed higher in invasive than in native populations, and the invasive plants lacked protection against specialist herbivores that are not affected by the alkaloids. In the native range of *S. jacobaea* the balance in defensive needs against specialist and generalist herbivores was maintained at intermediate levels, but invasive populations displayed the anticipated shift in balance. Invasion success occurred through the two stages of (1) release from the specialist-generalist trade-off followed by (2) increased chemical defences against generalist herbivores, and constituted a novel scenario that Joshi and Vrieling suggested might have wider value in assessments of invasive potential of species that have specialist herbivores in their native range.

Colautti et al. (2004) gave reasons for distinguishing different pathways of enemy release, including (1) regulatory release has an immediate impact whilst compensatory release may occur only over ecological or evolutionary time – with the latter the crux of EICA, above; (2) regulatory release seems to be more commonly involved than compensatory release; and (3) release of specialised defences evolved against co-evolved enemies is most likely to be skewed toward a compensatory release pathway. They emphasised, also, that a host may not experience a simple release from enemies, but an exchange, gaining enemies within the invaded range and that may elicit the same responses as enemies that have been lost. More perceptive and penetrating study of the enemy release hypothesis and the complex effects of natural enemies was advocated – these included (1) the 'enemy invasion hypothesis' (EIH) in which novel factors after invasion reduce (or even reverse) the net effect of enemies; and (2) the 'enemy of my enemy hypothesis' (EEH) in which natural enemies have greater effects on native competitors and the invading species benefit through apparent competition or hyperpredation, rather than enemy release. The components are summarised in Fig. 5.10.

5.5 Host Plant Shifts

Host plant shifts and changes in host plant preference by insect herbivores are common, and add to the intricacy of insect-plant associations: any alien plant has potential to induce novel insect-plant combinations, with largely unpredictable implications for conservation. Most documented examples appear benign but, in general, such novel interactions arising from alien plant introductions have three groups of outcomes: (1) the native insect adapts to the plant, may actively select it, and benefits from enhanced fitness and/or population size; (2) the native insect either does not recognise the plant as a suitable host, or exploits it 'casually' and without any significant effects on its wellbeing; or (3) the insect seeks the plant actively for oviposition, but cannot sustain development of offspring, to the detriment of the insect population and as a 'population sink' or 'ecological trap' (Chap. 4).

The first of these trends can lead to controversial conservation scenarios. In south eastern Australia the noxious introduced weed Chilean needle grass (*Nassella neesiana*) may prove to be an important additional food plant for larvae of the critically endangered Golden sun-moth (*Synemon plana*, Castniidae), an important flagship species for conservation of the highly fragmented native grasslands in the region and which are under major pressures for urban development (summary in New 2015). That situation creates an unusual dilemma in that *Nassella*'s formal status demands its eradication wherever it occurs, as a process that might constitute a serious additional threat to some populations of the sun-moth. At this stage, it seems that *Synemon* has simply added *Nassella* to its host range, but is abundant on some sites that are almost wholly occupied by needle grass (Richter et al. 2013).

The longer term consequences of such host shifts are usually unclear, but the classic example of the Edith's checkerspot butterfly (*Euphydryas editha*, Nymphalidae) demonstrates some possible evolutionary ramifications. In Nevada, *E. editha* rapidly evolved change from a declining native host plant to the increasing invasive *Plantago lanceolata* (Singer et al. 1993). At both sites where this rapid evolution was recorded, the proportion of insects preferring the new host increased and, as a result of genetic changes in one population, some insects then refused to

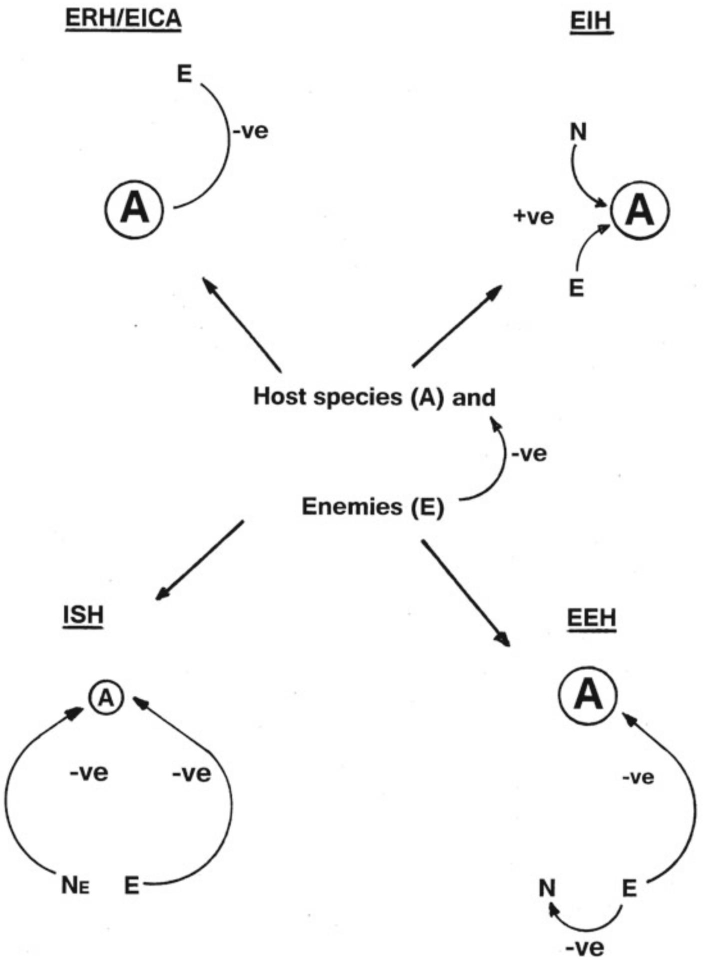

Fig. 5.10 The expected effects of enemies on the abundance or dominance of non-indigenous species, exemplified through a host species (A) in the centre of its native range being affected by natural enemies (E) that might have varying effects in the introduced range, where A becomes non-indigenous: ERH/EICA reflects reduction in number of natural enemies leading to increased vigour/fitness of A; EIH with disruption of complex species interactions reduces or reverses the impacts of enemies, such as through interactions with native species (N); EEH, host switching by introduced enemies leads to decreased vigour/fitness of native competitors (N), and proliferation of A; ISH, genetic bottlenecks lead to strong effects by a few introduced enemies (E) and by some already present (N_E), decreasing vigour of A; relative vigour of A indicated by size of symbol (Based on Colautti et al. 2004)

accept their ancestral host plant, *Collinsia parviflora*. The proportion of checkerspots utilising *Plantago*, assessed by distribution of larval webs (Singer et al. 1993) increased from about 5 % (in 1982), reaching 25 % (1985), and 53 % (1990); by 2005, Singer et al. (2007) estimated the proportion to exceed 98 %, so that the population had become near-monophagous on this alien host. If the native host is eventually restored to its original high abundance through remedial site management, the butterfly population might have lost any ability to use it – although other cases of host switching (amongst native hosts) discussed by Singer et al. (2007, and flowing from earlier contributions such as that by Singer 1983) demonstrate the checkerspot's ecological flexibility. This change was attributed to responses of oviposition preference to a plant that was, entirely by chance, more suitable to the insect than was the traditional host, and phenologically more suitable. Singer (1983) demonstrated how use of several (native) host plants can arise from the different behaviours of individuals of an oligophagous butterfly, in processes likely to have many parallels amongst alien plants and indicating that host range expansion might eventuate as (1) some individuals behave as generalists and discriminate little between host plants, ovipositing readily on different species; (2) the population contains individuals with different preferences, so that variations in popuations with different preferences affect variation in host use; and (3) one of the most highly preferred hosts is sufficiently rare and localised that most do not find it whilst searching, and lay on less preferred hosts. Both individual insect preference and ability to discriminate combine with availability of preferred hosts, and 'host specificity' is a continuous variable in the population. The wider studies of *E. editha* reviewed by Singer et al. (2007) demonstrated that, whatever the means by which a novel host plant is first adopted, rapid evolution can follow range shifts that include adoption of alien plants. However, at the time of the 2007 report, this adoption had not led to formation of new populations but was simply dietary change without spatial distribution changes, notwithstanding that *Plantago* is very widely distributed.

Many native insects can exploit invasive plants, but such unusual implications are relatively rare. Whilst they may have potential to affect the invasion process, in general insect herbivores have been found to perform more poorly on alien than on native hosts (Bertheau et al. 2010). The converse is generally attributed to the alien host's lack of chemical defences. As noted by Dai et al. (2014), most of those studies have limited scope in comparing the performance of native herbivores only on paired native and alien hosts and without attention to the duration of the novel associations. Native insects may take considerable time to accept novel host plants, and 'time since invasion' may be influential. The Chinese beetle *Cassida piperata* (Cassididae) that oviposited on an 'older' invasive (*Alternanthera spinosus*, Amaranthaceae, introduced in the 1830s) at similar levels as on two native hosts largely ignored a more recent invader (*A. philoxeroides*, introduced about a century later, in the 1930s) (Dai et al. 2014). In general, the beetle developed more slowly on alien than native hosts. Although based on study of freshwater crayfish (*Procambarus*) and aquatic macrophytes rather than insect hervbivores in terrestrial systems, the finding of considerable preference for feeding on alien over native plants led Parker and Hay (2005) to note that native herbivores can provide some biotic resistance to plant invasions, as a rather different response than from the predictions of the enemy release principle. A few published studies on terrestrial invertebrates report similar outcomes. The only insect example cited by Parker and Hay was for Orthoptera: Otte (1975) found three native North American grasshopper species (*Schistocerca* spp.) significantly preferring alien over native plants as part of a wider survey of their feeding preferences for stages of successional vegetation in Texas.

Whilst novel host plants for insect herbivores can be accumulated by 'oviposition mistakes', the wider themes of host shifting are complex. Agosta et al. (2010) discussed the concept of ecological fitting to demonstrate contributions of both current circumstances and evolutionary history to understanding this. Successful exploitation of novel environments or environmental conditions implies that the insects 'fit' by some characteristics they already possess. Because persistence depends on the colonists surviving within a novel and more-or-less unfamiliar array of species, at least some of the traits that facilitate this will have evolved elsewhere, and are then the basis for developing new ecological interactions. Each such colonising species is in some way pre-adapted to the novel circumstances. Shift to a new host may imply that the host possesses the same or similar resources as the 'old' host, or that the coloniser has abilities to persist on hosts beyond that familiarity. Arrival in a new geographical environment may impose the need to adopt new hosts, with ancestral hosts now unavailable, and lead to modification in wider traits of host use in the insect. In short, successful host shifts depend on both evolutionary history and characteristics of the species involved, both of which should be considered in seeking explanation.

Comparisons of insects on native and alien plants sometimes reveal considerable overlap of the assemblages, both in taxon richness and guild representation. The native legume *Virgilia divaricata* and the invasive Australian *Acacia mearnsii* in South Africa are one studied example (Van der Colff et al. 2015), in which more than 75 % of non-rare species (those for which four or more individuals were collected) occurred on both plant species, with 60 % overlap of herbivores and >80 % of most other guilds. This study contrasts with some that have found more native insect species on native than on alien hosts. It led Van der Colff et al. to imply that the alien tree might help to promote connectivity between isolated native insect populations associated with *V. divaricata* which, as a consequence of forest loss, now has a highly fragmented distribution.

Predominance of alien plant species in urban areas, where numerous species are planted as ornamental or wider amenity plants in parks and domestic or municipal gardens and other 'green areas', can lead to dependence on these by native insects whose native hosts have been lost, replaced or diminished. Presentation of such amenity areas may also involve removal of 'undesirable' native plants, such as many weedy species, that support native herbivores, and implement a wide range of sanitation procedures such as mowing or chemical applications. The long-term surveys of butterflies in Davis, California, enabled Shapiro (2002) to display that 29 of the 32 known locally breeding species are sustained in part on alien plants; 13 species (40 %) have no known native host in the area. Only three species have no known alien host, and three others depend wholly on alien plants for part of their breeding season when short-lived native hosts are not available. With losses of native food plants, Shapiro claimed that 'our urban butterflies are now deeply committed to a naturalised and cultivated alien flora'. Several notable native butterfly species (such as *Papilio zelicaon*, depending on the invasive *Foeniculum*) would become highly vulnerable if particular invasive plants were eradicated from Davis. Loss of native flora – with quoted estimates (Jahner et al. 2011) that up to two-thirds of the more than 2000 endemic plant species in California may undergo range reductions of more than 89 % over the next century – creates strong needs for native herbivores to adopt alien plants in order to persist. Species unable to do so are likely to decline. The surveys of California butterflies implied that the more widely distributed generalist species were more likely to use alien hosts, in contrast to the geographically restricted specialist species with much more limited natural host ranges (Jahner et al. 2011). The principle that such specialist species have heightened vulnerability in the face of such changes is widespread – but has only rarely been validated so comprehensively. Polyphagy begets ecological flexibility, and association of this with wide distributions exposes the species to a collectively wider array of potential hosts and dietary breadth. However, the full potential species richness of native herbivores on alien plants may take up to several centuries to achieve, but almost always with richness increasing over time since inroduction of the host (Brandle et al. 2008).

Wider community impacts may eventuate as native generalist herbivores adopt alien plants as food. Representatives of four families of generalist North American Lepidoptera were reared on cut foliage of plants that had become naturalised in the mid-Atlantic States region, with at least one native host also included in the trials for comparison (Tallamy et al. 2010), to test the hypothesis that, if common generalist feeders can grow and reproduce as well on alien plants as on native hosts, highly invaded plant communities may still support large numbers of the insects and also the insectivorous vertebrates that rely on that food. This was not supported – with only one exception, the tested Lepioptera species either died or developed extremely slowly on alien plants in relation to their 'normal' hosts. The inferences resulting were (1) the alien plants were unlikely to produce as much generalist insect biomass as the native plants they replaced as food, and (2) more specialised diets may occur in local populations of generalist Lepidoptera than when diet is assessed over the entire geographic range of the species. Tallamy et al.'s study implied that alien plant invasions might disrupt terrestrial food webs to the extent of reducing the insect food supply available for other consumers.

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Chapter 6
Alien Insects and Insect Conservation

6.1 Introduction

The vast numbers of alien arthropods across the world collectively impose major conservation concerns. Many insect invaders are presumed to be pests but, even for acknowledged pest species, debates can become divisive both in (1) assessing severity of impacts beyond an immediate pest context and (2) the remedial actions needed. The Australian Light brown apple moth (*Epiphyas postvittana*, Tortricidae) in California, where it was recorded first in 2007, is highly polyphagous with its larvae reported to feed on more than 200 plant species, including many crops. This discovery led to a massive eradication campaign. However, as discussed by Chen (2010), some entomologists doubt that it is really a recent invader but may have been in California for several decades over which it did not come to notice through any significant damage to crops. In that case, a highly expensive eradication campaign would not be needed, and is highly unlikely to succeed. *E. postvittana*, as a well-known and economically significant insect, simply indicates the problems that arise in seeking sound information on impacts and any remedial steps in a new, or previously undetected, environment where, essentially, the history and reality of invasion is unknown. Pest management, to a large extent founded on invasive insects of economic, social or ecological importance, continues to provide examples of the diverse impacts of invasive taxa, and parallels with conservation management – albeit often from different 'directions' of suppression or encouragement.

Much of this chapter reflects the debates over how best to harmonise the lessons from the two disciplines. Two major themes predominate: (1) the common ground between pest management and conservation, developed largely though debates over classical biological control (p. 135) and pressures to refine the practice; and (2) wider studies that concentrate on a few key focal groups of invasive insects that have contributed to understanding of how invasive insects, including notable pests, succeed in new environments. Both these themes must be considered in the wider

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context of numerous alien insects likely to be present and which represent a variety of origins, taxa, impacts and concerns (for Australia: New 1994).

Writing on Orthoptera, Lockwood (1998) discerned at least three conditions in which managing pests may come into conflict with conservation desires and ideals. These principles apply equally for many other insect groups, as (1) a species with pest potential may become threatened with extinction; (2) non-target species may be placed at risk by management practices; and (3) failure to recognise that, whilst targeting 'entities' (species), processes in ecology may also be as important – or more so – in conservation, so that disruption of ecological processes by management of a focal pest species may put both species and processes at risk. Several factors related to the above may lead to conflict between management and conservation goals – rare species, for example, may become more exposed during pest species outbreaks and then more vulnerable to the management processes. That observation flows from observation by Kemp (1992) that, at high densities, grasshopper communities in Montana, United States, included about 25 % more species than during later recovery periods when densities fell. Most known threatened orthopterans are continental taxa that may co-occur with pest species, and spatially restricted habitats, such as montane environments in which pest species may occur also harbour locally endemic co-existing taxa.

Much of the wider conservation concern from alien species in pest management arises from real or anticipated non-target impacts through pests or putative control agents feeding on, or competing with, native species either directly in the areas to which aliens are introduced, or through subsequent invasive spread to more natural environments. Those concerns, which manifest in practical contexts such as use of alien biological control agents for management of numerous insect pests, have generated much heated debate over priorities and procedures, but also led to serious considerations on assuring 'safety' of deliberately introduced species. The debate emphasised the need for pre-release assessment to determine (and, so, predict) risk of potential non-target interactions, with the major component of this being to determine feeding specificity to a level at which harm to native species could be obviated or reduced to tolerable levels. Polyphagous species are thereby generally rejected as candidates for deliberate introduction, and understanding the bases for narrower (monophagous or narrowly oligophagous) food selection increased. Scientific bases for screening potential classical biological control agents of weed or arthropod pests have done much to elucidate understanding of both incidence and mechanisms underlying undesirable impacts and to harmonise such practices with conservation need. Some level of specificity, reducing potential for undesirable side-effects, must generally be assured, with deliberate uses of more generalised consumers continuing to decline – but with their roles still to be clarified in many contexts. Much of the 'poor reputation' for safety of biological control agents flows from notoriously harmful examples from an era when environmental consequences received little attention, and when the focus was largely or entirely on efficacy of the agent. The changed perspective of modern activity would not allow many of those agents to be used, and the major calamities of the past seem unlikely to be repeated, or the reasons for any such occurrences be more clearly understood.

However, many conservationists urge wise consideration of the ‘precautionary principle’ in introducing alien species deliberately, so that risks are defined as clearly as possible, and the level of risk assessed as acceptable. Problems can arise because, although the principles of a release of a biological control agent or other alien being effective, safe, and necessary are clear, the amount of evidence needed to assess this has rarely been fully defined. As McCoy and Frank (2010) put it ‘the precautionary principle is problematic because it falls short of providing a prescription for action’.

The changing perspective and priority of ‘non-target impacts’ of alien pest management, discussed further by Lockwood (2000) has led to greater emphasis on ‘processes’ and, in Lockwood’s opinion, this represents a paradigm shift in biological control in appreciating and understanding ecosystems as networks of processes, rather than objects per se. Enlarging on his rangeland grasshopper experience, the management goal is there to save forage, in which killing grasshoppers is only one management component toward that end. In developing his earlier thesis, Lockwood (1993) considered that it is a valid null hypothesis at the ecosystem scale to consider native species to be beneficial (non-target) in sustaining ecological processes. Some rangeland grasshopper species that are important pests at high densities (outbreaks) prefer to feed on weedy or forb plants when at low densities during most of the time – so that suppression of the grasshoppers when at low levels could constitute a potentially serious impact on non-target, perhaps beneficial, species. Figure 6.1 indicates some of the interactions in rangeland that occur between target and non-target processes.

6.2 Generalist Predators

The ecological roles of Arthropod Generalist Predators (AGPs: Brockerhoff et al. 2010) are complex, reflecting their wide prey ranges, feeding across a range of trophic levels and them serving as resources for other predators, both invertebrate and vertebrate. Successfully invading AGPs can reach very high densities, with consequently high likely impacts – and with social Hymenoptera (below) they are regarded widely as amongst the most pervasive and damaging such invaders. Intentional introductions of any such generalists, with unpredictable consequences and ecological effects, are regarded as a severe conservation risk. Reviewed by Snyder and Evans (2006), both direct and indirect impacts can be demonstrated, any of which can influence community structure. Two of the classic examples they recapitulated (Fig. 6.2) show this contrast. The invasive Chinese mantis (*Tenodera sinensis*) in Delaware was associated with cursorial spiders leaving areas in which the mantis occurred (Moran et al. 1996), with the lower spider numbers presumed to reduce their predation on herbivores and so indirectly harm the plants. Addition of first instar mantids to open field plots induced this behavioural response, leading to fewer spiders there than in unaugmented control plots. The two possible mechanisms for this noted by Moran et al. were (1) predator avoidance behaviour or (2)

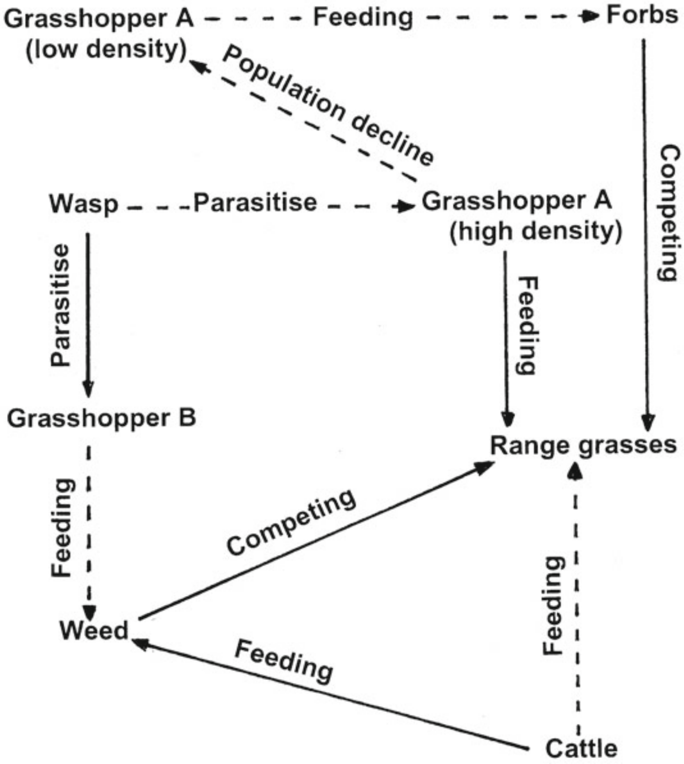


Fig. 6.1 Schematic simplification of the ecological entities and their relationships (*arrows*) in a rangeland habitat, to show the interacting nature of target (*solid arrows*) and non-target (*broken arrows*) effects. The scenario represents 'Grasshopper species A' that at low densities feeds on forbs that compete with range grasses but at high densities becomes a pest through feeding on valuable forage. In the latter conditions, a parasitoid wasp would be considered a beneficial control agent, but the same wasp becomes a detriment when it attacks 'Grasshopper species B' which feeds on a weed that competes with rangeland grasses (Based on Lockwood 2000)

numerical response to lowered prey abundance for spiders as a consequence of competition with mantid nymphs. But, because the mantids also feed directly on herbivores, the net impact is herbivore reduction and enhanced plant growth. In alfalfa fields in Utah, the invasive Seven-spot ladybird (*Coccinella septempunctata*) both suppresses Alfalfa weevils through direct predation and also counters this impact by eating the aphids that provide honeydew as a key resource for weevil parasitoids, so reducing the extent of their control (Evans and England 1996).

Impacts of generalist predators on individual threatened species are acknowledged as a serious concern, but details for many associations are unclear and, other than in clear pest impact evaluations or biological control contexts have often not been appraised. The potential direct impacts of the Red imported fire ant (p. 161) on a threatened species within its invasive range are exemplified by the Schaus swallowtail butterfly (*Papilio aristodemus*, Papilionidae) in Florida. The swallowtail is

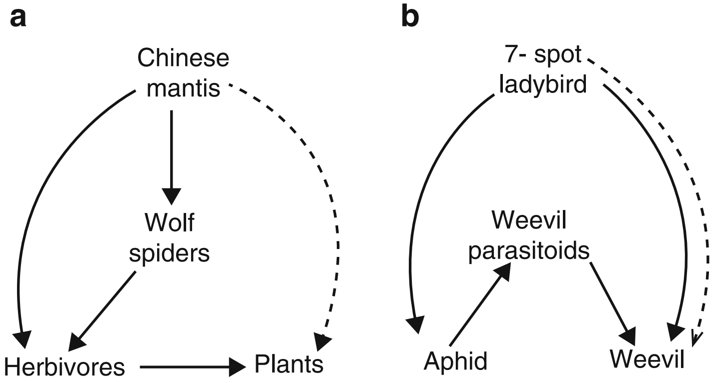


Fig. 6.2 Two examples of the impacts of invasive arthropod generalist predators on species interactions in the receiving community: (**a**) in old fields in Delaware, wolf spiders leave areas inhabited by the invasive Chinese mantis, with lower spider numbers then presumed to benefit herbivores and thus indirectly harming plants. Mantids, however, feed directly on herbivores as well, so net impact is herbivore reduction leading to enhanced plant growth; (**b**) in alfalfa fields in Utah, invasive ladybirds both suppress Alfalfa weevil through direct predation and weaken weevil suppression by eating the aphids that provide honeydew as food for weevil parasitoids, so simultaneously enhancing and weakening weevil control ('a' after Moran et al. 1996, 'b' after Evans and England 1996, as presented by Snyder and Evans 2006, see text)

listed as a federally endangered species due to a combination of destruction of its restricted hardwood hammock habitat, mosquito control and historical impacts of collecting, and the presence of the fire ant in its diminishing occupied area was a concern (Forys et al. 2001). Field trials revealed that all early stages of *P. aristodemus* were susceptible to ant predation, with the fire ants discovering exposed prey rapidly. Forys et al. suggested that fire ants are a threat to long-term *P. aristodemus* reintroduction programmes proposed for the area, and that a key need was to reduce fire ant populations.

A second example involves a classical biological control agent, the coccinellid *Coccinella septempunctata*, co-occurring with the endangered Karner blue butterfly (*Lycaeides melissa samuelis*, Lycaenidae) in Minnesota and Wisconsin (Schellhorn et al. 2005). Both occurred on the butterfly's sole larval food plant (*Lupinus perennis*), with eggs and larvae of the Karner blue easily accessible to the ladybird predator. Adult ladybirds can eat butterfly larvae. The coccinellid populations increase from the presence of large aphid populations as primary food, and benefit from both spring increases and overwintering adult population size, with the inference that Karner blue populations near agricultural cropping areas may be especially susceptible to predator spillover effects. Whilst Schellhorn et al. advocated maintaining a minimum isolation distance between aphid-bearing crops and known butterfly populations, they also noted that such a distance cannot yet be defined. However, their modelling exercise endorsed that increased predator density could increase butterfly mortality.

Relatively generalist alien predators or parasitoids introduced for biological control programmes (below) almost inevitably have potential for non-target impacts, and numerous such examples have been explored – either as simple records of non-target species being attacked or, much more rarely, assessment of adverse impacts through more quantitative investigations. Three examples of possible impacts of introduced biological control agents on Lepidoptera illustrate some of the ambiguities that can arise.

First, the effects of the polyphagous tachinid fly *Compsilura concinnata* on native North American silkmoths, Saturniidae. Exposures of sentinel larvae of the Cecropia moth (*Hyalophora cecropia*) and the Promethea moth (*Callosamia promethea*) revealed very high rates (69–81 %) of tachinid parasitisation (Boetnner et al. 2000), which may well have contributed to the spectacular declines of these saturniids in Massachusetts. Another study of these species (Kellogg et al. 2003) revealed equivalently high parasitisation in the first moth generation, but much lower rates (ca 20 %) in the second generation, and suggested that native hyperparasitoids affecting the fly may limit its impacts in some regions. As in many other contexts, differences in study methodology, habitats and taxa used can render comparisons difficult (Parry 2009).

Second, two parasitoids introduced to control Lepidoptera on Guam affected the local non-target *Hypolimnas* (Nymphalidae) butterflies, by attacking eggs (*Trichogramma chilonis*, Trichogrammatidae) or pupae (*Brachymeria lasus*, Chalcididae), as additions to the suite of native and other alien natural enemies attacking early stages of the butterflies (Nafus 1993). Both these generalist parasitoids were introduced to Guam in the 1970s; whilst their impacts on *Hypolimnas* seemed unlikely to endanger these butterflies, their capability to spread to other, perhaps more vulnerable, hosts implied need for extreme caution in releasing such species.

Third, the long-debated presumed extinction of the Levuana moth (*Levuana iridescens*, Zygaenidae) on Fiji from the tachinid *Bessa remota* was discussed by Kuris (2003). This case, discussed also by Sands (1997), demonstrates the ambiguities inherent in trying to assess the status of very scarce species. Both Sands and Kuris noted the rapid decline of this formerly important pest of coconuts following introduction of *B. remota*, but also raised the possibility that the moth is not extinct – despite this case having become somewhat of a classic as a claimed example of extinction due to classical biological control (Kuris 2003). However, it is also considered that other scarce Zygaenidae (notably the endemic *Heteropan dolens*) attacked by *Bessa* may indeed have been lost. Doubt has emerged over the real fate of Levuana, and even whether it is truly native to Fiji, or adventive.

Most studies of alien natural predators and parasitoids, many of them dealing with classical biological control agents (below), have focused predominantly on impacts on selected individual species – not least, because such investigations can be undertaken effectively in the new environments. However, as Memmott (2000) emphasised, 'the extent that biological control agents infiltrate natural communities is rarely investigated'. Manipulation of food webs, in conjunction with observational data to first assess the numbers of species (at all trophic levels) associated with the non-target species of concern, may help to reveal these impacts – but, especially for the rare or threatened species of conservation concern, achieving the detail needed may be impracticable. However, for increasing understanding of how invasive agents may lead to extinctions of native species through 'apparent competition' (with spillover from high agent densities on a common pest insect or weed targeted for control), Memmott suggested the approach of manipulating the density of the pest and monitoring impacts on the non-target species, as undertaken by manipulating some aphid species in England (Muller and Godfray 1997). There, decline of a second aphid species (the nettle aphid *Microlophium canosum*) was induced through a predatory ladybird feeding on both species, by manipulating density of the primary target (the grass aphid *Rhopalosiphum padi*) to redirect attack.

Habitat manipulations have demonstrated many ways in which the abundance, variety and effectiveness of natural enemies can be enhanced by changing environmental variety and resources. Those lessons extend to manipulative effects on invasive species, including alien pests (Jonsson et al. 2010), and led toward general principles for their management within the contexts of not harming native species and conserving (or enhancing) key ecological services.

6.3 Classical Biological Control

Classical biological control, predicated on reuniting an alien pest with it native natural enemies by introducing these into the novel area, represents a distinctive invasion route for those alien species (Hoddle 2004), albeit with the caveat that environmental safety has generally been considered and the introduction deemed likely to be beneficial, and endorsed formally by strong regulatory contexts and needs, and adequate peer review of the information available for each case. It has also been the most highly influential contributor to debate on the roles of introduced insects and other arthropods, with sometimes emotional controversy over their non-target impacts and safety after release into novel environments, but also furnishing the most comprehensive groups of factual evidence on the fates of introduced natural enemies and the risks they may incur. Although, by definition dealing with deliberately introduced predators or parasitoids, many of the principles and much of the rationale over procedures and evaluating safety extend unobtrusively to wider contexts of invasive species' impacts. One major difference between classical biological control agents and most other invasive species is that the former are subjects of considerable planning to maximise their chances of successful establishment and their 'safety' in the receiving environment, so that considerable biological knowledge is likely to be available. Inferences from the numerous published accounts vary enormously, with opinions on the impacts of biological control agents evaluated as from near zero to catastrophic and wide-ranging. Following classic papers by Howarth (1983, 1991), many authors have advocated greater care and precautions in releases of herbivores, predators and parasitoids and for the greatest possible assurances of safety, with a major context being fears of them causing extinctions of localised native insects adopted as prey or hosts by the agents. In discussing the safety of introduced non-indigenous classical biological control agents, Simberloff and Stiling (1996) concluded that (1) then current regulation of such introductions was inadequate and (2) probably no single protocols would prevent all harmful impacts, because 'ecologists simply cannot predict the effects of introduced species well enough to ever be certain'. They recommended, however, that protocols could indeed be vastly improved, largely accompanying a perceptual shift from general safety of introductions to a perspective that extensive research is needed to assess an introduction as probably innocuous – and adopting a 'guilty until proven innocent' perspective. They also called for an end to casual or ad hoc releases which at that time were still quite common. Nevertheless, in view of the polarising reactions to, and debates over, deliberate introductions of arthropods as biological control agents, some comment is warranted: several commentators have suggested that, in principle, any deliberate introduction could cause some perturbation and pose risk - but that risk may be minimal in relation to a wider 'cost-benefit' analysis or projection, and deliberately reduced by extensive pre-release screening tests. Samways (1988) noted the related conflicts and meeting points of classical biological control and insect conservation, and emphasised the critical importance of pre-introduction assessments, because 'Since established biological control agents cannot be recalled after introduction, any post-introduction monitoring is academic, albeit a valuable experiment' (Prinsloo and Samways 2001). Proposed benefits are usually centred on economic values, notably cost-effective crop protection, but operations such as weed control in natural environments clearly constitute environmental benefits. Environmental risks encompass impacts on non-target species, beneficial or other valued species, and the wider environment (Barratt et al. 2001), in all of which some level of uncertainty is almost inevitable. The variety and vitality of debates, with the volume edited by Lockwood et al. (2001) a valuable set of 'position statements' at that time and indicating the emotional fervour and conflicts the topics may arouse. In their introduction, Lockwood et al. emphasised the importance of developing acceptable compromises and selecting the least damaging options that incorporated the wellbeing of the varied groups of stakeholders in any individual exercise.

Rational assessment of non-target effects is necessary, not least to determine what level of risk – if any – is acceptable and to prevent what De Clercq et al. (2011) referred to as 'overly stringent regulations that would preclude promising agents from being developed'. That process can take various forms, as exemplified below, based on the reality that although 'benefits' can often be measured objectively, in financial terms, 'risks' cannot be evaluated fully in that direct way. As discussed by De Clercq et al., this led Bigler and Kolliker-Ott (2006) to promote a three-step process for assessment, involving (1) identifying the risks and benefits of releasing a given biological control agent; (2) determining the likelihood/probability and magnitude of each risk and benefit; and (3) ranking each, to assess whether the highest ranked benefit exceeds the highest ranked risk. A somewhat different approach is a matrix devised for New Zealand (Moeed et al. 2006), which includes a combination of seven levels of likelihood of risk (extremely likely, very likely, likely, unlikely, very unlikely, improbable, highly improbable) with five levels of impact (massive, major, moderate, minor, minimal) to produce seven rating levels, with 'highly improbable, minimal' the least concern. Such approaches can be developed at different scales, to constitute a 'risk index' across contexts and areas.

Whilst the importance of evaluating non-target impacts of introduced agents is almost universally acknowledged, just how to achieve this satisfactorily can remain problematical. Some retrospective analyses, giving the 'benefit of hindsight', have proved instructive. The braconid parasitoid *Microctonus aethiopoides* was introduced to New Zealand to control the lucerne-feeding weevil *Sitona discoideus*. The wasp attacks adult weevils and its non-target hosts in New Zealand comprise 19 native or introduced weevil species (Barratt et al. 2012). This increased knowledge of the taxonomic breadth of hosts was used for retrospective surveys in Morocco (the initial source of most *Microctonus* populations imported into Australia) and Australia (as the source of the New Zealand wasps, introduced with only limited survey at that time). This study emphasised the importance of establishing native host range efficiently and that host range testing should be undertaken in the area of proposed introduction, using the most up-to-date phylogenetic/taxonomic information available on complex host groups such as the weevils. Thus, Barratt et al. noted that changes in higher classification might have suggested a wider host range for *Microctonus*, and a correspondingly greater risk of non-target attacks.

Clear cases of adverse non-target effects, although acknowledged, have not always led to restraint over continuing introductions of the same agents, leading Cory and Myers (2000) to observe that some agents known to have negative non-target effects 'have continued to be redistributed in a frenzy of biological control enthusiasm'. Several of the examples they cited have been noted repeatedly in pleas for greater caution in such process The European seed-eating weevil *Rhinocyllus conicus* was introduced into North America to control *Carduus* thistles, but now also attacks several native species of *Cirsium* thistles there. This reduces their seed production, and also affects a native fly, *Paracantha culta* (Tephritidae), that feeds on the thistle seeds. As Louda (2000) demonstrated, this fly is only one of a number of native insects that feed on or in the inflorescences of native thistles, but exploits flower heads at the same stages and season as *Rhinocyllus*, so is subject to direct interaction if they occur together. Decreased numbers of *P. culta* were correlated with rapid increase of weevil numbers. This feeding by the weevil on non-target thistles was predicted before it was released, but the scale and importance of the impacts were severely underestimated; the strong preference then shown for *Carduus* was expected to select against significant use of native North American thistles. Louda's consequent recommendation for more extensive and penetrating risk assessment applies widely, and beyond biological control to a variety of other contexts involving deliberate introductions. As in some other cases, some unanticipated attacks are threats to native plants of conservation concern.

Cory and Myers suggested that a similar outcome may have occurred for *Cactoblastis* moths introduced from South America to control prickly pear cacti (*Opuntia* spp.), notably as one of the early classics of successful biological control in Australia. However, accidental introductions of the moths from the Caribbean to

Florida were associated with them feeding there on native cacti and becoming a severe threat to the localised and rare *Opuntia spinosissima*.

Predicting any such detailed impacts and risks has been acknowledged repeatedly as extremely difficult, and is perhaps even more so for higher level consumers employed against insects and related pest targets. The endemic Hawai'ian Koa bug *Coleotichus blackburniae* (Scutelleridae) is attacked by a number of parasitoids introduced to control Green vegetable bug (*Nezara viridula*, Pentatomidae), and these have become implicated in the bug's decline (Johnson et al. 2005). Surveys of the insects attacking *Coleotichus* on Hawai'i, Maui and Oahu demonstrated that the most important species were unintentionally introduced generalist invasive predators, notably spiders and ants, and implied that classical biological control agents had contributed rather little to its decline. As for *Rhinocyllus*, above, non-target effects of agents on *Coleotichus* were deemed predictable with hindsight, but their environmental range and magnitude would have been very difficult to anticipate. This principle is perhaps universal, and can be coupled with the reality that parasitoids and predators of insects 'clearly have characteristics that could allow them to impact nontarget organisms' but 'whether those characteristics actually result in nontarget impacts and the relative level and risk posed by those impacts is a question that can only be answered by empirical trials' (Orr et al. 2000, writing on augmentative release of egg parasitoid *Trichogramma* wasps used extensively to combat pest Lepidoptera). Non-target effects of mass-released parasitoids, such as *Trichogramma brassicae*, on endemic hosts in habitats adjacent to cropping areas, may occur (Switzerland; Babendreier et al. 2003). *Trichogramma* also exemplifies a category of biological control agents that engender concern because they are re-introduced at intervals – such as every year or every anticipated pest incidence. Laboratory studies revealed that *T. brassicae* is capable of attacking a wide range of Lepidoptera, including several on the Swiss Red List of threatened species and, whilst Babendreier et al. regarded risks to native species as low, emphasised the importance of understanding parasitoid searching behaviour as a component of risk evaluation.

Such scenarios led Follett et al. (2000) to explore the term 'parasitoid drift', to express the suite of ways through which an introduced biological control agent may come to attack non-target native species. They distinguished conditions of (1) host switching, characterised by the parasitoid concentrating on the most abundant and accessible host species; (2) host range expansion, in which the parasitoid commences to attack a new host species in addition to the primary host, irrespective of the density of the new host; and (3) host shift, where a parasitoid changes preferences from one host to another – with the close ecological analogy of an alien herbivore shifting to a novel host plant. Each of these three trajectories may occur amongst introduced biological control agents.

Some claims of extinctions or extirpations of native species from impacts of generalist classical biological control agents are based on rather incomplete information, and some such claims have later proved to be inaccurate, with rediscovery of the taxa involved. Non-target impacts of agents depend on the agent and species of concern being present together in space and time, as well as the accessibility and attractiveness (together, vulnerability) of the non-target taxon. Such information is basic to impact evaluations.

Refinements of biological control practice have necessarily incorporated both theory and practice and have contributed markedly to understanding alien species, and the ecology of their interactions in novel environments. Extensive refinements of screening tests for potential agents continue, with the aims of defining and understanding how specific they may be. Sound approaches toward assuring the safety of herbivores for weed control widely preceded such considerations for most predatory and parasitoid agents, for many of which the use of more generalist feeders has not altogether been excluded, and may even be advocated in a cost-benefit analysis. Classical biological control involving arthropod pests was developed largely in the context of crop pest management, with uses against environmental pests more recent (Van Driesche 1994), but is recognised as 'a powerful tool for suppression of invasive plants and insects in natural ecosystems' (Van Driesche et al. 2010). In contrast, early biological control attempts against plants only rarely focused on crop weeds, but far more on plants invading grasslands, forests and aquatic areas, all arenas with more 'natural' environmental values but also significant impacts on humanity as, for examples, affecting supply of forage, timber, and waterway access and navigation. The major need, historically, was to ascertain that any of those agents did not (or were unlikely to) attack beneficial insects or harm people. Wider environmental considerations have come to the fore only more recently, mostly from the early 1990s on. Van Lenteren (2001) recommended that a risk assessment for prospective agents should contain (1) a review of the target pest to explore its biology and the advantages and disadvantages of different approaches to its control; (2) full determination of the taxonomic status of natural enemies, using both traditional and molecular information; (3) information on the biology of the natural enemies; and (4) a safety evaluation of the agent's effects in the novel environment, on beneficial, threatened or other native taxa, with the conditions being that there should be no significant negative environmental impacts or such adverse effects on human/animal welfare and health. The main focus is thus on assessing the feeding specificity of the agent – a task that can never be absolute as it is impossible to rigidly test all alternatives to the target pest but for which credibility may be enhanced by approaches such as phylogenetic screening. For many historical programmes, little if any such rigid information was accumulated.

As Howarth (2001) emphasised, many agents may pose high risk of non-target attacks even though the probability of harm may be low. Again historically, relatively few introduced agents were monitored for spread and impacts after they were released – in part due to the (often false) supposition that they do not threaten native species. An extension of that practice has been a tendency to introduce potential agents to new areas before the target pests established, in anticipation that they may help to prevent that establishment (Ehler 1997).

Assessing the fate of classical biological control agents is a critical aspect of evaluation: as Carson et al. (2008) commented '… if we cannot evaluate when, where, and under what conditions, a biocontrol agent is effective, we have little means by which to weigh the costs and benefits of introduction'. Their five-component

Table 6.1 The components of a comprehensive protocol for evaluating the effectiveness of a biological control programme, based on agents introduced to control invasive plant weeds (Carson et al. 2008)

1. The agent should be released in randomly selected sites (release sites) that are paired with non-release (control) sites in a replicated manner, stratified across relevant temporal and spatial biotic and abiotic gradients
2. The abundance of the invasive plant species should be quantified in release and control sites prior to any agent releases and periodically afterwards
3. The abundance of the agent should be quantified on host plants in release and control sites
4. The agent should be experimentally suppressed on target plants in replicated subplots arranged in a stratified random manner in release and control sites
5. The responses of the associated plant community should be quantified in release and control sites prior to any releases and periodically afterwards

protocol to evaluate biocontrol agents introduced to combat weeds (Table 6.1) expresses the complexity and rigour needed in any such exercise if it is to be reasonably comprehensive – and this ideal has rarely been approached in practice. Indeed, several of the components appear very difficult to undertake within the common logistic constraints of such programmes. Nevertheless, they should stimulate much thought toward improving understanding of the processes involved in biocontrol monitoring and the guidelines needed for this.

Carson et al. also presented a series of six scenarios associated with the failure of biological control releases against invasive weeds, noting that the 'community perspective' these demonstrate can provide valuable insights for adaptive management. The scenarios are (1) native source limitation, in which populations of native vegetation needed to outcompete the alien invasive target are low, so that a shift from alien-dominated to native-dominated vegetation, even with agent impacts, does not occur; (2) novel weapons, generally chemicals produced by alien plants that impair native plants and microbial soil communities, so that a biocontrol agent can succeed only if it can negate the impacts of those allelochemicals; (3) static competitive hierarchies, where the agent may indeed reduce the invasive species, but that species continues to be dominant because it is a superior competitor and previous competitive hierarchies are not altered; (4) trophic shifts, an indirect effect in which the invasive plant species interacts with native species to change the likelihoods of their reestablishment, by altering other trophic levels (such as herbivores and predators) that affect their persistence; again, simply reducing abundance of the invasive by biocontrol may be inadequate; (5) invasive engineering, reflecting indirect effects of an invasive species on native vegetation through interactions in the abiotic environment – such as changes in soil chemistry affecting survival or fecundity: the invasive plants are essentially 'ecosystem engineers'; and (6) associated invasives, in which invasive species are replaced by co-occurring alien species which spread rapidly into areas previously occupied by the target invasive, and prevent native vegetation from returning. The above implies, as well-documented elsewhere (references in Chap. 3), that invader success may be influenced by abundance of other species that may or may not interact directly with the invader but change the abundance and

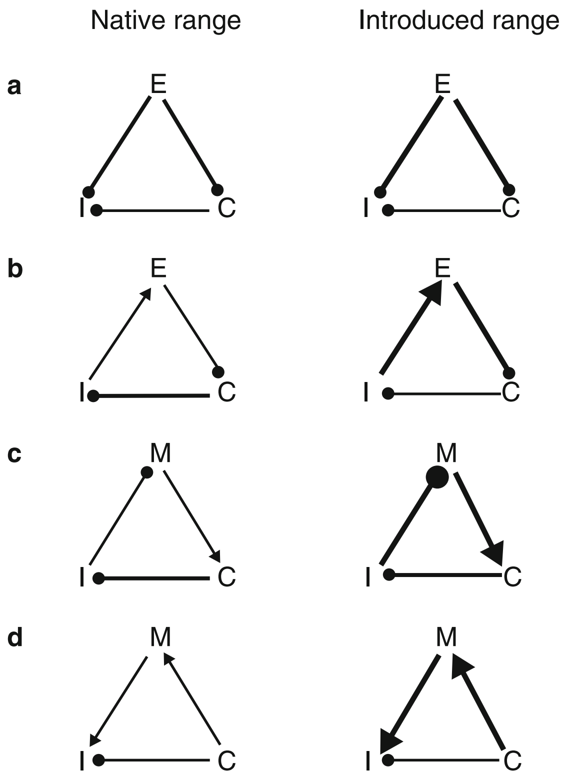


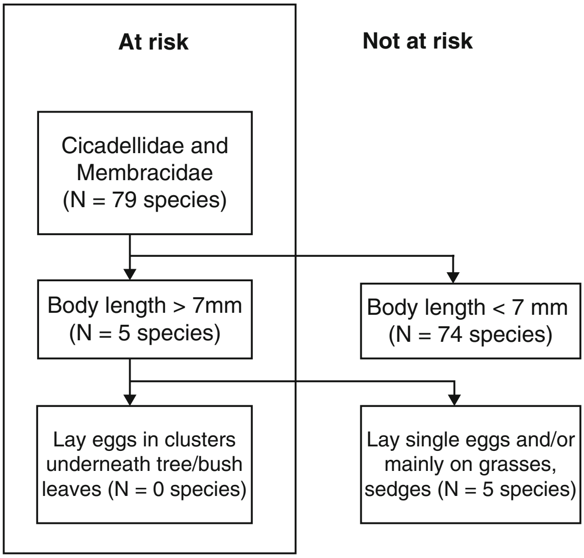
Fig. 6.3 Some hypothetical chains of interaction that may influence the success of introduced populations relative to native populations of the same species; *arrows* represent positive effects, clubs represent negative effects; relative thickness of lines indicates strength of interaction (measured per capita) relative to same interaction in other range (native or introduced); I is introduced plant species, E is enemy species, C is competing plant species M is mutualist. (**a**) if introduced plant species less vulnerable to generalist enemy attack in introduced range, competitors may benefit more from enemy release than the introduced species; (**b**) an introduced plant could facilitate its own success by increasing density of enemies which have stronger negative effects on competitors in introduced range than in native range because of difference in evolutionary history; (**c**) an introduced plant could indirectly suppress competitors by decreasing the density of their mutualists; (**d**) competitors in the introduced range may subsidise mutualists that benefit the introduced plant species (Mitchell et al. 2006)

influence of other species. Figure 6.3 indicates how native and invasive populations of the same species may differ in reflecting influences of other taxa (Mitchell et al. 2006, referring to conspecific native and introduced plant populations). Species introductions can clearly alter a plant's interactions with enemies, mutualists and competitors, and these may jointly affect the success of the alien population.

In a few cases of proposed introductions, low risk to receiving environments may be reasonably certain. The ichneumonid parasitoid *Sphecophaga vesparum vesparum* introduced into New Zealand to control invasive *Vespula* wasps (p. 164) was considered especially low risk (Beggs et al. 2008), because New Zealand has no native social wasps or social bees and it seemed very unlikely that any other possible hosts occurred: elsewhere the parasitoid attacks only *Vespula* hosts. *Vespula germanica* was reported first in New Zealand only in 1945 and within about a decade occurred across most vegetated areas of both main islands; *V. vulgaris* was present from (at least) the late 1970s and also spread rapidly. Both species were the focus of classical biological control attempts using *Sphecophaga* (Donovan et al. 2002), with screening tests implying that the wasps would not attack beneficial bee pollinators, themselves introduced.

Changes in natural enemies after they are introduced are difficult to predict, but increasing calls to appraise these occur as a component of wider risk analysis as a tool in reducing possible non-target effects (Vorsino et al. 2012). Many workers have contributed to the design and improvement of pre-release screening protocols designed to assure 'safety' of released agents, but post-release changes cannot be obviated and, increasingly, phylogenetic and evolutionary perspectives contribute to the various scenarios. Some may help to ascertain the need for rigorous screening, but the principle of practical screening is indeed well-entrenched in classical biological control. In New Zealand, Charles (2012) examined a case in which both the alien pest and the proposed classical agent differed greatly from any native species, and in which he claimed that no scientific case could be made for non-target host-screening to be undertaken before release. His perceptive argument involved the possible arrival (probably from French Polynesia, with the Cook Islands and Tahiti both now colonised by the bug) of the Glassy-winged sharpshooter (*Homalodisca vitripennis*, Cicadellidae, p. 154) and its vectored bacterial pathogen, with potential to become a serious pest of grapes, citrus and some endemic trees. In California, a key natural enemy of the sharpshooter is the egg parasitoid *Gonatocerus ashmeadi* (Mymaridae). The wasp co-occurs with *Homalodisca* in its native range, and is considered the optimum candidate agent for release in New Zealand should its host arrive. However, reviewing the biology of both these species in the context of the New Zealand insect fauna led Charles to recommend that this could be done safely without prior screening. Phylogenetic relationships of the sharpshooter were distinctive and host requirements of the mymarid unlikely to be met by any New Zealand resident species. In summary, the genus *Homalodisca* does not occur naturally in New Zealand or Australia, and the tribe (Proconiini) and subfamily (Cicadellinae) to which it belongs are likewise absent from New Zealand. This implies strongly that there are no related possible hosts for *Gonatocerus* to exploit. The native fauna of Cicadellidae comprises 79 species, and a single member of the related family, Membracidae, also occurs, and this is the only other bug family recorded as attacked by any species of *Gonatocerus*. Nearly all New Zealand cicadellids (74 of the 79 species) are much smaller than *Homalodisca*, many being less than half its size and too small to be considered as hosts (Fig. 6.4). None of the five large species lays massed eggs on the underside of foliage, as the primary conditions recognised by *Gonatocerus* in searching for hosts; one of these species, the adventive *Euacanthella palustris*, is a grassland species that probably lays its eggs singly. The risk of parasitoid spillover to native fauna was thus believed to be

Fig. 6.4 A schematic diagram to illustrate the criteria by which New Zealand native Cicadellidae and Membracidae are removed from consideration of risk of attack by *Gonatocerus ashmeadi*, should it be introduced to control the potentially invasive pest, the Glassy-winged sharpshooter (see text) (Charles 2012)

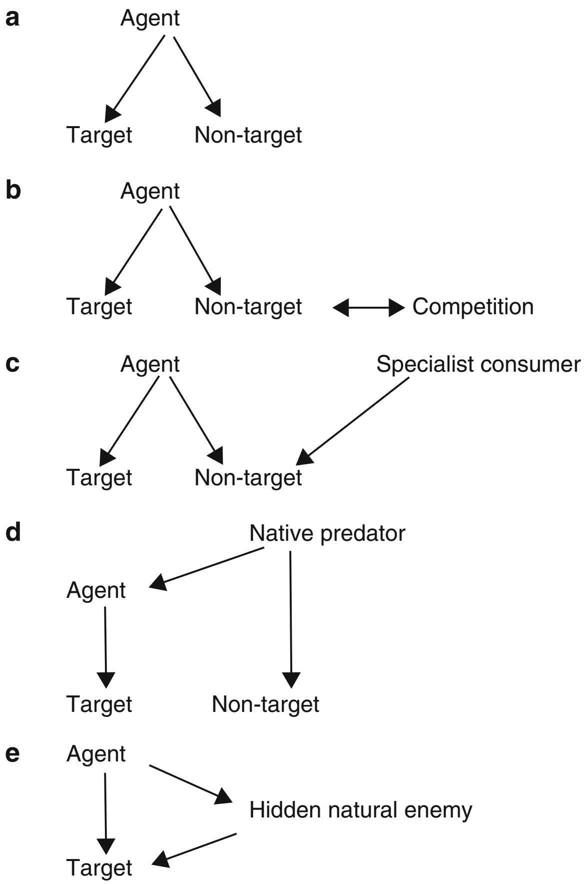


extremely low, with the consequence that, if necessary, *G. ashmeadi* could be released safely very soon after any arrival of *Homalodisca* – so avoiding the extensive delay necessitated by rigorous pre-release testing. It is very unusual for an entire fauna to be endorsed as 'safe' in this way.

The intended benefits of any classical biological control introduction include ongoing substantial suppression of the target pest, reduced pesticide uses and labour costs, and reversion to more natural ecological conditions. For weed control programmes, in particular, the last objective includes increasing more desirable native species as a means of increasing species diversity and restoring vegetation structure and associated ecosystem processes.

Testing for host specificity may be stringent, but some level of uncertainty is likely to persist when the prospective agent is introduced. As McEvoy and Coombs (2000) put it 'host specificity has its limitations as a safety criterion'. However, even highly specific classical biological control agents can impose 'indirect effects' on non-target species, as warned by Pearson and Callaway (2005). Many of these are never measured (Denslow and D'Antonio 2005), with such effects on invaded ecosystems even less so. Some are very difficult to anticipate, but arise from the form of interaction between agent and pest, reflecting both the strength of the interaction and the abundance of the agent. The scenarios envisaged earlier by Holt and Hochberg (2001) illustrate ways in which indirect impacts can occur. Represented in Fig. 6.5, the first four of these involve pathways in which the agent directly attacks a non-target species. The fifth example, however, simply requires the presence of some generalist natural enemy capable of exploiting the agent – a scenario designated 'enriched' (Holt and Hochberg 2001) in which the agent could be an extreme specialist on the proposed target species but still have impacts on other species in the receiving environment. If the agent then became sufficiently abundant,

Fig. 6.5 The structure of some community modules, indicating some interactions that can involve introduced biological control agents, and their consequences: (**a**) shared predation, where impacts on non-target taxa reflect interactions between agent and target; (**b**) mixed predation and competition, where impacts on non-target species are aggravated by presence of competing species; (**c**) exploitative competition, where the agent exploits a non-target species that is required by another non-target consumer; (**d**) enrichment, where introduction of the agent enriches the diet of a native predator, with impacts on non-target prey; (**e**) intra-guild predation, where the agent both competes with and attacks a non-target natural enemy (Holt and Hochberg 2001)



this interaction could become strong enough to benefit generalist natural enemies and indirectly affect taxa they attack. Examples postulated by Pearson and Callaway (Fig. 6.6) for weed control agents implied that the widespread argument that host specificity assures safety of the agents can be misleading. Although difficult to prove (and even more so to predict!), impacts can occur from both top-down (Fig. 6.6b) and bottom-up (Fig. 6.6c) interactions. The main need emerging was for deeper investigation of an agent's efficacy in order to better understand post-release impacts. Predicting host range of alien parasitoids and predators, accepted widely as a key need in classical biological control, encompasses three main groups of problems that can broadly be categorised as 'practical' (too many species, limited resources, varying levels of legal requirements), 'theoretical' (ecological contexts, as above, and difficulties of seeking generality), and 'treatment' (which sort of practical tests to undertake, scale and extent of tests needed, artificial test conditions, conditions and life stages to be used, and so on). Many were discussed in Van Driesche (2004), and review of published information may often give a preliminary framework for any potential agent (Sands and Van Driesche 2004). However, such

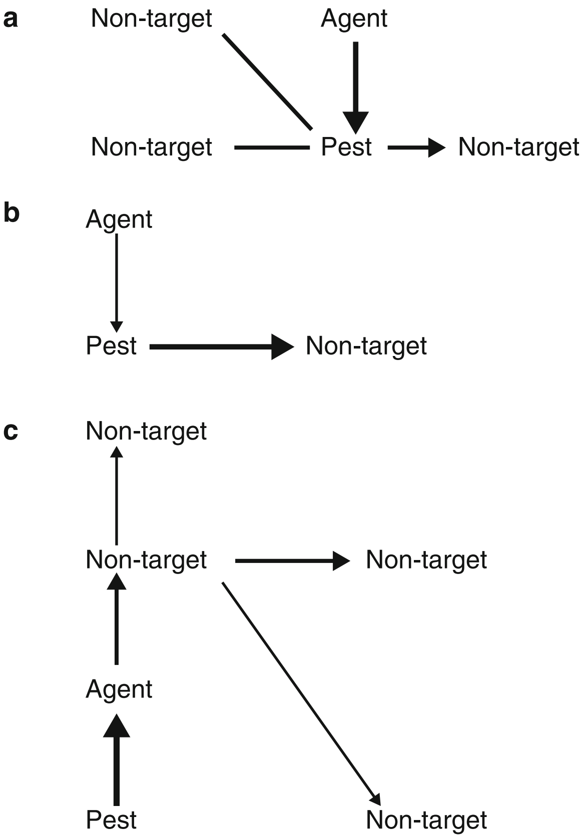


Fig. 6.6 Three examples of community modules showing pathways for indirect non-target impacts of host-specific biological control agents: (**a**) ecological replacement, where the agent strongly suppresses the target and enables releases of suppressed natives, but also weakens dependencies that have developed between the target and other native species, so negatively affecting those non-target species; (**b**) compensatory response, where the agent produces an overall top-down response but the target is only weakly affected because it displaces those negative impacts onto non-target species by compensatory responses; (**c**) food-web interaction, where overall interaction between agent and pest is strongly bottom-up, so that the agent becomes superabundant and then subsidises other natural enemies in the wider system – those natural enemies then translate that subsidy into interactions with other non-target species. *Arrow* direction indicates direction of dominant interaction, arrow thickness reflects strength of interaction; *lines without arrow* simply indicate some sort of dependence (Pearson and Callaway 2005)

coverage is often highly inadequate, with biases (such as toward pest species) and constraints from uncertain identifications and failure to recognise biotypes such as host races and biologically distinct populations. Groups of closely related and morphologically very similar taxa, each narrowly specific feeders, may be viewed only as a single polyphagous species – examples amongst parasitoid Hymenoptera are

Table 6.2 The parameters used to quantify the five selection criteria used to set priorities among non-target (NT) species for testing with entomophagous biological control agent candidates (EBC) (Todd et al. 2015)

Criterion	Parameters
Potential hazard posed by EBC to each NT	H1 Potential direct hazard
	H2 Potential indirect hazard
Potential exposure of each NT to the EBC	E1 Likelihood that NT will occur in receiving area
	E2 Likelihood that NT will occur in target species' habitat at the same time as the EBC is active
	E3 EBC's potential abundance
Estimated ecological impact that may result from NT being affected by EBC	I1 NT species' biomass
	I2 Food web links from NT to other organisms
	I3 NT species' key ecological function
	I4 NT species' resilience (ability to avoid the hazard or reduce exposure)
Assessed economic, social and cultural values of NT	V1 Value of NT to indigenous people
	V2 Conservation value of NT
	V3 Value of NT to society
	V4 Economic value of NT
	V5 Links from NT to species higher in the food web
Assessed ability to conduct tests with the NT	T1 Accessibility of NT
	T2 Generation time of NT
	T3 Rearing protocol for NT
	T4 Bioassay protocols for NT

not infrequent. Evaluation of unusual host records ('parasitoid errors': Sands and Van Driesche) may be important, and highly uncertain.

Satisfactory screening for entomophagous biological control agents for their impacts on non-target taxa is rendered difficult by the enormous variety of native non-target prey or hosts likely to occur in the introduction area, and it becomes necessary to select from these as appropriately as possible for the most informative candidates to be screened. The New Zealand model 'PRONTI' (Priority Ranking of Non-Target Taxa) was designed for this purpose, and sets priorities amongst species by five criteria. Discussed by Todd et al. (2015), these criteria were evaluated for a 'surrogate proposed biological control agent', the already present generalist predator *Polistes chinensis* (Asian paper wasp, p. 164), for this purpose treated as if it was a candidate for control of Lepidoptera pests in kiwifruit (*Actinidia deliciosa*, Actinidiaceae) orchards. The non-target candidate pool comprised 340 invertebrate taxa found in those orchards, and provided the information that could be used in ranking each species for priority for testing, using the selection criteria and parameters summarised in Table 6.2. Of these, the first two criteria (hazard, exposure) are the major drivers for priority, and the hazard features noted in the table encompass a wide variety of reported effects; scores, on scales of 1–10, were allocated to each parameter, with higher numbers assigned to information that implied high hazard risk but subject to some (specified) adjustments. 'Exposure' incorporated any modelling predictions for the agent, and the variety of ecosystems in which the agent and candidate non-target species were likely to occur – with highest scores given to species occurring in all ecosystems into which the agent was likely to move. The other criteria enlarge perspective by adding wider ecosystem impacts, consideration of cultural values, and of amenity to testing (for example, very rare species can not usually be tested because of their scarcity).

The PRONTI scheme thereby enables objective and transparent ranking of potential non-target species to set priority for screening. Depending on the potential agent, selection within these candidates could take various forms – for example, if only a limited number were at risk, all might be screened; if a wider array were considered vulnerable, selection might be across a range of genera or families; regulatory requirements might dictate that beneficial species are included; species might be selected against some PRONTI threshold score, and so on. A partial practical validation of this approach was obtained by identifying prey obtained directly from the wasps returning to nests in orchards, with the majority of prey species retrieved amongst those predicted to be at high risk, or related to such species at family level.

In order to pursue biological control of the Erythrina gall wasp (*Quadrastichus erythrinae*, p. 79) using natural enemies from the wasp's area of origin, determining that likely area was itself a complex exercise, undertaken through examining its impacts on a wide variety of possible host *Erythrina* trees (Messing et al. 2009). Botanic gardens in Hawai'i contained 71 of the approximately 112 known species of the genus, and these (covering much of the global range of *Erythrina*, and with origin of each species known or inferred strongly) were used in visual observations of infestation and damage levels. Female wasps were also presented with foliage of gall-free hosts in sleeve cages in a no-choice trial of host suitability. Tree species endemic to Africa appeared more resistant to the wasp than hosts from elsewhere, with complete absence of *Quadrastichus* from all species native to several African countries. Earlier presumption of Africa being the region of origin contributed to selection of Tanzania for searches for suitable agents. The study also revealed susceptibility of a number of *Erythrina* species from South America, where the wasp had not yet invaded, and the varied uses of the trees in that region implied the likely future need to defend them against the wasp's depredations.

Use of the predatory ladybird beetle *Rodolia cardinalis* to control the invasive Cottony cushion scale (*Icerya purchasi*) is one of the early classics of biological control. *I. purchasi*, native to Australia, has invaded more than 80 countries and has been reported to feed on at least 200 plant species across many families: it is of greatest concern in tropical and semitropical regions. Concerns over non-target predation by the ladybird have persisted, and its liberation onto the remote Galapagos islands (as the first recorded intentionally introduced insect to the archipelago, of more than 450 established alien insects there) in 2002 to target *I. purchasi* led to considerable debate and risk assessment, summarised by Causton (2004). The scale insect reached the archipelago on ornamental plants in 1982 and has colonised 15 islands, attacking more than 60 endemic or native plant species. Because earlier information was considered insufficient to demonstrate impacts of *Rodolia*, further tests, including feeding range trials with potential non-target species, were

Table 6.3 Some considerations in designing screening tests to assess possible impacts of the ladybird *Rodolia cardinalis* as a potential control agent for *Icerya purchasi* on the Galapagos Islands (Causton 2004): the criteria used to select native species for inclusion in the feeding range trials

Criterion	Rationale
Species closely related to *Icerya* or other Margarodidae	Wide assumption that species taxonomically close to the target pest are more likely to be attacked
Species previously reported as prey for any *Rodolia* species	Habits of congeners may be useful indicators of potential feeding range
Species morphologically or physiologically similar to *Icerya*	Olfactory or visual cues produced by scale insects are often necessary to stimulate coccinellid feeding: such prey characteristics may influence prey selection by *Rodolia*
Species that live in close proximity to prey of *Rodolia*	Possibly at risk, as increased likelihood of spill-over prey, together with natural enemies on *Icerya* or other possible prey as risk from competition or intraguild predation from increased encounter rates
Invertebrates of conservation value that might interact with *Rodolia*	Toxic reactions produced by feeding, could transmit to insectivorous vertebrates

undertaken. Criteria used to select test species for trial mirror the development of such approaches for other predators (Table 6.3). The last category considered possible toxic reactions produced by feeding, so that insectivorous birds (including some Galapagos finches, and others) are amongst the potentially vulnerable taxa. The detailed considerations listed by Causton (2004) reflect the complexity of designing reliable screening tests for, even, a reasonably well studied predator. Conservation considerations include that, whilst temporary foraging on non-target taxa is sometimes considered acceptable to sustain agent populations when the target species is in very low numbers, such behaviour might be highly undesirable in environments such as the Galapagos, in which impacts on endemic (or threatened) species could easily result. Almost inevitably, series of screening trials such as above – however well planned – must be incomplete, but the major outcome for this case was that potential detrimental impacts of *R. cardinalis* were minimal in relation to the immediate threats of damage to native flora by uncontrolled *Icerya*. Monitoring of the release continues (Causton et al. 2004). This case is one in which, following Wagner and Van Driesche (2010), 'classical biological control is proving an essential tool for protecting native species, communities and ecosystems'.

The acceptance of temporary non-target foraging, as above, has broader ramifications. Lynch et al. (2002) discussed the importance of the 'transient impacts' of introduced biological control agents, a theme that has only rarely been incorporated into release plans. Modeling exercises from parasitoid introductions demonstrated circumstances in which even little-preferred non-target hosts might undergo severe population reductions, and even local extinctions, in transient periods soon after parasitoid introduction. At that time the agent population is likely to increase rapidly on its initially abundant target host and, as that host declines increased parasitoid populations may spill onto a non-target host on which there is no potential to sustain the agent over any long period. Lynch et al. noted four reasons to study the importance of these transient effects, and stressed that monitoring programmes should be in place before the agent is released in order to detect these. The stated reasons are (1) that the problems have been ignored widely in favour of theoretical studies on other aspects of host-parasitoid systems, notably community assemblages and stability parameters; (2) transient impacts may have serious consequences for non-target species, even if these are markedly less preferred than the target host; (3) even on marginal hosts, local extinctions may occur that – whilst not necessarily individually critical – may contribute to wider metapopulation dynamics and declines; and (4) they are difficult to study in the field, not least because they occur rapidly, and only once in any given release location.

The wider perspective of 'revenge effects' flows from increased numbers of introduced control agent species used to increase reliability of pest control leading to problems that are even more difficult to solve. They can arise through four main pathways (McEvoy and Coombs 2000), namely (1) limited resources are diverted from other, more profitable, alternatives for managing the pest; (2) one agent undermines another, more effective, agent species and leads to increased pest density; (3) the pest is replaced by another that is even harder to control; and (4) non-target effects that offset any benefits attained. All have conservation importance, but the main purpose of listing them here is simply to emphasise that those concerns extend well beyond the commonly-cited non-target impacts that dominate much conservation discussion. Neglect of already established alien agents and of their native functional analogues may be unwise.

Coextinctions of specialised herbivores due to invasive plants have probably been underestimated substantially (Dunn 2005). A second well-documented example also involved an invasive scale insect (the invasive Ensign scale, *Orthezia insignis*, Ortheziidae) which threatened the endemic Gumwood (*Commidendrum robustum*, Asteraceae) on St Helena and was targeted for suppression as a means to promote wellbeing of specialist insects on that tree (Fowler 2004). By 1993, after its initial detection in 1991, the scale had killed more than 100 of the approximately 2500 gumwood trees present. Projections implied that all trees could succumb by 1995, and that other endemic species of *Commidendrum* were also at risk. Releases of the ladybird *Hyperaspis pantherina* were undertaken in 1993, with the knowledge that any feeding on other Homoptera there was not considered important: all Coccoidea on St Helena were introduced, and most were pests. Abundance of *Orthezia* was initially fostered by large numbers of alternative host plants (such as lantana), and there was no evidence of attack by any existing natural enemies (Fowler 2004). Following the ladybird's introduction, scale numbers fell dramatically (a 30-fold reduction) from 1993 to 1994, with correlated increase of predator numbers on gumwoods, and no further problems had been reported after 1995, so that restoration projects involving weed control around the two relict stands of *Commidendrum* have been undertaken.

Any predator or parasitoid that is maintained at high abundance by feeding on a common pest species could potentially help drive a rare but vulnerable non-target species to extinction (Memmott et al. 2007), a theme historically termed 'apparent competition' (after Holt 1977). Non-target interactions can be (1) direct, if the agent attacks a non-target host/prey or (2) indirect, when the impact occurs through shared natural enemies, a scenario that may be clarified through construction of food webs.

An early demonstration of the possibilities arose from study of the relative impacts of a shared parasitoid wasp (the long-resident *Anagrus epos*, Mymaridae), which attacks eggs of both the resident endemic Grape leafhopper (*Erythroneura elegantula*, Cicadellidae) and the congeneric invading Variegated leafhopper (*E. variabilis*) in California's San Joaquin Valley (Settle and Wilson 1990). *E. elegantula* declined in parallel with spread and rapid increase in abundance of *E. variabilis*. Different attack levels by *A. epos*, with the native species suffering higher attack rates than the invasive leafhopper, apparently shifted the competitive balance between the two leafhoppers strongly in favour of the invasive species. Settle and Wilson (1990) distinguished two rather different categories of impact: (1) during the initial invasion phase the parasitoid reduced the native Grape leafhopper to lower levels, facilitating spread of Variegated leafhopper under conditions of markedly reduced interspecific competition with the native; and (2) later, as the Variegated leafhopper increases past the level of becoming dominant, it contributes to an increasing proportion of the collective parasitoid population, leading to higher parasitisation rates for grape leafhopper than would be experienced in the absence of the invading host. Because this occurs only later in the continuing invasion, it becomes important only after the invader has become dominant – so is a consequence of the invasion rather than an initial 'driver' (Settle and Wilson 1990).

Some introductions of insects for classical biological control involve taxa that fill, or are purported to fill, roles not found in the receiving environment, so have additional novelty. The chances of any short-term non-target effects are usually assessed as nil to very low, and the organisms involved unlikely to intrude into wider ecosystems or ecosystem processes. Two rather different examples of such introductions are (1) alien dung beetles (Scarabaeoidea) from southern Africa and Europe introduced to Australia to break down dung of farm animals in pastures, and (2) specialised parasitoid flies (Phoridae) that attack fire ants (p. 90), and are possible biological control agents for some key species of *Solenopsis*. Each has revealed further subtleties in post-release outcomes from deliberate introductions of suites of ecologically complementary species.

The history of the Australian dung beetle introduction campaign (Doube et al. 1991; Tyndale-Biscoe 1990) reflected that most native (and highly endemic) species are restricted to forest and woodland areas, and that few are common in more open grasslands or cleared pasture. Most are also adapted, and restricted, to exploiting pellet-like marsupial dung and could not degrade the large dung pads produced by cattle and other stock. Accumulations of cattle dung persist to cause pasture staling and provide breeding substrates for nuisance flies (Waterhouse 1974). To redress this, a programme was initiated to introduce dung beetles capable of rapidly degrading dung of domestic stock, with climate matching focusing selection on the native faunas of parts of Europe and southern Africa. The principle of seeking potential control agents in areas with climate similar to that of the proposed introduction areas is adopted widely, with the hope of removing one field of adaptation that would otherwise pose selection pressures on the introduced population, and facilitate their establishment. Forty-one species (of the 52 alien dung beetle species screened in quarantine conditions) were initially released, with serial introductions leading to assemblages of alien species with varying patterns of seasonal activity and differing feeding and dispersal habits. Climate and habitat matching were the major keys to success, as well as some manipulations of biology such as by controlling diapause. Several introduced species disperse strongly, with Ridsdill-Smith and Edwards (2011) noting the natural spread of several taxa over much of the continent where conditions suited. They also noted possible competitive effects, with the native *Onthophagus ferox* declining by up to 97 % following establishment of the introduced *O. binodis* – possibly related to diurnal patterns of activity whereby the latter gains precedence for diurnally-produced fresh dung pads.

Initial releases of alien dung beetles encountered virtually no interspecific competition, but intensive competition later became frequent amongst introduced species, with five to six species commonly occurring in the same dung pad (Doube et al. 1991). Dung degradation has been highly successful, and introduced beetles have become a major component of Australia's dung insect communities with considerable restructuring of those communities in open pastures, but some wider impacts have not been appraised in detail. The major practical outcomes have been dung burial and nutrient recycling, control of dung-breeding flies and (more rarely) control of parasites such as intestinal nematodes of cattle.

Phorid flies (*Pseudacteon* spp.) parasitise various species of *Solenopsis* fire ants, some of which are amongst the most potent invasive insects (p. 90), Several South American fly species have been released in the United States, where *Pseudacteon tricuspis* and *P. curvatus* now co-occur with fire ants over much of their range, and no native analogue parasitoids occur. The flies were expected both to kill fire ants directly and disadvantage them relative to native ants by inducing behavioural changes. The extensive literature on the intricate relationships between *Pseudacteon* and *Solenopsis*, reviewed by Morrison (2012), reveals considerable ambiguity over factors that regulate fire ant populations. The scenario supporting 'top-down' control reflects (1) a diversity of parasitoid fly species that produce a range of pressures on the ants; (2) a continually high abundance and activity of these *Pseudacteon*; (3) a high rate of mortality from parasitisation; (4) lack of refuges for host ants, or lack of capability to adapt to the parasitoids; and (5) shifting the outcome of interspecific competition with competing ants. Contrastingly, Morrison characterised 'bottom-up' control by (1) low parasitoid diversity; (2) low or fluctuating parasitoid activity; (3) low rates of mortality from parasitisation; (4) presence of refuges or host ants having ability to behaviourally adapt; and (5) little or no impact on outcomes of interspecific competition with competing ants. The latter scenario may have only little, perhaps seasonal, impact – but without long-term declines of the ants. Morrison (2012) suggested that any impacts of *Pseudacteon* on fire ants are small and may be compensated by rapid increase of ant populations. There was little evidence of any strong top-down effects, and it is likely that *Solenopsis* populations are regulated primarily by other factors. *Pseudacteon* species are highly host-specific, and appear to have minimal (if any) non-target impacts, but will assuredly persist in areas to which they have been introduced, for as long as fire ant hosts are available. Whilst Morrison recognised that the most potent natural enemies of *Solenopsis* might actually be other South American ants, he noted that introductions of these 'are not seriously contemplated' in view of likely harmful impacts elsewhere – but other natural enemies, combined with habitat restoration, may be components of future suppression attempts against fire ants.

Other modes of biological control using natural enemies have implications for insect conservation, but not all directly involve alien predators or parasitoids; they are noted briefly below.

6.4 Neoclassical Biological Control

More immediate concerns arise from a related, but ecologically very different, approach known as 'neoclassical biological control'. This deliberately creates new ecological associations, with natural enemies that are acknowledged as capable of changing their ecological interactions in a novel environment – and are expected to do so. It is based on the importation and release of putative biological control agents to control native pest insects related to the agents' natural hosts, with the expectation that the agents will attack the target pest with which they have had no historical association or co-occurring legacy. The practice thereby has a very different ecological foundation from classical biological control, in forming new ecological linkages rather than seeking to reinstate previous associations in a new place. The approach thereby involves introducing novel relatively generalist feeders to become permanent members of the new fauna, with expectation that they will exploit native taxa and implication that they might also feed on co-occurring species. As Lockwood (1993) commented 'Host ranges of the exotic organisms are essentially unknown … so ecological safety assurances are unfounded'.

Two early examples dominated early discussion. The major concerns were voiced initially in relation to control of rangeland grasshoppers in North America, as a diverse group in which species that are pests and of conservation concern often occur together, and are sometimes closely related. Debate arose from proposals to introduce two Australian agents to North America to control the few significant pest species of grasshoppers. Both a fungus (*Entomophaga praxibuli*) and an egg parasitoid wasp (*Scelio parvicornis*, Scelionidae) were proposed for introduction without thorough host range trials and, of equal concern to conservationists, with no plans to monitor the impacts of these agents on non-target taxa after they were released (Lockwood and Ewen 1997). Denial (in 1994) of the application to introduce the wasp was not on these grounds, however, but because it was considered likely to suppress other, related, grasshoppers that can control rangeland weeds – it was designated as an 'indirect plant pest' under the United States Federal Plant Pest Act.

The second example was of a European braconid wasp, *Peristenus digoneutis*, imported to North America to control native mirid bugs, most notably the Tarnished plant bug (*Lygus lineolaris*, a major pest of fruit and vegetable crops). Day (1996) reported that it also attacked other bugs but tended to 'prefer' *L. lineolaris*. It was also a likely control agent for a second pest species, the European bug *Adelphocoris lineolatus*, on alfalfa.

Use of pathogens in this way also poses problems. Deliberate introductions of non-specific pathogens, whose fate after release can be extremely difficult to assess, continue to cause conservation concerns. A microsporidian, *Paranosema* (previously *Nosema*) *locustae*, experimentally introduced to Argentina to control grasshoppers in the Pampas region, was considered to have potential for 'pathogen pollution' (a global threat in biodiversity conservation: Cunningham et al. 2003). It was introduced with knowledge that it is a generalist, capable of attacking numerous host grasshopper species (Bardi et al. 2012). About 50 grasshopper species (approximately a quarter of the Argentine fauna) occur in the Pampas, but only about 6 of these are targeted for control as serious pests that cause losses to crops and forage during their outbreaks. All the resident species are natives. Field samples indicated that the pathogen was distributed very patchily – but also that many, perhaps most, of the Pampas grasshopper species may be susceptible, with several localised species perhaps the most vulnerable. For rare species, other grasshoppers may function as pathogen sources or reservoirs. Bardi et al. noted *Scotussa daguerrei* as the only species under risk of possible extinction from *P. locustae*: it was narrowly distributed within a range confined to the Pampas, found only in small numbers, and field infestations were confirmed. All 21 other infected species found were more widely distributed and common, but two less abundant taxa could face local extirpations.

6.5 New Association Biological Control

A rather different emphasis occurs in 'new association biological control' (Hokkanen and Pimentel 1989), again involving importation of novel agents but with a somewhat different premise and drawing on the evolutionary history of interaction between a native natural enemy and its target. In the past, and reflecting the concept of classical biological control, agents have been selected from amongst the pest's spectrum of natural enemies in its native area, so with re-establishing historical associations forming what Hokkanen and Pimentel (1984) termed the 'old association'. Their contrasting proposal of 'new association' then applies to natural enemies from other sources, which lack such coevolutionary history and historical interaction with the target but are naturalised in the area in which control is needed once a novel pest occurs. One possible consequence of such long coevolutionary association (old association) is that the enemy becomes less effective in controlling the target pest, and the latter becomes more resistant to the natural enemy attack – with the association establishing a balance that allows both parties to persist and become insufficient to suppress the target species. In such cases, it may be useful to seek 'new association' biological control agents that have no previous evolutionary history with the pest, but with similar trophic interactions to the 'old' enemy and with the supposition that the pest may be highly vulnerable to attack by the newcomer, so encouraging a renewed mortality. Following Hokkanen and Pimentel (1989), such new association biological control was then estimated to have a considerably (they noted 75 %) greater chance of success in pest suppression than the long-coevolved natural enemy alone. This putative benefit may need to be balanced against any non-target impacts from polyphagy of the new agent. The original target pest that prompted the initial introduction of the natural enemy is often closely related to the new target, with the consequence that those species are most likely to form new associations are also the most likely to affect non-target species. Several species of Coccinellidae feeding on Tomato-potato psyllid (*Bactericera cockerelli*, Psylloidea) are potential new association agents. O'Connell et al. (2012) examined several of these; two (both originally from Australia: *Cleobora mellyi*, *Cryptolaemus montrouzieri*) had been established in New Zealand for at least 40 years, so that risk of significant non-target impacts may be low. Few such detailed investigations to compare co-occurring agents have been undertaken. The native mymarid parasitoid of the Glassy-winged sharpshooter (*Homalodisca vitripennis*, p. 142) has long coevolved with this primary host in California. Considering novel introductions of related species of *Gonatocerus* to enhance and complement impacts of *Gonatocerus ashmeadi*, Irvin and Hoddle (2010, 2011) compared details of their laboratory 'performance' under controlled conditions. *G. tuberculifemur* (s.l.) is a widespread parasitoid of proconiine leafhoppers in southern South America, and was imported into quarantine in Texas (2001) and California (2002) for comparative trials with *G. ashmeadi*. However, part of the imported stock proved to be a further (new) species, *G. deleoni*, so that the ensuing trials encompassed two distinct new association egg parasitoids of *Homalodisca*. Neither of these species outperformed *G. ashmeadi*, and conclusions on the value of the two additional parasitoids were similar in (1) they may have difficulty in establishing in areas where *G. ashmeadi* is present and (2) potential increased impacts of release in California may be negligible unless they perform better under field conditions than laboratory trials indicated, or can exploit some role not currently undertaken by *G. ashmeadi*. More comprehensive investigation may be warranted but the initial results endorse *G. ashmeadi* as still the most effective natural enemy for use against the sharpshooter.

6.6 Conservation Biological Control

Some of the problems of non-target fears from classical biological control agents have been partially allayed or addressed through advocacy for 'conservation biological control', through which the pest arena is modified to favour native naturally occurring predators (mostly generalists) and parasitoids to concentrate from the local environment – so that 'control' then involves only native species and ramifications from alien introductions of parasitoids or predators are bypassed. That primary motivation to effect pest management without creating novel interactions through alien introductions, except by changed abundance of some higher trophic

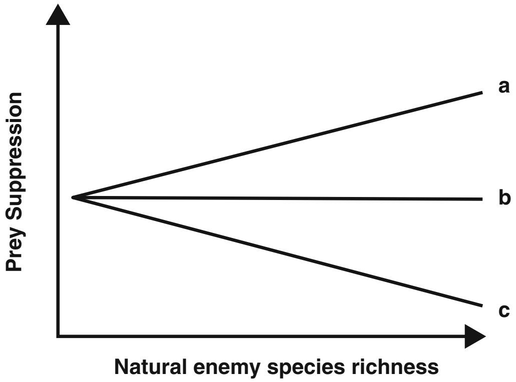


Fig. 6.7 Relationships between species richness of natural enemies and prey suppression by biological control: (**a**) a positive relationship through conserving natural enemy diversity can occur through natural enemies occupying different feeding roles; (**b**) there may be no relationship between enemy diversity and biological control, such as when natural enemy species are functionally redundant and share/compete for the same feeding role, or when negative and positive effects of increasing diversity counteract; (**c**) conserving natural enemy diversity can weaken prey suppression, such as when intraguild predation occurs. Both 'a' and 'c' may also occur through sampling effects; both are also shown here as linear relationships, but may take other forms; in 'a', conservation and biological control are complementary goals, in 'b' they are compatible, in 'c' they are conflicting (Straub et al. 2008)

level residents that could conceivably lead to spillover effects, can nevertheless lead to complex ecological considerations with conservation importance. Alien species become involved through the twin contexts of their impacts on native natural enemies, and for (plants) augmenting resources such as nectar and pollen as food for the adult native predators and parasitoids. Series of studies on relationships between natural enemy diversity and pest suppression (summarised by Straub et al. 2008) have raised questions of compatibility between conservation of natural enemy diversity and control outcomes in this and other forms of biological control. Three categories of relationships were discussed by Straub et al. (Fig. 6.7), with intraguild predation an important consideration. For example, a larval parasitoid inside a host can be consumed by a predator devouring that host, a situation that reflects two different natural enemies attacking the same individual pest, as 'coincidental intraguild predation'. Straub et al. also demonstrated 'omnivorous intraguild predation', in which one enemy consumes another enemy independent of the shared prey, so that consumption of the within guild prey does not then coincide with any impact on the pest.

Conservation biological control usually involves the spillover of native natural enemies across crop boundaries, to reach both the crop and adjacent non-crop areas, and much of its benefit derives from those predators and parasitoids with sufficient dispersal ability to undertake such movements. As Tscharntke et al. (2007 [2008]) emphasised, structurally complex landscapes can then enhance chances of pest management by facilitating presences of accessible natural enemies near the crops of interest. They argued that complex landscapes with well connected crop/noncrop mosaics should confer considerable benefits. Increases in landscape complexity are central to many such exercises, with measures such as field boundary management and mosaic plantings or intercropping common as counters to the large-scale agricultural intensification that effectively excludes many locally uncommon natural enemies. Dependence on, and protection of, the richer native natural enemy assemblages may depend on proximity to natural source areas and refuges, a perspective that contrasts with management focused largely on generalist predators with high dispersal ability and long promoted for pest management in more intensively changed areas. For conservation biological control to be effective, the natural enemies contributing to management must be present in the pest's habitat, colonise from a larger distance, or be easily recruited from nearby areas.

6.7 Some Major Taxonomic Focal Groups

Understanding the roles in insect conservation of invasive alien insects has developed from studies of many taxonomic groups, and amalgamation and integration of numerous different study priorities, contexts and interests. However, a few taxonomic groups stand out as having attracted most attention and concerns – and, so, providing key information for aiding understanding. The primarily ecological and economic implications of alien pests, predators, and parasitoids are thus complemented by wider perspectives derived from less 'applied' ecological studies from which outcomes can have serious conservation implications for native insect species and ecosystems.

6.7.1 Social Hymenoptera

The roles of alien social Hymenoptera generate, perhaps, a greater range of impacts and concerns than any other insect order. Many of those exemplified elsewhere in this book and by New (2012) have far-reaching cascade effects, reflected in features such as pollinator declines, assemblage changes, losses of specialist species and numerous impacts of predation and competition.

6.7.1.1 Ants

Invasive ants have commanded enormous attention to interpret and counter their impacts, not least because many interact directly with human welfare as well as being major threats to native biota, and their sheer numbers bring them forcibly to attention. The relatively few cases of deliberate introductions of ants for biological control are by far outnumbered by those that are inadvertently spread, mainly imported as stowaways in containers and commercial supplies (Rabitsch 2011). Invasive ants are one of the most prominent insect groups that threaten native biodiversity in many parts of the world, and have been studied far more intensively than most other invasive taxa. Those studies have led to clarification of the features that render them highly successful invaders (Holway 1999), and impacts extend well beyond other insects to include numerous other invertebrates, most vertebrate groups, and plants, as well as wider impacts on the environment. Nineteen species, of a total of more than 200 alien invasive ants, are regarded as 'highly invasive', and 5 are listed on a compilation by the World Conservation Union of a hundred of the world's worst invasive species (Lowe et al. 2001, 2004). Competitive displacement of native taxa by invasive ants occurs widely with impacts reflecting the individual capabilities of different species in the receptor environments. Statements such as 'Invasive ants are spreading rapidly through the Pacific, moving from island to island, killing off native species' (Wetterer 2007) may appear alarmist and exaggerated. Many of them are not.

Displacement of native arthropods by alien tramp ants is well-documented, although some cases are inferred by post-invasion spatial patterns, rather than as direct temporal sequences of samples spanning pre- to post-invasion. Reasons for specific displacements, likewise, are often inferred, but the lists of features involved overlap broadly with those that facilitate invasions. From the 'victim's viewpoint', exemplified for invasion of the Little red fire ant (*Wasmannia auropunctata*) in the Galapagos Islands (Lubin 1984), features associated with vulnerability included being (1) species of the transition zone between forest and arid regions, with high *Wasmannia* density; (2) terrestrial or arboreal species, overlapping broadly with *Wasmannia* distribution; (3) species of small to medium body size, with soft exoskeleton; (4) species lacking active defence, such as chemical defences, or those relying on crypsis; and (5) insectivorous or nectar/honeydew feeders that overlap directly with *Wasmannia* for food needs. In contrast, species more likely to escape from *Wasmannia* included (1) arthropods associated strongly with the arid zone or high elevations, occupying areas with only low *Wasmannia* density; (2) species with non-overlapping microhabitats, such as being plant-borers, cave-dwelling or hypogaeic; (3) larger species with strong exoskeletons and chemical defences; and (4) primarily herbivorous species, with non-overlapping food requirements. Many studies on displacement of native arthropods involve Argentine ant (below). For example, displacement of native pollinators by this ant whilst seeking floral nectar may be widespread, reflecting its superior exploitation tactics. Lach's (2008) study in the Cape region of South Africa suggested that displacement of endemic arthropod pollinators may be a conservation concern. Diminished floral arthropods on the Green tree pinch plant (*Leucospermum conocarpodendron*, Proteaceae) might also have consequences for other plants that depend on those pollinator species. Whether such effects occur, discussed also in a related study by Lach (2007), is related to a variety of factors, including (1) whether displacement from the focal species' inflorescence leads to pollinator population declines; (2) whether other plant species compete for the same pollinators at the same time, or whether these interact in some sequential manner; (3) whether the Argentine ants also visit other inflorescences in the same plant community, and (4) the extent of pollen limitation for plants within the community. However, knowledge of invasive ant impacts in above-ground environments is far less than of impacts on ground-dwelling arthropods – in reality, their impacts on plants may be relatively far greater than implied by the wealth of studies on ground level biota.

The global transfers of ants have thus for long caused concerns in conservation, and the extent of invasions is still rather uncertain. A review by McGlynn (1999) reported 147 species (in 49 genera) as aliens in some way, and records have continued to proliferate and diversify. Several more recent evaluations quoted by Miravete et al. (2014) led them to imply that the number of ant species introduced and established outside their native range is far greater than the number documented. Indeed, on a global scale, the number of species introduced in temperate regions could be 3.5 times the number so far recorded, with two-thirds of those species established. The most invasive species (including most of the tramp species, below) are able competitors with native ant species and readily displace many of these. McGlynn distinguished between 'invasive species' and 'tramp species', in that invasives monopolise food resources from native ant species, while tramp species simply occupy roles/niches not exploited by native ants. This distinction, however, seems not always to be heeded – but implies that tramp ants are not a threat to native taxa because they lack obvious negative impacts or remain associated with anthropogenic environments. One example of an 'impact' from the above distinction is of the alien *Lasius neglectus* and the native *L. grandis* foraging for honeydew of the aphid *Lachnus roboris* on oak trees in Spain (Paris and Espadaler 2009). Ecological dominance of *L. neglectus* enabled it to monopolise *Lachnus* colonies, in turn increasing honeydew production of tended colonies – with the invasive ant supporting its higher activity by this increased food supply.

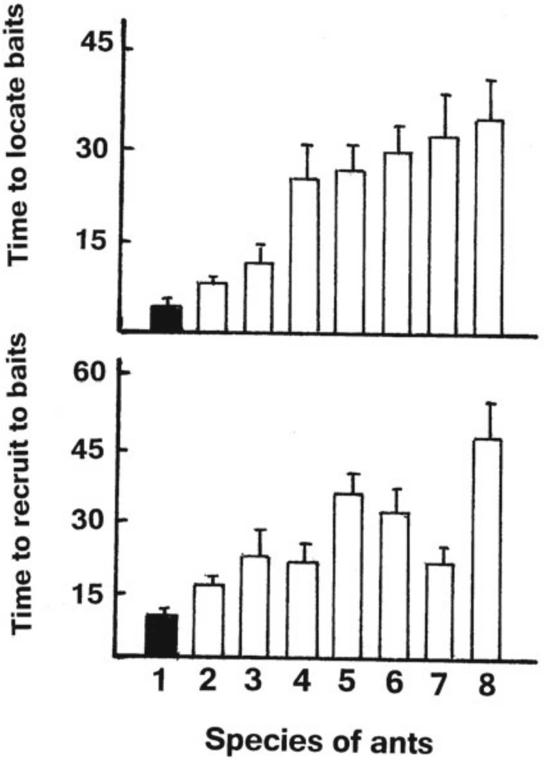
Displacement of native ants by invading tramp species (below) raises many possible consequences but, as Lach and Thomas (2008) noted for Australia, few of these have been interpreted fully, notwithstanding that domination of food resources and competitive interactions are commonly associated with reduction of native species diversity. The relative risks from each key tramp species are largely unknown, but identifying native species or processes that may be especially vulnerable may facilitate development of well-targeted eradication efforts rather than the more widespread use of toxic baits that currently dominate control programmes and have largely unknown – but suspectedly significant – non-target effects. Lach and Thomas used the example that eradication of a pest ant from a fragment of vegetation inhabited by a myrmecophilous lycaenid butterfly may be more realistic and worthwhile than removing it from an entire metropolitan area – but such fine-scale manipulations are clearly limited.

The prime focus of Wetterer's (2007) comment (p. 157) (the African big-headed ant, *Pheidole megacephala*) is regarded as amongst the worst of a series of 'tramp' ant species spread predominantly by humans in commerce and that subsequently invade natural ecosystems whilst also maintaining strongholds in anthropogenic environments. They are regarded as amongst the most ecologically harmful of all invasive insects. Tramp ants can displace many native species, and disrupt or destroy long-coevolved mutualistic associations of native species and key ecological processes. Their impacts have been assessed in many situations, but perhaps nowhere more disturbingly than on the Hawai'ian archipelago, where no native ants occur. Predominance of invasive ants was also evident on Surprise Island, New Caledonia, where seven alien species accompanied a single native species, *Pheidole oceanica* (Cerda et al. 2012). The different habitats examined were dominated by different alien species but the overall 'top dominant', assessed from recording interactions at honey/peanut butter baits, was *P. oceanica*, which recruited large numbers of workers at baits and aggressively excluded other species. This Pacific native ant is clearly able to resist invasion by some tramp ants, as a form of 'biotic resistance' reported also for several other native ants against invaders. Two life history traits were suggested (Cerda et al. 2012) to possibly advantage that outcome – the very efficient mass recruitment system (whereby a mean of 40 workers were attracted to baits in their study) and the occurrence of a soldier caste: *P. oceanica* was the only species with big-headed workers on the island. Several key Pacific region tramp ants, however, were absent from Surprise Island. Those 'superdominants' (notably *Pheidole megacephala* and *Wasmannia auropunctata*) monopolise food resources, and it is likely that their absence on Surprise may be a key factor in allowing *P. oceanica* to prevail there. Better understanding of invasibility of native ant assemblages may come from parallel studies in areas where individual tramp invasives are still absent.

Holway (1999) elucidated the mechanisms through which competitive displacement by the Argentine ant (*Linepithema humile*) occurred, comparing both exploitation competition and interference abilities with each of seven native ant species it encountered in invading riparian woodlands in northern California. Manipulative field experiments showed that Argentine ants found baits and recruited workers to them at least as rapidly as the native ants, whether they occurred together or in separate areas where natives were not exposed to *Linepithema*. The native ants shared a feature reported also in other ant assemblages, that a 'competitive trade-off' occurred in which exploitation and interference capabilities were negatively correlated. The species differed in dominance ranking (the order of ranking in increasing success in deterring Argentine ant workers in one-to-one interactions) and discovery and recruitment ranking (where the species are ranked by decreasing order of discovery of fixed distance baits and recruitment to these) (Fig. 6.8). *L. humile* discovered and recruited to baits much more rapidly than did native ants, as evidence of excellent exploitation ability, and were also highly dominant in interference trials, shown by them displacing most native species from baits. It appeared to be free of the trade-off implied for native species, and which facilitates their coexistence in native assemblages. The strong competitive advantage of *L. humile* is enhanced by its massive supercolonies, unicolonial entities that can achieve enormous population sizes.

Studies of *Linepithema* at the leading edges of their advance – their 'invasion front' – showed that both direct aggressive encounters with native ant species and competition for food through interference with foraging activity and excluding from food resources occur (Human and Gordon 1996). The former category included preventing native ants from establishing new colonies, by predation on winged

Fig. 6.8 Baiting trials used to compare the time taken by Argentine ant (1, *Linepithema humile*, *black bars*) to (**a**) locate and (**b**) recruit to baits placed I m from nest entrances, in comparison with various native ant species (*open bars*) in California. Native species, from *left* to *right*, are 2 *Aphaenogaster occidentalis*, 3 *Dorymyrmex insanus*, 4 *Tapinoma sessile*, 5 *Formica moki*, 6 *Monomorium ergatogyna*, 7 *Liometopum occidentale*, 8 *Formica aerata* (Holway 1999)



queens. Displacement of native ants from invaded areas is complex, and can also involve invader-induced emigrations, but with the almost inevitable outcome of reduced richness of native ants in many invaded areas.

Less well understood are the ways in which the tramp ant species interact with each other, a scenario that is likely to become far more common as they continue to spread to co-occur and interact (Bertelsmeier et al. 2015). Because they share many features – those characteristics that comprise the ant 'invasive syndrome' (Passera 1994) and more widely characterise successfully invasive ants (Wittenborn and Jeschke 2011, below) – and are highly effective generalists, their interactions might be expected to differ from those between invasive and native species. Interference competition was examined experimentally among all possible paired combinations of seven invasive ant species, both as single individuals and 'group of ten' levels. The seven species differed greatly in their 'performance' (Bertelsmeier et al. 2015). The top dominant competitor was *Wasmannia auropunctata*, and the least dominant was *Pheidole megacephala*, noted above as one of the most notorious invaders in this group. Four species interacted aggressively with all others, whilst the other three tended to avoid aggressive encounters by being indifferent or escaping from potential opponents. The four aggressive species were thought likely to exclude each other, but the other three could probably coexist, possibly also with one or

Table 6.4 The results of comparative analyses of traits to distinguish the features of alien ants in North America. The following features characterise alien ant species (Wittenborn and Jeschke 2011)

Large colony size
New nests founded by queen with workers, rather than by queen alone
Not socially parasitic on other ants
Sterile workers
Monomorphic workers
More than one queen/colony (polygyny)
Small body size
Equipped with functional sting

more of the aggressive species. Other factors, such as local microclimate differences, that might affect the outcome of encounters remain to be explored, but the unexpected behavioural heterogeneity amongst these highly invasive species is a salutary endorsement of need to consider each species separately.

Characteristics of invasive ants in North America (42 of the 93 alien ant species there), and comparison with native species, supported a number of previously advanced presumptions about features of invasive species (Wittenborn and Jeschke 2011). As examples, colonies of alien species (1) contained more queens and (2) more workers than native species colonies; (3) parasites are found less frequently, and workers are (4) more frequently monomorphic, (5) smaller, and (6) more frequently sterile. Analysis of all these traits led to listing of a suite of features that characterised alien ants when compared to native species (Table 6.4).

A more specific interaction between tramp ants in Texas showed that the spread at high density of the recently (around 2002) introduced *Nylanderia fulva* can eliminate Red imported fire ant (*Solenopsis invicta*) and replace it as the dominant invasive ant in the region (LeBruhn et al. 2013). Earlier in its history in the region, *S. invicta* had displaced both the Argentine ant and the Black imported fire ant (*Solenopsis richteri*) to become the then dominant species. *N. fulva* has invaded both natural and urban environments. Pitfall trap surveys showed the strong impacts of this species on *S. invicta*, with all colonies displaced within about a year of high density invasion, and species richness and abundance of other ants also reduced – effectively countering trends for the native fauna to recover from the earlier fire ant invasion. Within the disturbed grassland areas surveyed, *N. fulva* affected local ant assemblages non-randomly, producing clear differences from assemblages in nearby uninvaded areas. Most small-bodied ant species were either unchanged or increased in abundance, whilst large-bodied species all declined. Small-bodied ants were disproportionately represented by tramp species, so that the net outcome was assessed as reduced biological and functional diversity and extensive biological homogenisation. Removal of local or regional species, whilst not affecting globally distributed tramp species, has significant implications for ecological integrity and is coupled with wider reductions in arthropod abundance. Other studies cited by LeBruhn et al. (2013) attributed resistance of small-bodied ants to displacement by several key invasive species to either (1) their underground foraging affording protection or (2) being opportunists or cryptic species, but also suggested the alternative of them being resistant to nest-raiding. Small body size had been demonstrated as important in establishment of tramp ants, leading to assemblages that contain many introduced species. Implications from this particular case could be much wider than at present evident, as LeBruhn et al. noted that *S. invicta* is almost universal in non-forested habitats in the region, whilst *N. fulva* also reaches high densities in forests, so that the forest fauna may be under greater threat from *N. fulva*.

Many interactions of invasive ants with native biota are complex. Exploitation of native Hawai'ian plants, for example, has intricate influences on plant reproduction but may also have positive effects by reducing herbivory through predation. Ants are found at high densities on the endemic shrub *Vaccinium reticulatum* (Ericaceae) and exploit nectar heavily (Bleil et al. 2011). They also eat and remove larvae of the introduced plume moth *Stenoptilodes littoralis* (Pterophoridae), which pierce holes in flower buds and feed inside them. Tramp ants such as *Linepithema humile* (Argentine ant) and *P. megacephala* were observed taking the moth larvae. In that study, measurements of viable seed set implied that invasive ants protected flower buds and flowers by reducing impacts of *Stenoptilodes*, contrasting with many other reports that summarise only severe adverse impacts from invasive ants on the archipelago. Bleil et al.'s study indicated that such positive effects should be considered, together with probable negative effects on pollination (in this case, by native *Hylaeus* bees, of which very few were seen) in assessing their net impacts.

The massive attention justly accorded to tramp ants has tended to overshadow the roles of other invasive ants that have remained relatively innocuous and not intruded significantly on human interests. For Hawai'i. Krushelnycky (2015) noted a total of nearly 60 introduced ant species, and found 10 of these on understorey trees in the mesic forests of Oahu. Only about a third of his 384 samples included ants, and fewer than 10 % had five or more individuals. Both frequency and abundance were dominated by *Plagiolepis allaudi*, which comprised 491 of the total of 714 ants captured. Collectively, little evidence of any effect on native arthropods was found – but suggestions of impacts on native Lepidoptera were raised, through the higher numbers of larvae of two endemic groups in samples with fewer than five ants. *Hyposmocoma* spp. appeared sensitive to ant presence, and larvae of the predatory *Eupithecia orichloris* (Geometridae) were not found in samples with the higher numbers of ants, although they were present in about 10 % of the low ant abundance samples. Krushelnycky suggested that the apparently low impacts inferred for many native arthropods simply reflected the low ant densities, and could become more evident if ant densities rose.

Studies on invasive ants have also illuminated the distinction between 'passenger' and 'driver' aspects of interpreting the severe impacts attributed to them, with some support for the 'back seat driver' role, in which the invader is facilitated by earlier disturbance that has already caused some declines in local biodiversity and subsequently causes further declines, rather than being the initial primary cause of declines (Berman et al. 2013). This role was confirmed for invasive ants In New Caledonia, demonstrating clearly that biodiversity loss was an outcome of disturbance and invasion, with the two localities studied by Berman et al. contributing different, complementary, information. One involved comparison of native ant diversity at paired burned (disturbed, 5 years previously) and unburned sites, some invaded by *Anoplolepis gracilipes*. That survey yielded 52 ant species (45 natives) across 26 genera. The second study assessed ants along a successional gradient from rainforest to human-caused savanna in the long-term absence of fire, in an area being invaded by *Wasmannia auropunctata*, often considered a disturbance specialist. It yielded 54 ant species (50 natives) in 21 genera. Native ants were resilient to fire in the first survey, but markedly lower in richness in invaded burned sites. The second survey showed strong correlation between ant diversity decline and high *Wasmannia* abundance. Both supported the back seat driver hypothesis. Even if associated primarily with disturbance in New Caledonia, the invasive ants clearly contribute to declines of native taxa, so that conservation must consider both disturbance reduction and invasive ant suppression.

In Sulawesi, Indonesia, agroforestry (represented by three categories of cacao plantings, collectively a substantial anthropogenic disturbance) promoted the occurrence of the Yellow crazy ant (*Anoplolepis gracilipes*). In part, this was apparently because management of the cacao crop had negative impacts on native ants that depend on trees for nesting and foraging (Bos et al. 2008). Practices such as thinning stands of trees can facilitate crazy ant invasion, threatening the potential of such cultivated land to conserve native tropical ant diversity. Relative ant richness in natural forest (40 species) and in cacao plantations (66 species) implied the value of the latter system, but many of the former group (treated as more specialised ‘forest species’) did not occur in the cacao areas. In agroforestry areas, richness declined when *A. gracilipes* was present, with forest ants those most susceptible. *A. gracilipes* was the most common ant in agroforestry areas, but was not found in natural forest. Bos et al. noted that the dominance by this invasive ant in such tropical agroecosystems may threaten potential of cultivated forests for wider biodiversity conservation. Comparative studies on attraction of ants to different food baits (tuna, peanut butter, jam) on Tokelau revealed that food preferences may facilitate coexistence of some native ants with *A. gracilipes* (Sarty et al. 2007). The crazy ant dominated ant visitations to tuna and jam baits, but was relatively scarce at peanut butter baits, where four other species could thus gain this food. More widely, insects living on plants with extrafloral nectaries may be particularly susceptible to effects of invasive ants. That *A. gracilipes* increases its aggressive behaviour and recruitment to foraging sites as extrafloral nectar supply increases was used by Lach et al. (2015) to evaluate its impact on an Australian native butterfly, *Vindula arsinoe* (Nymphalidae) in the Wet Tropics rainforest of northern Australia. The butterfly’s larvae feed on both the introduced vine *Passiflora foetida* and the native *Adenia heterophylla* (Passifloraceae), on which the native ant *Oecophylla smaragdina* is replaced by the invasive crazy ant. Both ant species attack *V. arsinoe*, but the lower activity levels of *Oecophylla* mean that they are less likely to find the prey: attack rates by *Anoplolepis* were much higher, simply because of their higher numbers and activity. Lach et al. cautioned that those findings should raise concerns for Lepidoptera of conservation importance in areas invaded by this ant.

The Yellow crazy ant is perhaps now most notorious for its dramatic ecological impacts on Christmas Island (p. 76) but studies such as the above on other regional invasions contribute to wider understanding of its success and factors that might restrict this. On Bird Island (Seychelles) the very high ant densities were associated with major changes in invertebrate communities and impacts on native birds (Hill et al. 2003). It is most abundant there in deeply shaded areas but can forage in open areas when ground temperatures are low (Gerlach 2004). Although it has excluded many large invertebrates (such as a large ant *Odontomachus simillimus*, and crabs), cockroaches remained abundant in ant-infested areas – probably, as suggested by Gerlach, because high cockroach densities mask any predation impact, or because reduction of other predators by the ant benefits them. Even when harmful impacts are not apparent, reasons for this are thus often unclear.

Most invasive ants have been studied relatively little in relation to intensive investigations of the most notorious tramp species but may nevertheless also have far-reaching impacts. One such species, *Pachycondyla chinensis*, native to eastern Asia, has become widespread in parts of the United States. There, it disrupts ant seed dispersal mechanisms (myrmecochory) in forest environments, notably through causing large declines in the key seed-dispersing species *Aphaenogaster rudis*, described by Rodriguez-Cabal et al. (2013) as a keystone mutualist, so disrupting myrmecochory and reducing abundances of ant-dispersed plants.

6.7.1.2 Wasps

The major impacts of eusocial vespid wasps flow from their being generalist predators, often occurring in very large numbers, dominating the environments they enter, and eating vast numbers of local insects and other invertebrate prey. Several examples of the far-reaching impacts of invasive wasps have been noted earlier in this book (p. 40, 87, 141), and some – notably invasives in Hawai'i and New Zealand – have been documented in considerable detail. *Vespula* spp. in New Zealand (Beggs et al. 2011) are amongst those that have provided salutary warnings for wide ecological impacts, with clear evidence of threat to individual arthropod species and changes to ecosystem functions and native community structure. Globally, Beggs et al. (2011) identified 34 species of Vespidae that are known to have been introduced in some way to new areas, but noted that the seven most invasive species are all eusocial, with their ecological impacts accompanied by considerable concerns for human health.

Most studies of vespine and polistine invasive wasps emphasise the large variety of prey arthropods taken, with several focussing on concerns for Lepidoptera through predation of larvae. Thus, *Polistes chinensis* in New Zealand (Clapperton 1999) and *P. versicolor* in the Galapagos (Parent 2000) both include high proportions of caterpillars in their prey. Experimental studies of impacts of *Vespula* wasps on Lepidoptera in New Zealand beech forest involved placement of sentinel larvae of the Kowhai moth (*Uresiphta polygonalis maorialis*, Pyralidae) on potted plants in beech forest sites in the Nelson Lakes National Park (Beggs and Rees 1999), where wasp densities were manipulated by poisoning to assess impacts with different levels of wasp abundance, as well as likely seasonal effects. Survival rates of both small and large moth larvae declined with increased wasp density and, at the times of peak wasp abundance, their chances of survival were very low. At the wasp densities observed in the study sites, Beggs and Rees calculated that wasp densities must be reduced by 'at least 88 %' to conserve the more vulnerable Lepidoptera species present. Those species occurring as larvae predominantly in spring (before the peak wasp season) may persist, whilst those found from January to April (the time of peak wasp activity) are likely to be severely reduced, or extirpated, but with the precise impact depending on the spectrum and abundance of other prey and of honeydew on any given site.

6.7.1.3 Bees

The most familiar pollinating insects, bees, include many alien species, which fall into two main categories. Some have been introduced historically and widely to provide pollination services, and some of these have become naturalised and feral in areas of introduction. Literature on some of these, including extensive debate over impacts and conservation concerns of honeybees (*Apis mellifera*) and bumble bees (*Bombus* spp.) is both voluminous (Goulson 2003) and often polarised. These social species are regarded by different parties as economically indispensable or as severe invasive and ecologically harmful invasive pests. A second category, far less studied, comprises unintentionally introduced invasive bees, some solitary and some of which have become widespread and abundant beyond their natural ranges. Invasive bees are a geographically widespread concern in conservation, but many of their purported impacts need further investigation. Indicating the variety of concerns, Goulson (2003) listed broad categories of negative impacts as (1) comperiton for floral resources with native species; (2) competition for nest sites, such as cavities in wood and ground; (3) possible co-introduction of parasites and diseases that might spill over to native species; (4) increased pollination of invasive weeds, such as becoming primary pollinators of sleeper weeds; and (5) disruptions to the normal pollination systems of native plants.

The Wool carder bee (*Anthidium manicatum*, Megachilidae) has undergone rapid expansion in range, and the aggressive behaviour of males in defending territories (using their abdominal spines to batter and disable other bees, whether conspecific or not) affords them some advantage. It is now the most widely distributed species of this genus and the most widespread unmanaged bee species (Strange et al. 2011), and occupies a wide range of habitats. In North America its potential distribution may depend more on the floral resources of urban gardens than on climatic conditions – in Utah, part of its invaded range, winter temperatures fall below −20 °C, and the bee's incidence in warmer urban areas may help counter effects of such extremes. *A. manicatum* uses a wide range of flora. Its impacts are not yet clear, but Strange et al. (2011) noted that the 32 native *Anthidium* species in western North America might be adversely affected by this newcomer.

In Australia, the recently detected alien *Halictus smaragdulus* (Halictidae), with its high relative abundance, long seasonal activity and possible preference for introduced flowers (in New South Wales), deserves further investigation to determine its impacts (Ashcroft et al. 2012).

The long-tongued alien bee *Braunsapis puangensis* (Allodapini), distributed widely across south east Asia, has become widespread in Fiji. It colonised many islands and a wide range of elevations there in a relatively short time (Groom et al. 2015), perhaps aided by brood rearing in both wet and dry seasons. The continuing spread of *Braunsapis* has important implications, listed by Groom et al. as (1) enhanced crop pollination, complementing the native short-tongued bees and perhaps providing a functional buffer against any future losses of *Apis mellifera* from disease invasions; (2) enrichment of weed species, with possible detrimental effects on agriculture by promoting non-palatable or competitive weeds; (3) threats to native pollinators, if *Braunsapis* became abundant, with other introduced bees (p. 78, 177) that have also become widespread compounding possible competition with currently undocumented native pollinator systems; and (4) tracking social adaptations to new habitats, with the possibility that, if the bee's invasion of Fiji represents enemy release, selection might then favour non-social nesting and so decrease colony size and increase potential for dispersal. Groom et al. (2015) suggested that Fiji presents an 'unequalled opportunity' to explore whether such traits arise, but their detection would entail commitment to long-term monitoring.

6.7.2 Lepidoptera

The conservation of Lepidoptera, a paramount theme in insect conservation, incorporates aspects of many alien plants and natural enemies, but relatively few Lepidoptera are themselves invasive. Most of those (other then strictly stored products species essentially restricted to domestic environments) are pests of field crop plants (some *Pieris* butterflies), forestry or orchard or ornamental/amenity plants, and targets for suppression in those contexts. Spread of a few other invasive Lepidoptera to possibly compete with native species or affect naturally restricted host plants also causes concerns. Most species, however, are deemed innocuous.

The Geranium bronze butterfly (*Cacyreus marshalli*, Lycaenidae) (p. 18) poses complex conservation problems as it continues to expand its range in southern Europe, where fears have been expressed that it could cause 'serious economic and environmental losses' (Quacchia et al. 2008) through affecting both native geranium host plants and the other, native, Lycaenidae that feed on these. *C. cacyreus* is multivoltine, and may have potential to outcompete native univoltine species such as *Aricia nicias* and *Eumedonia eumedon*. Under nursery conditions, the butterfly can be controlled by insecticide uses, but continuing spread into natural environments and uncertainties over its progressive host range expansion to include native *Geranium* species is a continuing concern.

Most attention to alien Lepidoptera has historically fallen on a small number of stored products pests, some of which are almost cosmopolitan but almost wholly confined to highly anthropogenic environments, and those accompanying valued species – such as the wax moths (*Galleria melonella*, *Achroia grisella*, Pyralidae) found in honeybee hives, and pests of crops and ornamental plants. Those of direct conservation importance are relatively few. In addition to *C. marshalli* (above), Lopez-Vaamonde et al. (2010b) noted three other alien Lepidoptera in Europe that may also have potentially high ecological impact: (1) *Diaphania* (or *Cydalima*) *perspectalis* (Crambidae, native to Asia) could threaten box hedges and plants used as ornamentals; (2) *Cameraria ohridella* (Gracillariidae, p. 69) with possible adverse impacts on *Acer* spp. through competiton; and (3) *Paysandisia archon* (Castniidae, native to South America) as a threat to natural populations of Europe's only native palm tree.

6.7.3 Coleoptera

6.7.3.1 Ladybirds

The native British ladybirds (Coleoptera, Coccinellidae) have recently been affected severely by invasion of the Asian *Harmonia axyridis*, a ladybird predator used widely for biological control of pest aphids, and already implicated in declines of some native species in Britain (Roy et al. 2012; Roy and Brown 2015). This impact occurs conjointly with large-scale land use changes, and the native fauna was selected as a suitable taxonomic group to assess the impacts of these two major drivers of biotic changes. Comont et al. (2014) noted that documentation of the native fauna, including coordinated mapping of incidence at a 1 × 1 km grid level over mainland England, Wales and Scotland, and knowledge of feeding habits and preferences were both very sound templates against which to assess changes that affected distributions. The modelling exercise (undertaken using distributional data at the above scale) incorporated a wide range of traits, and commenced with a prediction that 'large, polymorphic, multivoltine species with a wide diet breadth but with limited overlap with *H. axyridis* are more likely to colonise and resist local extinction in comparison to species not exhibiting these traits'. Results implied that *H. axyridis* has important influences on native ladybirds, with their species-specific responses reflecting overlaps of resource use with the alien species. Urban land cover was a key influence increasing local extinction and reducing colonisation. Overall, this survey implied that continued spread of *H. axyridis* in Britain will lead to extinctions of native species, with those species overlapping in resources and in urban areas the most vulnerable. Wider impacts on native insects in North America are also highly probable. Koch et al. (2003), for example, recognised *H. axyridis* as a potential hazard to immature stages of *Danaus plexippus*, a scenario investigated later by more formal risk assessment (Koch et al. 2006).

Ladybirds have a venerable history of introductions for biological control of pest insects, mostly of Homoptera such as aphids or coccids: Evans et al. (2011) cited 179 species introduced into North America alone by the mid 1980s. However, most early introductions evinced no conservation concerns, and Evans et al. postulated that this might have reflected that most of those introductions were of species highly specialised to feed on coccids and which had relatively little potential for non-target impacts. With later importations of much more generalised aphid predators, perhaps most notably of *H. axyridis* and *Coccinella septempunctata*, major concerns arose from their very broad feeding habits and potential to spread into a wide range of ecosystems. *H. axyridis* is resilient to pathogens and parasitoids in comparison to some other coccinellids, leading Roy et al. (2011) to predict that it could benefit both from enemy release and EICA (p. 119) in its invasive range. Both are also large-bodied species with high reproductive output, and Evans et al. listed a suite of reproductive traits shared by these two species that may predispose them to invasion success: high fecundity, ability to be multivoltine, ability to reproduce rapidly under diverse conditions, inhibition of oviposition in the presence of other ladybirds, and ability to resorb eggs. Intraguild predation can disrupt biological control programmes if other natural enemies are consumed, whether these be predators or parasitoids of arthropod pests or the herbivores employed for weed control. Some native North American ladybirds (perhaps most notably *Coccinella novemnotata*) have declined throughout the continent, and predation by *C. septempunctata* is one of the factors implicated in this. Four mechanisms have been designated as causing losses to native coccinellids (Evans et al. 2011), as (1) competition, especially scramble competition for food amongst larvae; (2) intraguild predation; (3) habitat selection by adults as indirect effects of competition; and (4) interspecific hybridisation. Sharing of parasitoids is amongst other themes that need further study to assess their impacts. Responses of individual species differ considerably, but broad competitive exploitation by alien species and related to dietary overlaps between native and alien species (Bahlai et al. 2015) is a key element of many declines. Active conservation of native species, notably through refuge habitats such as forests in agricultural landscapes, may provide some resilience to alien species impacts – and design of such landscapes to include refuges may be an important means of conserving native ladybirds, with the potential benefit of their proximity to cropping environments as aids in pest management. From Bahlai et al. (2015), habitat use by some native coccinellids supported the ‘habitat compression hypothesis’ whereby native species survive in natural or semi-natural habitats whilst invasive specie dominate disturbed (cultivated) habitats, a scenario that can apply to many groups of invasive natural enemies.

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Chapter 7

Other Alien Invertebrates

7.1 Introduction: An Overview

Insects, by their massive diversity and ecological variety, almost inevitably dominate many accounts of invasive invertebrates, but numerous other invertebrates are also commonly aliens – and, as for insects, some have considerable ecological or applied importance. Some are vectors of parasites or diseases that can affect native hosts, as in some examples noted below, and their control may entail other impacts. Even for many which pose few assessable impacts on native insects or others, ramifications of controlling them may still cause concerns. Drenches used to rid domestic stock of intestinal parasites (including alien species), for example, may lead to pesticide residues persisting in dung, with possible effects on the dung-feeding community. Residues of the broad spectrum antiparasitic drug ivermectin, amongst others, have been implicated in disrupting development of dung-breeding flies. It has been used widely against ectoparasites of stock, but concerns have been raised since the late 1980s, and ivermectin has also been shown to prevent emergence of some alien dung beetles in Australia. Some coprophagous scarabaeoids may avoid dung from treated cattle, whilst others may be attracted to it. A single cattle injection of ivermectin was effective in killing larvae of the dung-breeding fly *Orthelia cornicina* (Muscidae) for up to 32 days after treatment (Wardhaugh and Rodriguez-Menendez 1988), mirroring outcomes reported elsewhere for several related Diptera, and also killed dung beetle larvae.

Effects transcending trophic levels also occur. Houseflies (*Musca domestica*) reared to puparial stage with exposure to ivermectin and then exposed to the wasp parasitoid *Muscidifurax zaraptor* (Pteromalidae) demonstrated changes in host quality (Floate and Fox 1999), with concentration of =/> 0.25 ppm reducing the number of emerging parasitoids from hosts that survived to this stage. Faecal residues might also influence relative abundance of different potential hosts in dung, in addition to individual host quality.

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Related concerns arise from a variety of parasites, including some of the 101 alien mites and ticks reported in Europe (Roques 2011). Few of these are considered directly harmful to native insects, even if they have insect hosts. The south east Asian parasitic mite *Varroa destructor*, which is confined to its original host (the Asian honeybee, *Apis cerana*) in its native range, has now spread throughout Europe as a major cause of decline of *Apis mellifera*, and is a severe threat to the apiary industry in many parts of the world. Despite an incursion (which was eradicated) of *A. cerana* in tropical Queensland in 2007, *Varroa* has not yet established in Australia, and fears that it might do so and severely affect honeybee pollination services render *A. cerana* a high priority for biosecurity inspection and early detection. *Varroa* appears to be quite specific to the two recorded hosts, and fears have been expressed that the extensive mortality of domestic and feral bee populations could hamper pollination to some scarce, potentially vulnerable plants. However, and despite the host switch from *A. cerana* to *A. mellifera*, and the taxonomic complexity within the few species of the mite, no additional hosts have been reported, and no hybridisation has been detected between mites from the two host bees. Possible consequences from any extension of highly virulent mites from *A. mellifera* to other hosts not previously exposed to it could become a concern (Beaurepaire et al. 2015).

The spread of diseases from alien to native bees is viewed as one of the greatest threats from invasive bees, with the historical records from honeybee and bumblebee vectors clear evidence of this occurring repeatedly (Stout and Morales 2009). The very heavy parasite loads carried by some commercial bumblebee stocks may lead to increased spillover to native populations, and Meeus et al. (2011) also noted that higher parasite virulence might be evolved through commercial rearing operations and that movement of commercial stocks might disrupt local natural patterns of adaptation between hosts and parasites. Elimination of parasites from commercial stocks, and routine screening for parasite incidence, are highly desirable – but Meeus et al. thought such steps unlikely to be adopted widely unless compelled by law. Nevertheless, and despite lack of detailed knowledge of many taxa, pathogen spillover apparently contributes to declines of susceptible native bumblebees. Many bee parasites/pathogens, in contrast to *Varroa*, are able to infect many bee species. The natural ranges and virulence levels of most of these organisms are unknown, leading to concerns over accidental or undetected introductions to countries and continents where they do not occur naturally, through movements of bees for commercial pollination services. Goulson and Hughes (2015) noted the strong – but circumstantial – evidence that parasites associated with commercial bumblebee colonies can cause substantial harm to wild bumblebee populations. The accidental importation of the microsporidian *Nosema bombi* to North America has been implicated in declines of five native species, some of them formerly abundant and widespread and one (*Bombus franklini*) becoming extinct (Cameron et al. 2011). Those declines commenced soon after start of the commercial trade in bumblebees – but, in the absence of direct documentation of those movements, the cause cannot be confirmed. The hypothesis of *Bombus* declines being due to *N. bombi* was broadly supported by demonstration that declining populations had significantly higher infestation levels of the parasite, and also lower genetic diversity than co-occurring

Table 7.1 Strategies proposed to mitigate the risks of further impacts from the commercial trade in bees on bee health (Goulson and Hughes 2015)

Prevent entry of parasites to factory or apiary	Received bees to be free of parasites
	Ensure food is not parasite-contaminated
	Ensure other materials, such as recycled hive boxes and other materials, are avoided or sterilised to remove parasite spores
Break infection cycle in the factory or apiary	Strict hygiene measures to prevent spread of parasites: sterilise equipment, change clothing before moving between rooms – prevent accidental transfers
	Parasite screening: routine screening of bees to enable early detection and eradication of parasites; screening protocols available for most bee parasites
	Curing: often overlooked that there are no known methods for curing any bumble bee parasites; methods available for many honey bee parasites; more attention needed
Mitigation from factory to farm	Shipment. Conditions may cause stress that can lower bee resistance to parasites: minimise shipping time and associated storage time; provide adequate nutrition during transport; avoid exposure to extreme temperature or other stressors
	Parasite screening on arrival, to ensure colonies are parasite-free: much regulatory modification may be needed to enforce this
	Escape prevention – 'excluders' on hives to prevent dispersal of queen bumble bees or swarms of honey bees; netting (etc.) on glasshouse windows to reduce risks of escape
Mitigation measures in policy	Encourage use of native bees where possible, in preference to importing non-native species; difficult to enforce in view of needs for pollination, but a key move in preventing parasite transmission
	Restrict spillover of parasites from honey bees by improving their health, and restricting their use in/near areas with rare/vulnerable native bee species
	Monitor numbers/prevalence of parasites in wild bees to help identify potential problems at an early stage

populations of non-declining species. Both syndromes are realistic predictors of declines, but the precise cause remains unknown (Cameron et al. 2011). One South American analogue is more certain. A parasite (possibly more than one, because the identity has not been confirmed, with the two leading contenders being the neo-gregarine *Apicystis bombi* and the trypanosome *Crithidia bombi*) is hosted by the alien *Bombus terrestris*, which is spreading rapidly in South America and associated with losses of the native *B. dahlbomii* to approach a state of likely imminent extinction. This decline is occurring at a rate that Goulson and Hughes commented 'could only plausibly be explained by pathogen spillover'. Extent of wider pathogen transmissions between different bee species is unknown, but there is clear need to reduce likelihood that these processes prevail through commercial operations. Goulson and Hughes (2015) listed a number of proposed mitigation strategies (Table 7.1), citing some practical difficulties (such as there being currently no cure for any bumblebee parasite), and the urgency for incorporating these measures into policy – not least by fostering the uses of native bees rather than continuing to depend on imported stocks. More broadly, Goulson and Hughes also listed the 14 bee parasites hosted by honeybees (10 species) or bumblebees (4) for which evidence exists of anthropogenic spread to other bees.

The numerous invertebrate groups with alien species in Europe (Roques 2011) include some with little evident direct importance for insect conservation – the 20 terrestrial Platyhelminthes, for example, include 12 predatory species which could clearly come into contact with insects as potential prey, but no such records have been traced, and most environmental concern has focused on their impacts on native earthworms, notably from the New Zealand *Arthurdendyus triangulatus*. The other eight species are internal trematode parasites with medical or veterinary implications. Likewise, nearly half (24 of 53 species) of alien nematode worms are internal parasites of vertebrates. Three, however, infest cockroaches, but no conservation concerns have yet emerged. The American pine wood nematode (*Bursaphelenchus xylophilus*) has become a major threat to pine forests in southern Europe, and could perhaps influence interactions between native herbivores and the trees. The nematode causes a wilt disease that leads to sudden death of the trees. Most concerns have arisen for Stone pine (*Pinus pinaster*) in Portugal, where the nematode is transmitted by the native beetle *Monochamus galloprovincialis* (Cerambycidae). A wider range of beetle vectors, including Cerambycidae, Curculionidae and Scolytidae were noted by Toth (2011). About 34 % of the Portuguese forest (about a million hectares) had been affected by about 1999, and attempts at control were facilitated by a European Union subvention of almost Eu 24 million from 2001 to 2009 (EPPO 2009). Isolated outbreaks in Spain have been eradicated by measures that included a clearcut area of up to 3 km radius around the infested tree.

Any generalist predators that become invasive in areas occupied by rare or threatened insects may pose threat. The endangered Cromwell chafer beetle (*Prodontria lewisii*, Scarabaeidae) is a narrowly endemic flightless beetle now known only from the remnant 81 ha Cromwell Chafer Beetle Nature Reserve in the South Island of New Zealand. That reserve has been invaded by the Australian Redback spider (*Latrodectus hasseltii*, Theridiidae), reported from New Zealand first in 1981 and known to take a very wide variety of prey. Surveys of the spider and its prey in the reserve revealed substantial predation on the chafer, with 278 corpses found in spider webs (Bryan et al. 2015), both occupied (212) and unoccupied (66). Over 5 weeks, 422 chafers were found to have been killed, and surveys extended over 8 weeks of the beetle's 11-week activity period. Although detailed population estimates of the chafer were not available, the mortality found indicated a likely strong impact, augmenting other risk factors from mammal predation and habitat degradation from rabbit activity and alien plants (Barratt 2007).

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Chapter 8
Alien Vertebrates and Insect Conservation

8.1 Introduction: An Overview

The roles of alien vertebrates in insect conservation are cited most commonly as the direct impacts of predation – notorious examples include impacts of rats, mice and mustelids on remote islands or other isolated environments such as New Zealand, and impacts of introduced fish, notably trout, on aquatic fauna in Australia. Both have numerous parallels elsewhere. Attempts to locally eradicate such taxa for conservation of notable threatened insects recur, but some lead to conflict. Trout for example, are distributed widely from commercial or government hatcheries for recreational angling, and licence fees may be a significant revenue source, together with supplies of gear and bait. However, some New Zealand weta now survive largely or only after translocations to small offshore islands from which rodents have been eliminated, and some aquatic arthropods persist only in the upper reaches of streams inaccessible to alien predatory fish.

Relict populations of other New Zealand insects have survived on islands that have remained mammal-free. Likewise, the endemic Lord Howe Island stick insect (*Dryococelus australis*) is believed to have been eliminated from the island by rats, and survived only on the isolated Ball's Pyramid, from where a single pair founded an intricate captive breeding programme that saved the species from almost certain extinction (Honan 2008; Wilkinson 2014). Plans to release the insect on several small islets near Lord Howe await confirmation of success of complex baiting programmes to eliminate rodents. Invasive rodents (several species of rats, and house mice) are renowned for their broad feeding habits and their impacts on large-bodied invertebrates, especially on islands, where impacts are varied and often severe (St Clair 2011). Extinction of an undescribed carabid beetle, *Loxomerus* sp., on Antipodes Island, New Zealand, was attributed to predation by mice (Marris 2000), with mice considered to have major impacts on the island's invertebrates. Larger beetles and orthopteroids are the most often-cited susceptible insect prey groups, with terrestrial snails also commonly considered vulnerable. A high proportion of

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island studies are from New Zealand or the Southern Ocean – but a number of published studies on rodent impacts there are ambiguous, in that comparisons of some rat-infested and rat-free islands have demonstrated insect absences from the former but without clear evidence that the focal species ever really occurred there. Such 'natural experiments' of comparisons are exemplified by survey of the Middle Island tusked weta (*Motuweta isolata*), which was found only on the rodent-free Middle Island in the Mercury Island group (New Zealand), and not on the other islands that supported *Rattus exulans* (Stringer et al. 2014). As with the Lord Howe Island stick insect (above), the endemic Fregate giant tenebrionid beetle (*Polposipes herculeanus*, Tenebrionidae) on the Seychelles underwent rapid declines (a reported 80 %) in the 5 years after Fregate Island was invaded by *Rattus norvegicus* (Parr et al. 2000), with Thorsen et al. (2000) noting that it was 'under a very real threat of extinction in the wild'.

Not unexpectedly, St Clair's review showed that larger-bodied invertebrates are especially susceptible to rodent predation, and large size may be a strong predictor of risk. A variety of indirect effects also occur from rodents, perhaps most commonly through their impacts on plants that host notable insect species. These associations may be very difficult to prove, but several correlative inferences cited by St Clair for New Zealand indicate representative examples. Two of these are (1) the large weevil *Hadramphus stilbocarpae* became locally extinct at the same time as considerable reduction of its host plant (*Stilbocarpa lyelli*) by *Rattus rattus* soon after its invasion; and (2) regeneration of Karo (*Pittosporum crassifolium*) is inhibited by *Rattus exulans*, and after eradication of the rat from Korapuki Island, the endemic scale insect *Coelostomidia zealandica* feeding on this host also recovered.

Eradication of alien vertebrates, most commonly mammals and especially from small islands, is a frequently attempted management tactic: the numerous cases reviewed by Clout and Veitch (2002) collectively include many different taxa and areas – the taxa included feral predators (such as cats), introduced pigs, goats and smaller herbivores, as well as rodents and mustelids, demonstrating the wide variety of trophic cascade impacts likely to affect native taxa, together with physical impacts such as soil compaction and vegetation trampling by larger mammals. Genovesi (2005) quoted an unpublished figure of 156 such eradications in New Zealand, for example. The predominant target group, feral and other invasive mammals, have been eliminated from more than 90 islands there, providing excellent opportunities to establish additional populations of threatened insect species – a predominant national theme that Watts et al. (2008, 2012) claimed to be 'certainly leading the development of reintroduction biology for insects'. This claim follows from a long history of translocations of threatened vertebrates in New Zealand, notably birds and tuatara onto predator freed islands, and Watts et al. (2008) noted that this itself could prove problematical for some later invertebrate transfers, because introduced native insectivorous vertebrates could pose an additional threat, and reduce options over which invertebrates might be moved there. Most such vertebrate eradication efforts (Chap. 9) have not been designed to specifically favour native invertebrates, and so differ from the Lord Howe Island example, above.

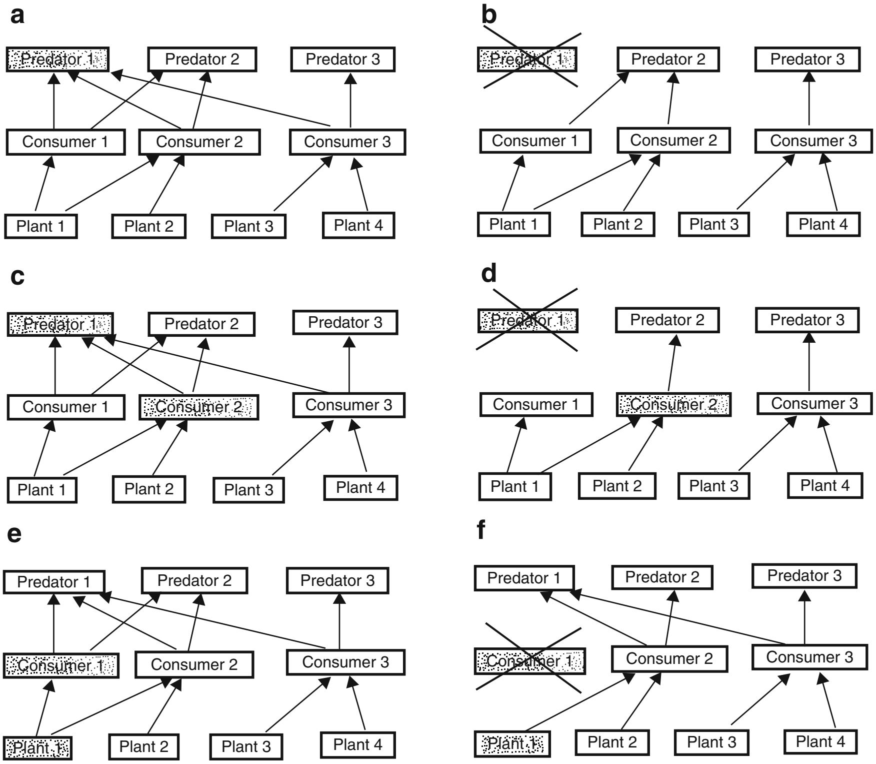

Fig. 8.1 Representations of some 'idealised' food webs to indicate variety of trophic interactions between species; *shaded boxes* represent alien species, unshaded boxes represent native species. Structures are (**a**) a community with a single alien predator; (**b**) removal of that predator increasing native prey populations; (**c**) a community with an alien predator and an alien herbivore; (**d**) removal of only the alien predator releases the alien herbivore population, with cascading impacts on two plant species; (**e**) a community with both an alien herbivore and an alien plant species; (**f**) removal of only the alien herbivore releases the alien plant population (Zavaleta et al. 2001)

Every eradication attempt, however, is an individualistic exercise and, as Zavaleta (2002, following Zavaleta et al. 2001) claimed, 'there will always be some surprise outcomes'. Even for successful eradications, secondary ecological consequences may include (1) releases of populations of other alien species; (2) declines in native species; and (3) failures of native species and ecosystems to recover after the target invader has been removed. The core of such uncertainty, as Zavaleta showed, is the variety of interactions amongst alien species, and between aliens and natives, and the ways in which these may influence food webs. Thus, a variety of contexts can occur for ecological release following removal of an alien species (Fig. 8.1), and together include a suite of possible outcomes, some through enforced dietary changes leading to novel competitive interactions.

The ecological context for an eradication can thus be complex, leading Zavaleta et al. (2001) to urge the need to assess each exercise in the context of the overall ecosystem that is being managed, that the assessment should, ideally, include both pre-eradication appraisal to help remove or reduce unwanted effects, perhaps through different techniques being employed, and post-eradication studies of the effects on both the target taxon and the invaded ecosystem – within which changed trophic relationships may become a serious concern. Many workers (such as Mack et al. 2000) have pointed out that attempts to control biological invasions are often most effective when they include a broad ecosystem-wide strategy rather than more limited focus on individual invaders. That philosophy needs understanding of why invasive species flourish, so that the underlying causes of their success can be opposed.

For many vertebrates, eradication on any but very local scale is unlikely; many indeed are naturalised and absorbed – even welcomed – into local culture, with any harmful impacts overlooked or unknown because of other societal or sectoral benefits. Some, however, demonstrably harm local biotas, and historical impacts of others cannot now be assessed realistically. Two contrasting examples noted below indicate some of the concerns for insect conservation; both involve human recreational interests.

Alien predatory fish are a major concern in freshwater bodies. Release of predatory salmonid fish for recreation/sport activity is widespread, with large stocks reared under aquaculture conditions for liberation into natural waterbodies in many parts of the world. Their wide diet includes numerous invertebrates, including insect larvae, as a cause of concern for localised freshwater species. In south eastern Australia, for example, very few stream systems remain free of one or both of Brown trout (*Salmo trutta*) or Rainbow trout (*Oncorhynchus mykiss*), with continual augmentative releases from a government hatchery boosting stocks for recreational fishing. Early analyses of gut contents of Victorian fish samples (Butcher 1947) revealed numerous insect taxa, including a high proportion of terrestrial insects in the diet of Brown trout. Many suggestions of threat are made, but those for native insects in Australia are overshadowed by losses of native fish and amphibians attributed to trout predation. Likewise, harmful impacts of salmonids released into Hawai'i have been 'simply presumed to occur' (Englund and Polhemus 2001). Possibility that upland stream releases of Rainbow trout on Kauai, following some 60 years of restocking from the 1920s on could threaten populations of endemic damselflies (*Megalagrion* spp.) led to surveys indicating that those streams still sustain diverse populations of these and other native insects. Those damselflies, however, have been shown to be susceptible to other alien fish, mostly Poeciliidae (Englund 1999), but in the more recent surveys *Megalagrion* larvae comprised only a tiny fraction (0.3 %) of Rainbow trout diet. The habitats of *Megalagrion* and some other endemic Hawai'ian aquatic insects (notably some Diptera) are quite restricted and may be largely inaccessible to trout that feed predominantly on terrestrial drift. Other observations on Odonata, in Australia (on trout feeding on the dragonfly *Hemicordulia tau* in New South Wales: Faragher 1980) and South Africa (Samways 1999), implied rather different effects. *H. tau* was significant in the diets of both trout species, but they did not affect its long-term survival because of seasonal variation in prey spectrum and lake water levels. In South Africa, the distribution of the threatened *Ecchlorolestes peringueyi* may have been reduced by Rainbow trout but it occurred only in streams above waterfalls, presumed to be refuges from downstream trout that could not encounter them. Clarification of refuges from predatory trout for native species is a complex task, as demonstrated for a New Zealand stream mayfly, within a wider discussion of refuges resulting from coevolutionary history with native fish. For *Nesameletus ornatus* (Nesameletidae), Townsend (1996) suggested that effective use of refuges might reflect such coexistence but with arrival of a novel predator, native insects might not show the appropriate responses, and become vulnerable. Mayfly larvae from a stream with Brown trout showed strong nocturnal foraging behaviour which was not evident in nearby streams with native galaxias but no alien trout. In this example, the refuges may have developed since *S. trutta* arrived, with time (nocturnal activity) and space (beneath stones during the day) both contributing to this. Trout may restrict some prey species to areas with refuges, such as dense aquatic vegetation, as Macan (1966) showed for the damselfly *Lestes sponsa* in Britain. In a further example (Macan 1965), rare species of Corixidae (Hemiptera) were eliminated from a pond to which trout had been introduced. In addition to direct predation, losses may flow from long-evolved characteristics of the prey species in predator-free environments. Thus, for South Africa, de Moor (1992) noted that larvae of several ancient groups of aquatic insects had developed conspicuous behaviour patterns in rivers and pools that supported only a very small endemic fish fauna, but have consequently suffered ‘severe impacts’ from alien fish.

Many concerns over impacts of Poeciliidae have come from introductions of Mosquito fish as generalist predators and biological control agents to reduce pest mosquito vectors. Two species, *Gambusia holbrooki* and *G. affinis*, both native to the United States, have been introduced to many parts of the world, and have since been classified as amongst the world’s worst invasive species. They are associated commonly with declines of amphibians as well as fish and invertebrates. Following Shulse et al. (2013), who confirmed that *Gambusia* can reduce invertebrate abundance through non-selective predation, mosquito fish are claimed widely to reduce natural ecological values of wetlands. Hoddle (2004) noted that about 70 countries have permanent populations of *G. affinis*, largely initiated by its promotion for mosquito larval control by the World Health Organisation up to 1982.

The Asian pheasant (*Phasianus colchicus*) has been naturalised in Britain for at least 1000 years, and is reared in large numbers for shooting. Neumann et al. (2015) reported that as many as 37 million pheasants are released annually in Britain, many initially into open-topped woodland pens from which the birds gradually move and settle in the local landscape. Recommended release density of 700 birds/ha is frequently exceeded, with numbers in some pens documented by Neumann et al. reflecting far higher densities. Possible impacts on ground-active invertebrates from this recreational stocking activity were studied by pitfall trap sampling in pens and at local control sites, using carabid beetles as a major focal group. No major differences in invertebrate abundance, or in richness of Carabidae or Staphylinidae were initially found between treatments. However, the within-pen samples showed changes in the carabid species complex towards those species associated with grassland and arable fields – a trend linked with reductions of woodland vegetation in the pens to encourage understorey growth. Losses of species that were large (>17 mm body length) or active mainly in spring increased as pheasant density increased. Neumann et al. could not confirm the cause(s) of this, but suspected predation by the pheasants as well as direct habitat disturbance effects. The high pheasant density pens also yielded higher numbers of detritivore groups, such as snails, isopods and millipedes. Suggestions for changes included maintaining recommended release densities, and considering reducing rearing pens in environmentally sensitive areas where such impacts may be significant, as well as considering changes in seasonal release patterns to benefit spring-active beetles.

Highly invasive birds are often acknowledged generally as harmful, but specific examples of threat to individual threatened insect species are sparse. The Common myna (*Acridotheres tristis*, Sturnidae), listed amongst the world's worst invasive species (Lowe et al. 2004), is notorious in and near urban areas of eastern Australia, where it competes aggressively with native wildlife. Their ecological impact (although 'their true effect on the environment and agriculture is largely unknown': Old et al. 2014) is regarded as severe and includes predation on native insects, including some of signaled conservation interest. Thus, recorded prey include Golden sun-moth (*Synemon plana*, p. 120) and the Perunga grasshopper (*Perunga ochracea*, Acrididae) in the Australian Capital Territory, where this flightless forb-feeding vulnerable orthopteran also occurs on remnant grassland patches.

Invasive vertebrates span all major taxonomic groups, and a considerable variety of ecological roles – they are responsible, for example, for dispersal of many invasive plants, most notably woody species (Reymanek 2000). Widespread processes such as domestic stock grazing on native vegetation, or replacement of native vegetation by more desirable alien pasture forage species simply exemplify the variety of major ecological changes that result – with little or no knowledge of impacts on native invertebrates. Temperate grasslands, in particular, have been modified extensively for such agricultural intensification, with alien plants and stock vital contributors to human welfare.

The woody shrub *Rosa rubiginosa* (Rosaceae) has become a serious weed in parts of the South Island of New Zealand, and was formerly planted extensively as a garden ornamental. Larvae of the endophytic wasp *Megastigmus aculeatus* (Torymidae) feed within the endosperm of rose seeds, which are eaten by the introduced Australian Brushtail possum (*Trichosurus vulpecula*), an abundant arboreal pest marsupial. These three species are all introduced to New Zealand, and have not co-evolved. Collections of fresh possum faecal pellets retained under room temperature conditions were inspected for wasp emergences over the next 6 months (August to February). Rouco and Norbury (2013) also collected samples of ripe fruit directly from *Rosa* bushes at the same time as they collected the possum pellets, for comparison of wasp infestation levels. By February, 146 adult wasps had emerged from 700 pellets; 88 % of the pellets contained rose seeds, and 19 % of pellets yielded wasps. For unconsumed rose fruits, 42 % were infested by *Megastigmus*, but survival of wasps was no higher than from possum-consumed seeds. The small wasp is believed to have very limited natural dispersal ability and, as individual Brushtail possums in the study area have home ranges of up to 54 ha, they may play a role in dispersing the wasp far more effectively than likely by its own powers (Rouco and Norbury 2013).

Emphasis on alien mammals and fish as the most highlighted vertebrate taxa that threaten native insects has tended to overshadow impacts of other taxa, most notably reptiles and amphibians. Few specific cases have been documented, but predation by the North American Green anole lizard (*Anolis carolinensis*) on the lycaenid butterfly *Celastrina ogasawarensis* on the Ogasawara Islands of southern Japan is believed to be the major cause of the butterfly's rapid decline – to a state that Nakamura (2010) regarded it as 'in extreme peril' on the one island on which it then existed. Conversely, some native vertebrates may be significant predators of alien insect pests: *Peromyscus* mice and other small mammals were a major cause of mortality of Gypsy moth pupae in North America, for example (Liebhold et al. 2005).

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Chapter 9
Countering Impacts of Alien Species

9.1 Introduction: Assessing Management Needs

The numerous concerns over invasive species' impacts, whether the alien species be insects, plants or others, display the intricacies of their interactions with the native biota they encounter, and give them a substantial collective and central role in insect conservation practice. Writing generally on invasive insects, Liebhold and Tobin (2008) noted that most accidentally introduced species only rarely reach high population levels, and are commonly not noticed. Management needs can differ considerably according to the invasion phase of concern, as (1) arrival – international quarantine, inspection; (2) establishment – detection, eradication; and (3) spread – domestic quarantine, barrier zones. The contexts of 'biosecurity' are founded largely in assessments of the risks of not detecting the alien species (Hulme 2011), with the important provision that it has indeed been identified correctly.

Testament to their importance, largely under the rather different priority of human welfare, alien species are a major focus as pests, nuisances or other threats to human interests – roles that create need to suppress or eradicate them, and can bring them into some conflict with conservation needs. Their spread into non-anthropogenic areas, exemplified repeatedly in earlier chapters, causes many alien species to be regarded as threats to native species and native-dominated localised ecosystems. Indeed, the title of Low's (2001) book discussing alien species' impacts in Australia ('Feral future') aptly summarises the variety present, and the diversity of alien insects on the continent (New 1994) is simply one aspect of this. The Australian scenario is by no means exceptional, but the natural previous isolation of the biota there renders many invasives easily recognisable amongst the highly endemic fauna and flora. Most have arrived in the 200 years or so since European colonisation.

Increasing numbers and variety of invasive insects and other taxa are related strongly to globalisation, with increasing international freight and passenger transport (including international tourism) being trends that Rasplus (2010) predicted

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Table 9.1 The seven objectives used as guidelines for formulating the 'IUCN Guidelines for the Prevention of Biodiversity Loss caused by Alien Invasive Species' (IUCN 2000)

1. To increase awareness of alien invasive species as a major issue affecting native biodiversity in developed and developing countries and in all regions of the world
2. To encourage prevention of alien invasive species introductions as a priority issue requiring national and international action
3. To minimise the number of unintentional introductions and to prevent unauthorised introductions of alien species
4. To ensure that intentional introductions, including those for biological control purposes, are properly evaluated in advance, with full regard to potential impacts on biodiversity
5. To encourage the development and implementation of eradication and control campaigns and programmes for alien invasive species, and to increase the effectiveness of those campaigns and programmes
6. To encourage the development of a comprehensive framework for national legislation and international cooperation to regulate the introduction of alien species as well as the eradication and control of alien invasive species
7. To encourage necessary research and the development and sharing of an adequate knowledge base to address the problem of alien invasive species worldwide

will continue to expand and influence economies and global ecosystems to increasing extents. A recent Australian government report (in August 2015), for example, noted that in the past decade the volume of air passengers to Australia had increased by 80 %, of sea containers by 82 %, and of bulk cargo by 16 %. The ineffectiveness of formerly formidable geographical barriers in preventing spread of organisms throughout the world is undoubted, with previously effective natural boundaries such as oceans or mountain ranges that enforced isolation and allowed characteristic regional biota to evolve now largely succumbing to human behaviour, trade, global trade and related activities – and with this homogenisation coinciding with losses of many of the world's most complex and restricted biomes. Discussing how globalisation increasingly facilitates the spread of invasive species, Meyerson and Mooney (2007) noted that research is rarely conducted simultaneously at the three relevant scales. Thus, mechanisms and impacts revealed at a local scale may not apply at larger spatial scales. Larger, regional, studies have tended to focus on patterns of invasions rather than their impacts, and global scale studies have emphasised commerce and travel in order to predict risks and formulate policy. Greater integration across these scales to develop more holistic approaches to preventing and evaluating invasions is advocated widely.

Guidelines on the roles and management of alien species, devised through the World Conservation Union (IUCN 2000), have become a platform for advance toward effective appraisal and, where necessary, reaction to suppress undesirable or harmful invaders. Those guidelines were formulated with a series of seven objectives (Table 9.1) that collectively summarise the major conservation concerns that arise and the primary needs for management of alien invasive species. Each must be based on the best information available, together with understanding and communication across all relevant sectors and community groups. The guidelines cover both unintentional and deliberate introductions of species and, where necessary,

Table 9.2 The themes needed to comprise an 'ideal' web-based integrated tool for biosecurity involving capability to predict, detect, and manage invasions of arthropods (After Rasplus 2010)

1. Identify the most likely future arthropod invaders
2. Provide generic and accurate identification tools, including global DNA listing of barcodes, of the most invasive species
3. Compile biological information on those species in nature and, where possible, their invasive range
4. Predict where such aliens might potentially thrive, and their future distributions under climate change
5. Estimate the full costs of the most likely alien arthropods
6. Quantify and map risks associated with these non-indigenous species, and prioritise them

eradication or other control; the values of effective communication and education are also emphasised. The guidelines do not single out any particular invasive groups, but the conservation themes and 'messages' apply widely to insects, not least through the published 'Background' sentiments that 'The impacts of alien invasive species are immense, insidious, and usually irreversible' and, further 'They may be as damaging to native species and ecosystems … as the loss and degradation of habitats'.

Linking with themes discussed earlier, Rasplus suggested the need for an integrated biosecurity tool for invasive arthropods, and that it was necessary to include components integrated to address the themes summarised in Table 9.2. Whilst the notes included in this table currently appear somewhat idealistic, they emphasise the major urgent needs for the future. Simply, increased extent and variety of worldwide transport of goods and people increase chances of accidental transfers of species. Many of these are difficult, or impossible, to anticipate. Transport of used vehicle tyres, for example, is an important pathway for some mosquitoes (Culicidae) – as summarised for *Aedes albopictus*, a treehole-breeding vector of several important diseases (including dengue fever and yellow fever), and which has been distributed widely from its native Asia by this method (Eritja et al. 2005). Tyre shipments from China were implicated in the first importations of the mosquito to Albania and the United States, amongst others.

The impracticability of effectively inspecting all consignments in the accelerating pattern of global trade and people movements has dictated that efforts to detect invasive invertebrate pests of plants has focused more on priority pathways than on threats from novel commodities or markets (Smith et al. 2007). This approach may be quite effective – 89 % of the 114 human-assisted introductions to the United Kingdom from 1970 to 2004, for example, were associated with movements of plants, most notably of ornamental plants imported for garden or horticultural purposes.

Management of invasive alien species necessarily considers six key themes that emphasise both the importance of a wide range of environmental processes and the limited capability to provide sound predictive information as management becomes necessary. The themes, as stated by Hulme (2006), are summarised in Fig. 9.1. For any given invasive species, they are (1) expected impacts on the receiving environ-

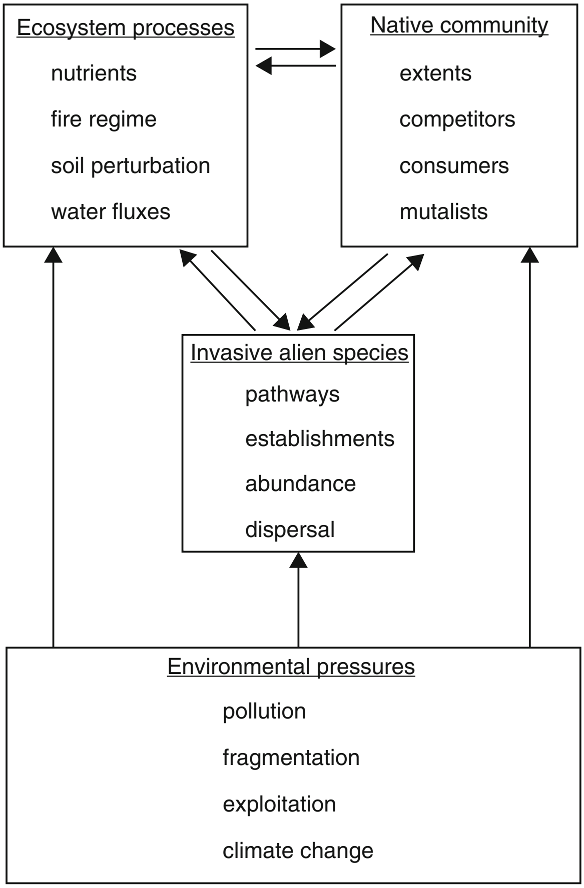

Fig. 9.1 Key linkages among different components that need to be considered in planning attempts to manage invasive species. Targetting aspects of individual invasive species' ecology may not lead to sustainable management outcomes if roles of environmental pressures, ecosystem processes and native community are not adequately considered (Hulme 2006)

ment and economy; (2) the variety of technical options available for management; (3) how easily the species may be targeted for management; (4) the risks associated with different management options; (5) the likelihood of success of defined management strategies such as eradication, containment or control; and (6) the levels of public concern and stakeholder interest. Collectively, these themes emphasise that, whilst a target species is the central primary concern, management must consider many other areas related to ecological, political and economic 'working environment' that may constrain ideal management through lack of resources, concern, priority and understanding, together with ignorance of the species' full range of potential impacts. Lack of detailed knowledge or awareness of the impacts of most alien species on native biota is taken commonly to mean that they are not harmful, but fuller risk assessment is a clear need in many cases. Most conservation concerns over threat have come from herbivores or generalist predators and parasitoids, but numerous aspects of species displacements and disruptions of intricate ecological constructions are unknown and, in most taxa, have not yet been appraised. The

Table 9.3 The impact categories of invasive species listed under the two major groups of impacts, as listed by Vaes-Petignat and Nentwig (2014) (numbers 1–12 correspond with listing in Table 9.4)

Environmental impacts
1. Impacts on plants or vegetation through herbivory
2. Impacts on animals through predation or parasitisation
3. Impacts on other species through competition
4. Impacts through transmission of diseases or parasites to native species
5. Impacts through hybridisation
6. Impacts on ecosystems
Economic impacts
7. Impacts on agricultural production
8. Impacts on animal production
9. Impacts on forestry production
10. Impacts on human infrastructure and administration
11. Impacts on human health
12. Impacts on human social life

widespread perception that (1) limited known attack by invasive species on native species and (2) relatively low abundance of the aliens in natural ecosystem denotes low risk, is dangerous to adopt uncritically; such situations can change rapidly if aliens increase in abundance and distribution as conditions alter. Brockerhoff et al. (2010) urged the need for 'innovative risk assessments' such as (for New Zealand in their context) exploration of the invertebrates exploiting New Zealand plants occurring as ornamentals or invasives elsewhere in the world, with such species likely to represent future biosecurity risk.

Attempts to assess and predict impacts of alien species accurately and consistently, and to provide realistic bases for comparisons across taxa, continue to challenge the ingenuity of biologists and managers alike. Within Europe, a 'generic impact scoring system' based on analyses of published information, and derived initially for mammals and birds, has more recently been applied to terrestrial arthropods (Vaes-Petignat and Nentwig 2014). The scheme incorporates six environmental impact categories and six economic impact categories (Table 9.3), each with five impact levels (ranging from minor ['1'] to major ['5'], with an additional zero impact level when no impact has been detected or is known. The scheme is scale-independent and was promoted as easily adaptable as new information accrues, and in allowing comparable impact scores that enable science-based recommendations for management priority. It also applies to countries where a given species is not yet present but is likely to invade, so facilitating preventative or early detection measures. The analysis was based on 77 species, all alien to Europe (p. 17) and each represented in more than 20 European countries, with the additional parameters of ensuring inclusion all terrestrial arthropods included in a priority list of the region's

Table 9.4 The highest ranking invasive alien arthropod species in Europe, based on the summed scores of each of the 12 impact categories listed in Table 9.3 (Vaes-Petignat and Nentwig 2014)

	Impact categories												
	Environmental						Economic						Total score
Taxon	1	2	3	4	5	6	7	8	9	10	11	12	
Varroa destructor	0	5	0	5	0	5	5	5	0	3.5	1	1	30.5
Linepithema humile	2	2	4	0	0	4	2	0	0	3	0	0	17
Harmonia axyridis	0	4	2	0	0	3	3	0	0	2.5	2	1	16.5
Frankliniella occidentalis	2	0	0	3	0	3	4	0	0	3	1	0	16
Bemisia tabaci	2	0	0	3	0	3	4	0	0	3	0	0	15
Aphis gossypii	2	0	0	3	0	3	3	0	0	3	0	0	14
Tuta absoluta	2	0	0	0	0	3	5	0	0	3.5	0	0	13.5
Aedes albopictus	0	1	0	0	0	3	0	0	0	2	3	3	12
Callosobruchus chinensis	1	0	0	0	0	3	4	0	0	2.5	1	0	11.5

Of the 77 taxa appraised, 53 scored less than 10

worst invasive aliens (DAISIE 2012) and of up-to-date consideration of the most recent invaders by including species recorded first in Europe after 2000 if now present in eight or more countries there. Collectively, the taxa represent 13 orders and 38 families, with ranking by 'impact points' across the 12 categories leading to definition of the most harmful species – the mite *Varroa destructor* was followed closely by Argentine ant and representatives of several insect orders, but with most species scoring only lowly (Table 9.4).

Increased surveillance to detect insects and other arrivals at ports and airports is a complex and labour-intensive process, and an important component of biosecurity. Transport hubs are key foci for alien species introductions, and surveillance to detect arrivals is a critical aspect of invasive species management. Thus, international arrivals on aircraft are frequent and varied. Surveys of cargo planes arriving at Miami International Airport, Florida, (by direct inspection of two randomly chosen aircraft each day for a year [September 1998–August 1999], by specifically trained officers) yielded 157 insect pests in 33 families (Caton et al. 2006). These included five 'high risk' pest species and, whilst most contaminated flights had only one or two species, three to seven species occurred on some flights from Central America. This study, as for several related investigations, displays the considerable array of such hitch-hikers that can arrive undetected. That most introductions of alien insects in Europe are associated with international trade in ornamental plants (Kenis et al. 2007, 2008) endorses the need for enhanced biosecurity attention to this pathway. Sap-feeders and detritivores were the predominant guilds represented, and in surveys for Austria and Switzerland, external defoliators were under-represented. More than half the insect introductions to Europe were on cut flowers, potted plants, seedlings or bonsai. The last is notable – nearly twice as many pest insects were intercepted on bonsai trees as on timber, and these include many aphids and several cerambycid beetles.

Table 9.5 Summary of the numbers of quarantine interceptions in Australia of four major insect orders for which species level identifications were available, 1986–2005 (Caley et al. 2015)

Order	Number of interceptions	Number of species
Hemiptera	4,797	222
Coleoptera	34,163	524
Diptera	787	107
Lepidoptera	5,866	245

Effectiveness of intercepting insects at customs borders is extremely difficult to assess, and several investigators have revealed the uncertainties that persist. Australian border interceptions of four large insect orders (Hemiptera, Coleoptera, Diptera, Lepidoptera) for 1986–2005, for example, showed that most incursive species over that period were not intercepted. The three main inferences were (1) arrivals occur through means that are not subject to inspection; (2) inspection effectiveness is low; and (3) lack of taxonomic information prevents effective detection and reporting. All contribute to the impression that border security may not here be an effective early warning system for many invertebrates (Caley et al. 2015). Preparatory lists of 'pest species' amongst those four orders confirmed that they are the predominant taxa of concern: 138 (of 180) species categorised with a potential pest impact, and 210 (of 253) with potentially high economic impact were included. The relative abundance of interceptions is summarised in Table 9.5, whilst the numbers of interceptions (Fig. 9.2) confirmed that few species were intercepted commonly. The most likely occurrence was of fewer than ten records, but a few were much more common – even up to about 10,000 occasions. Nevertheless, of the 91 successful incursions over that period, only 13 were intercepted at least once, confirming the probable low likelihood of quarantine interceptions.

The valiant attempts of quarantine officials are almost always hampered by the extent and complexity of needs to discover organisms such as small insects or plant seeds among the mass of trade goods and human traffic. The 'pet trade' (p. 44), for example, can be very difficult to detect and regulate. Sampling incoming goods and people by risk assessment (based, for example, on place of origin, kind of goods, selected target species, and quality of packing and declared prior treatments) is a formidable task, and it is inevitable that many potentially invasive organisms will continue to arrive. Global surveillance is very uneven, in itself a possible tool in inferring origins; the Tasmanian thrips recently found in California (Sullivan 2014, p. 70) has recently been found in Hawai'i, and Sullivan suggested that it was far more likely to have arrived from California than directly from Tasmania. Even for small Pacific islands, where some of the greatest concerns over invaders occur, increased trade and tourism creates complexity. The first 6 months of a quarantine and inspection system for the Galapagos Islands led to detection of 33 arriving invertebrate species, at only a sixth of the system's capacity needed to fully undertake the programme (Causton et al. 2006).

An allied problem for many such remote islands, but also for many continental environments is that the resident biota has not been characterised fully; many a

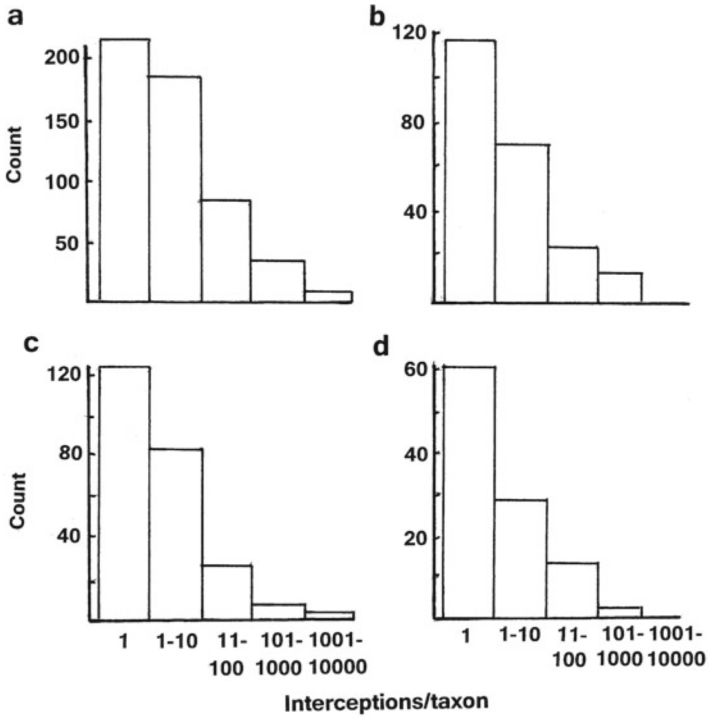

Fig. 9.2 Interceptions of insects by Australian quarantine: counts of interceptions (1986–2005) of four major insect orders, with frequency of interceptions/taxon shown, (**a**) Coleoptera, (**b**) Hemiptera, (**c**) Lepidoptera, (**d**) Diptera; note that the x-axis is logarithmic in scale (Caley et al. 2015)

small wasp, fly or beetle intercepted at a border cannot be (1) identified to species level easily and (2) distinguished as a previously resident species or a new potential incursive. Additional subtleties, such as length of residency among the former category, add to difficulties of evaluating whether any response to a current discovery is needed, or would be redundant. Tracing probable origins of newly-discovered or other significant aliens can lead to effective searches for natural enemies in their native area and help clarify their subsequent evolutionary changes. Genetic studies may help to trace arrival pathways and times or sequences through clarifying patterns and rates of genetic changes. The very widespread Red imported fire ant (*Solenopsis invicta*, Chap. 6) is one such case, for which recent study (Ascunce et al. 2011) provided evidence that all the world's invasive populations are derived from the original North American invasion rather than from multiple arrivals from South America.

Systematic surveillance for arrival or spread has the twin foci of general monitoring for invasive taxa and targeting individual species, the latter sometimes with intensive campaigns that can be rendered effective by good knowledge of the focal species. Monitoring of the spread of Gypsy moth (*Lymantria dispar*, p. 29) in North

America along the leading edge of the population front, for example, involved deploying about 100,000 pheromone-baited traps during the male moths' flight period, as the 'Slow the Spread' campaign (Tobin and Blackburn 2007).

Increasing contributions by 'citizen scientists' to recording incidence and distribution of key invasive species are becoming key elements of such surveys, as in many other aspects of natural history data accumulation. Recent technological advances, such as the use of smartphones with series of recognition applications for such purposes, as discussed for western Europe (Adriaens et al. 2015), facilitate rapid and verifiable (photographic) recording.

Needs for more general monitoring for arrivals, especially of known or potential pest species have also led to some ambitious and innovative suggestions. Deployment of a global network of 'sentinel plantings' within established botanic gardens and arboreta was recommended for monitoring for invasive forestry pests (Britton et al. 2010) as an avenue toward early detection of those threats. Using their diverse plant collections, observations of any unusual pest on an introduced plant, or of a local pest found for the first time on an alien host, may have value for workers elsewhere as adding to the wider knowledge of pest incursions. Monitoring of expatriate plants is a recognised component of improving predictions of incursions (Mack et al. 2002). Many other monitoring schemes, in many parts of the world, contribute to the continuing knowledge of alien arrivals. The United States 'Port Information Network' maintained since 1988 provides a continuing database on incidences of pests of potential quarantine importance, in which arthropods (mostly insects) comprise around 60–65 % of records of approximately 53,000 identifications annually (Mack et al. 2002). These can be related to mode of arrival, with most insects travelling in wooden packing or crates, or on nursery stock as the most frequent pathways of entry.

More widely, the general structure of a system for predicting invasiveness of alien species combines knowledge and understanding of species' biology with the wider context of invasion biology, in order to assign parameters that are meaningful in predicting the likely outcome and extent. The scheme devised by Mack et al. (2002) (Fig. 9.3) depends on characters relevant to each stage of the process (summarised in abbreviated form in Table 9.6).

Impacts, commonly the major driver of conservation concern from invasive species, represent only part of the information needed by managers for considering actions that must be assessed also on costs and feasibility as well as ranking within a suite of other needed activities. Parker et al. (2006) schematised the decision process faced for action (Fig. 9.4) by ranking invasive species by current or projected impact and the feasibility of control. The impacts are normally defined by the extent of ecological change produced, but Parker et al. suggested that impacts could, rather, be defined by the feasibility of restoring sites once the invader has been removed. The two subsets of the figure indicate categories for species already present and those that are not present but must be kept out as biosecurity priorities.

Management of any invasive species is complex, as modern insect or weed pest management amply demonstrates, through innovative approaches that draw on any relevant aspect of the species' biology to devise methods that are – to the highest

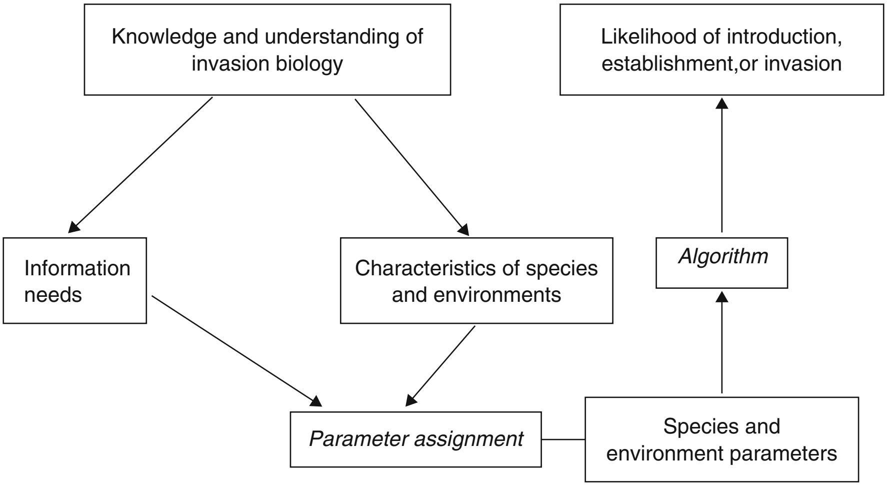

Fig. 9.3 General structure of a system for predicting the invasiveness of alien species, based on initial knowledge enabling assigning parameters to species' characteristics and subsequent use in algorithms to estimate likelihood of invasion (see text) (After Mack et al. 2002, with permission by the National Academy of Science, courtesy of National Academies Press, Washington DC)

levels possible – environmentally safe, economical and effective. Such processes in agroforestry or other economically important environments are generally well-resourced, and so contrast with many invasives whose impacts are primarily of conservation concern rather than having direct economic importance. Planning such an operation thus requires considerable foresight to ensure a sound approach and outcome. As Green and O'Dowd (2009) showed for *Anoplolepis gracilipes* with its massive impacts on Christmas Island (p. 76), success of any response depends on many factors, combining willingness, capability, effective communication, and the best available experience and knowledge of the species' ecology. Thirteen 'hard-won insights' from that exercise (Table 9.7) have much wider relevance, but parallels have rarely been itemised in such succinct form, or with such effective support and resources available.

9.2 Eradication

Once any undesirable alien species has passed though the post-establishment 'lag phase' and become invasive, some form of suppression is commonly advocated. Natural declines of serious invasive species can occur, but reasons for these relatively rare events are largely unclear. The Yellow crazy ant (*Anoplolepis gracilipes*, p. 76), invasive in northern Australia, was studied by Cooling and Hoffman (2015) who showed that five populations on small sites (up to 3.6 ha) disappeared, and two others on larger sites (8.6, 15 ha) declined substantially. Although precise

Table 9.6 Information needed to support the scheme for predicting invasiveness of alien species summarised in Fig. 9.3 (Abbreviated from Mack et al. 2002): factors for the three successive stages of arrival, establishment and invasion, for invasive arthropods and plants

Stage	Feature	Information needed
Arrival	History	Details of frequency and interceptions outside native range
	Rate of movement from source to potential distribution	?wide geographical range; ? wide range of environments; ?strong association with imported products; ? high frequency/likelihood of trade transfers; ? high population densities in native range
	Survival during movement	?dormant resting stages; ? likely to survive transport
	Escape from safeguards	?detection likely; ? any recognised detection/mitigation procedures
Establishment	History	Details of naturalisation or establishment outside native range
	Environmental suitability	?climatic suitability; ? similarity to native range;
	Resources	?suitable hosts available; ?biotic resistance affecting survival in new areas
	Demographic/environmental suitability	?propagule pressure high; ? dormant period; ? parthenogenesis; ?high growth rate and rapid development
Invasion	History	History of invasiveness elsewhere
	Host/habitat availability	?resources associated with disturbance or cultivation; ? potential hosts contiguously distributed
	Dispersal	?effective means of dispersal (natural or assisted)
	Growth	?high reproductive output; ?related to native species in invaded areas; ?biotic resistance limiting growth

colonisation dates were not documented, that swift declines were possible was shown by disappearances at two sites within 2 years of arrival, possibly due to stochastic effects. Factors suggested as possibly contributing to declines on the larger sites included bush fires (most savanna sites in the Arnhem Land region are burned at least every 2 years), pesticides, migration, resource overuse, and pathogens/parasites. Eradication of tramp ants is notoriously difficult, and attempts to do so have drawn on many aspects of modern pest management and proved most successful on small isolated islands or atolls. Thus, Spit Island (6.07 ha), the smallest island of the Midway Atoll (in the central Pacific) was the site for attempts to eradicate *Solenopsis geminata* by using a specific formicide bait (Plentovitch et al. 2010). Non-target effects were found on other arthropods, including cockroaches and crickets – most of them also alien – as well as other ants. That island is unusual in that the

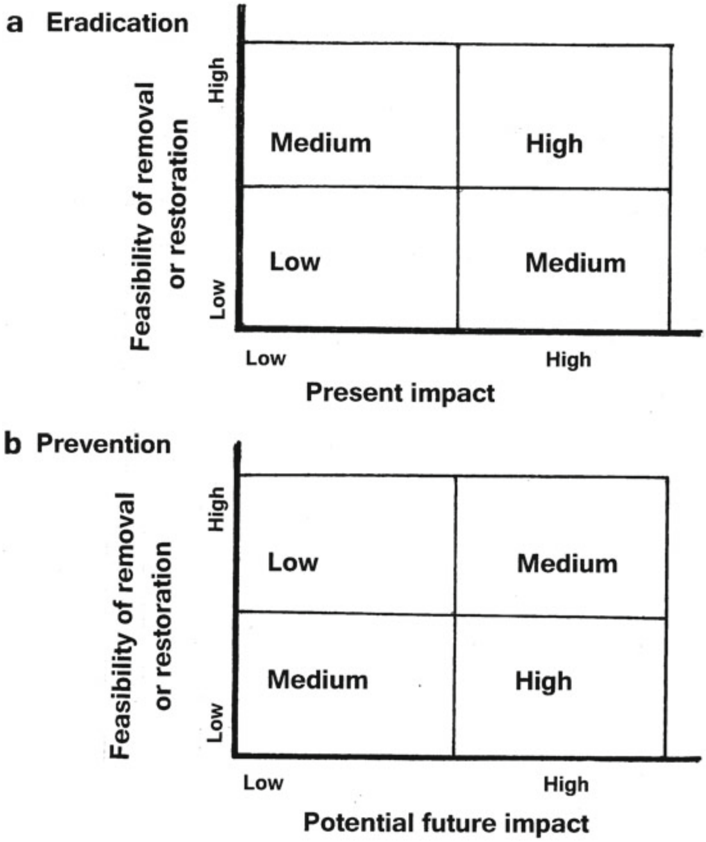

Fig. 9.4 Indicative scheme of the processes faced by policy makers and managers who need to decide which alien species they must (**a**) eradicate or control once already present in the local environment, or (**b**) keep out, if they are not already present (Parker et al. 2006)

ground-dwelling insect community is almost wholly alien, so that rather few native species could be affected. Nevertheless, lack of knowledge of the bait impacts on any particularly susceptible native species (Plentovitch et al. cited *Caconemobius* crickets and other native detritivores) implies need for some caution, and prudent uses of baits. Baiting programmes are commonly suggested for alien ant eradications, especially from small or isolated areas – Burwell et al. (2012), for example, advocated this approach for removing *Pheidole megacephala* from coral keys on the Great Barrier Reef (Australia).

Whilst eradication of alien species is viewed as a key conservation need, doing so can sometimes present formidable problems. Public attitudes to eradication of invasive alien species vary enormously, with different stakeholder groups often having markedly disparate perceptions of the relative harmful impacts and benefits of the focal species. Many such people, however, may have only limited appreciation of the problems, and education and public awareness campaigns associated

Table 9.7 The series of ‘hard-won insights’ relevant to undertaking rapid response to invasion by an invasive alien invertebrate, derived from practical experiences of attempting to control Yellow crazy ant, *Anoplolepis gracilipes*, on Christmas Island (Abbreviated from Green and O’Dowd 2009, by permission of Oxford University Press)

1. The human dimension – need for ‘bottom-up’ effort by people directly involved
2. Solid support of science by good natural history - seriousness of problem conveyed through understanding of ecological aspects of the invader, with natural history fundamental to clarifying the wider implications of invasion
3. Capacity for responsive funding – ‘crisis management’ unpredictable, and cannot be planned in many operational budgets
4. GPS/GIS technology – vital to locate sites accurately, delimit supercolonies, and target aerial operations
5. Public awareness – increased awareness at all levels helped focus management attention
6. Clear demarcation of responsibility – single authority avoids cross-jurisdictional disputes and related delays and confusion
7. Bridging the ‘science-management interface’ – cooperative programme to meet challenges of management and harmonise different priorities of scientists and managers to achieve primary goal
8. Competing resource demands – diversion of resources from other programmes (in this case including weeds and feral cats) as well as wider issues in the wild (on Christmas Island including refugee detention facilities and phosphate mining)
9. An independent steering committee – independent of management authority, to review, guide, advise, and including representatives of scientists, managers, policy makers and other major stakeholder groups
10. ‘Successful response sometimes requires a healthy dose of luck’ – draw on previous experience and recognise value of chance experiences and opportunities
11. ‘Successful response requires quick thinking’ – accidents, unplanned events and circumstances, happen and may require rapid changes to plans and problem solving
12. ‘Who you know is as important as what you know’ – networking with other groups proved pivotal, gaining experience, facilities, ideas and key contacts
13. Isolation and tight timelines can be overcome – effective coordination to counter remoteness on the island and effective advance planning to accommodate shipping schedules

with proposed management are a clear need to ensure the most coordinated outcomes (Garcia-Llorente et al. 2008). Most such programmes have targeted vertebrates or plants, and Genovesi (2005) noted that no eradications of alien invertebrates had then occurred in Europe. Elsewhere, insect eradications have almost always focused on key pest species of wide economic or welfare relevance, for which political and financial support has been readily forthcoming. Thus, three of the four introduced *Bactrocera* fruit-fly species (Tephritidae) were eradicated from Nauru by a combination of male suppression and protein baits (Allwood et al. 2002). Following initial report of the flies on Nauru in 1992, the eradication campaign lasted from October 1998 to December 2000. There, as more generally, early detection and concern were considerable advantages in control, with need for rapid response to new invasions of damaging insect species. Surveillance for priority invasive species is a key need. Allwood et al. noted that the isolation of Nauru could reduce risks of re-introductions of the flies, and that the exercise had considerable additional benefits in training local people and improving quarantine inspections for such invasives.

The ‘release’ of other invasive species previously present in unobtrusive roles or low numbers following eradication of key target aliens is difficult to anticipate. One possible example is the extinction of Black rats (*Rattus rattus*) on Bird Island (Seychelles) being followed by rapid increase of the crazy ant *Anoplolepis longipes* (Feare 1999). Rat eradication was completed in late 1995 and by 1997 the ant had expanded to occupy about half the 80 ha island, with consequences including deaths of land crabs, disappearance of the endemic skink from infested areas, impacts on native birds and ‘the killing of large numbers of insects, especially large beetles’. Feare speculated that eradication of the rat reduced predation on the crazy ant, which had remained in low abundance for several years since it was recorded first in 1991, and enabled it to subsequently expand dramatically.

Eradication of invasive aliens, advocated continually and widely, is itself subject to possible non-target effects. In general, as Clout and Veitch (2002) commented, some non-target deaths may be acceptable if (1) eradication of the alien species is achieved and (2) recovery of the non-target species is likely to be rapid. However, other undesirable consequences may ensue. Following Zavaleta et al. (2001), Clout and Veitch noted (1) ecological releases of invasive plants after introduced herbivores are removed and (2) prey species irruptions after predator removal. Knowing sufficient of the biology of the eradication target is key to undertaking the programme, together with assuring that sufficient resources are available to complete the project under clear and defined leadership. Any eradication success, of course, can be negated if the species reinvades. For a number of key insect pests – Liebhold and Tobin (2008) cited the Mediterranean fruit fly, *Ceratitis capillata*, and the Gypsy moth, *Lymantria dispar*, as examples – repeated eradications following reinvasions have indeed been necessary, with the process still being cost-effective. Difficulties of selecting approaches to eradicate invasive insects were exemplified in speculation over the Lime swallowtail butterfly (*Papilio demoleus*, Papilionidae), almost certainly likely to invade Florida from the Caribbean area (McCoy and Frank 2010) and then feared to pose a severe threat to the citrus industry and also threaten native swallowtails – larvae of some also feeding on citrus. The ‘popularity’ of butterflies may engender adverse public reactions to any control measures pursued; classical biological control could threaten non-target congenors; biological control by generalist predators may be a very long-term exercise with uncertain outcomes and probably be ineffective; and chemical control could disrupt ongoing biological control of other citrus pests. The optimal course of action was unclear. Similar dilemmas are not uncommon.

Many workers have asserted that the most effective way to reducing the spread of an invasive organism is to first suppress outlying (edge) populations and move progressively toward the centre of the range as eradication proceeds. Some modelling studies, such as that on the spread of *Bombus terrestris* in Hokkaido, Japan (Kadoya and Washitani 2010) support this premise. Any such model must rely on sound basic knowledge of the factors that may influence rate of spread – in this example, the bumble bee’s spread depended on the proportion of woodland in the landscape, and the climate (measured as snow depth) influenced this, but suppressing the peripheral colonies was the best of several control options available.

Unanticipated effects of attempts to eradicate invaders are more likely to occur when the number of invading species is increased (Chiba 2010), and can flow from (1) trophic interactions between alien and native species; (2) native species feeding on or otherwise using invasive plants; and (3) when dominant alien species inhibit invasions by other species. Chiba's studies on the fate of land snails (*Ogasawarana* spp., Helicidae) on Anjima (Ogasawara Islands, Japan) in the face of an invasive plant (*Casuarina stricta*, forming a thick forest that excludes native vegetation) and Black rats (*Rattus rattus*, associated with severe declines of snails by predation) showed removal of *Casuarina* to be associated with loss of snails, indicated by decreased density of living snails and increased numbers of shells showing marks from predation. The thick litter produced by *Casuarina* appeared to provide refuges for the snails from rat predation. In this example, for conservation of the endemic snails eradication of the rat should occur before eradicating *Casuarina*. It is likely that many analogues to this scenario occur for insects, and such cases emphasise that eradication of alien species for practical conservation of native taxa may need to be planned very carefully, and often as relatively long-term campaigns.

The broader perspective of managing alien species discussed by Bull and Courchamp (2009) emphasises that such programmes cannot be assessed fully by decrease or loss of the single focal species alone, but also on the successful subsequent recovery of the invaded ecosystem. Any adverse flow-on impacts from the alien's loss are a key consideration for management. Management difficulty increases as the number of invasive species present increases and creates larger numbers of novel interactions (Zavaleta et al. 2001). Aliens in the later stages of colonisation are more likely to replace the functional roles of native species. Success of single species eradications could thereby lead to impacts on the ecosystem, or on species that are a primary focus for conservation. Ecological release of a second invasive species previously controlled by the now-eradicated herbivore or predator/parasitoid is perhaps the most common such outcome, and can be predicted only from substantial prior knowledge of the interactions involved. In theory, any species that undergoes ecological release as a result of removing a species from the ecosystem has the potential to influence subsequent species interactions and abundance.

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Chapter 10
Invasions and Insect Conservation

10.1 Introduction: Insects in the Anthropocene

This book endorses much of the theme expressed by Vermeij (1996) – that in invasion biology ‘particulars of individual cases have obscured broader patterns’ – but in the intervening years since his essay the variety of examples and of contexts across which many taxa can be appraised have increased considerably. However, the four main foci suggested by Vermeij for seeking generalities (Table 10.1) remain valid, and tantalising in their complexity.

Many biologists have focused, overtly or tacitly, on only one of these themes but, in arguing that study of invasion biology should be integrated more widely into biology and draw on the broad principles of ecology and evolution, Vermeij foreshadowed recent debates on the validity of any distinct ‘invasion biology’, and calls for precise understanding of terms such as ‘invasive’ (Shah and Shaanker 2014). None of this, however, lessens the reality and often irreversible impacts and importance of biological incursions, linked with accelerating development of Anthropocene environments. General predictive rules for the processes remain elusive. One popular ‘rule’, known widely as the ‘Tens Rule’, asserts that approximately 10 % of arriving species become established and, of these, about 10 % become invasive and are widely considered ‘pests’ in the new environment. Those (very generalised and approximate) ratios and impacts are often difficult to both detect and measure – not least because details of most of the numerous resulting ecological interactions are not fully understood (Jaric and Cvijanovic 2012), so that caution is necessary in applying this (or any other) suggested rule and in so conveying misleading messages to management authorities. Extending from this, Jaric and Cvijanovic also urged extreme caution in seeking to introduce species with no apparent or documented effects on receiving ecosystems.

Roles of alien species, and their potential to become invasive and harmful in their new environments, are often highly uncertain. Predicting success of invasion remains so, and Prins and Gordon (2014a) urged that ‘In ecology neither modelling

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Table 10.1 The four key themes suggested to help seek generalities beyond the particulars of each individual invasive species (After Vermeij 1996)

1. How invaders differ from non-invaders in the arrival, establishment and infestation phases of invasion
2. How regions or communities that have produced many successful invaders differ from those in which few resident species have been able to extend their ranges
3. How recipient ecosystems with many successfully established invaders differ from those in which few species have invaded
4. How invasion affects evolution of the invader itself and of species in the receiving community with which the invader interacts

Table 10.2 The series of hypotheses derived from ecological theory and used by Prins and Gordon (2014a, b) to explore how biological invasions may occur

Hypothesis
1. A species will not be able to invade an area that has abiotic conditions that are outside its physical tolerance levels
2. The extent of an invasion is negatively correlated to species diversity of functional guild competitors in the invaded environment
3. An invasive species will not be able to replace a native species if they occupy the same niche and are in all other ways equal
4. A species will not be able to invade areas that harbour pathogens (that cause disease) or predators (that prey on the invading species) that it has not encountered before
5. A species will not be able to invade an area if its coevolutionary species (those necessary for parts of the invader's life cycle) is/are not present in the area
6. Species that occur at low population densities in their natural range will not be invasive
7. A species will not be able to invade an area if it has a lower use efficiency of its limiting resource than a native species that occupies the same location
8. Species can more easily invade highly disturbed areas; this disturbance can be man-made or natural
9. Species from older lineages are more vulnerable to being replaced by invasive species that occupy a similar niche
10. A species will only be able to invade an area if it has a life-history strategy which is more r-selected (or 'weedy') than that of the species which already is occupying the niche
11. There are no rules concerning whether a species is invasive or not; it all happens by chance

nor theorising, although they are great fun, is a substitute for the hard work of case-by-case reasoning'. That comment arose from asking 34 experienced field ecologists writing on the Australian environment and their individual specialised fields within this to appraise a series of 11 ecologically based hypotheses dealing with invasion (Table 10.2). None of the 20 major chapters in the resulting book dealt with invertebrates but the considerable variety in levels of support for each of the various hypotheses arising from expert opinion of better understood vertebrate and plant taxa demonstrates the uncertainties involved. In some cases, hypotheses were rejected, and some authors could not address particular hypotheses even when those represented basic or traditional tenets of community or population ecology.

Two revealing outcomes were (1) each hypothesis was rejected by at least one author, and (2) other than rejections, no single hypothesis received unequivocal support. Only two hypotheses (numbers 8, 10 in Table 10.2) appeared to withstand reasonable scrutiny but even they were occasionally rejected – and the thoughtful discussion in the concluding chapter (Prins and Gordon 2014b) is important and sobering reading in leading to their conclusion that the outcomes of invasion events are not predictable. This reflects that the interactions between populations of animals and plants in natural communities are too complex to necessitate any regular or predictable outcome when a new species is introduced. Field research may be the most important avenue toward improving this situation.

A comment by Komdeur and Hammers (2014) that ‘Any species could, in principle, establish successfully somewhere, but some species are more successful than others. It is of great interest to conservation biologists to identify which species have a greater chance of successful establishment’ encapsulates much of the thought and effort attending modern studies of invasion biology. The variables outlined in Chap. 4, linking with the hypotheses noted above, display the difficulties of doing this reliably or consistently.

No species’ range in an area in which functional dispersal is possible is likely to be static, except in relation to limitation by distribution of more static critical resources. Most native species continually expand or change their distribution range as conditions alter and, paralleling true alien invaders, can enter novel areas and ecological communities in ways that are not conventionally regarded as ‘invasive’. Over recent decades, such local distribution changes attributed to climate change have been reported in many groups of organisms. The northward movements of Lepidoptera and Odonata in Britain, for example, have been studied in considerable detail (below) and are paralleled by less effectively documented southward range changes in Australia and elsewhere in the southern hemisphere. Some such movements are accompanied by corresponding vacation of range at the other extreme, again as conditions change. Accompanying range changes, invasive species may undergo substantial changes to their developmental patterns in a new environment as they adapt to new climates and ecological contexts, sometimes with changes in voltinism and diapause regimes.

10.2 Climate Change

The gradual elevational and latitudinal shifts in native species’ distributions attributed to climate change are an increasing focus in conservation, as new associations and interactions occur and can parallel those associated with more ‘conventional’ alien invasions. Putative influences of global warming reflect the widespread scenarios that temperature and precipitation are important determinants of species’ regional distributions through influences on physiological parameters, and set limits to elevational and latitudinal ranges of many taxa (Wilson et al. 2007). However, firmly establishing any such causal link between range limits and climatic factors is difficult: as Gaston (2009) noted, relevant evidence may take the form that conditions that exceed levels within the current range preclude completion of the normal life cycle or impose excessive mortality. Experimental studies on the Pine processionary moth (*Thaumetopoea pityocampa*, Notodontidae) are one of few examples of attempts to link range expansion with increased winter temperatures marking climate change (Battisti et al. 2005), highlighting need to explore such trends for species that may require management as their range expands and, in some cases, indicating the urgency and relative priority amongst invasive species.

There is little doubt that climate change (broadly 'global warming') has enabled many alien species to expand their ranges and rates of invasion. In surveying the themes involved, Walther et al. (2009) noted (1) new opportunities for introductions; (2) facilitating colonisation and reproduction; and (3) enabling population persistence and spread. However, additional complications occur, and can hamper clear interpretation of how such changes eventuate. Some European insects, for example, have both spread gradually northward as warming occurs and also now occur in isolated populations far 'ahead' of the natural diffusive spread as a result of human-aided dispersal.

A practical problem in dealing with climate changes is simply that many effects are relatively long-term and difficult to predict or evaluate, so that needs for any attention or management may not become clear until after change is well-entrenched. The complex implications of climate changes for invasive species can create very different concerns from those for non-invasive species, with those concerns centering respectively on control or conservation (Hellmann et al. 2008), and additional species possibly becoming unwanted invasives. From the sequence of well-defined stages of the invasion process (Chap. 3), Hellmann et al. discussed five possible consequences of climate change as (1) changes to mechanisms of transport and introduction; (2) changed climatic constraints on the invading species; (3) changed distributions of existing invasive species; (4) changed impacts of existing invasive species (including biocontrol agents); and (5) changed effective management strategies for those invasive species. Applicable to many different taxa, and not mutually exclusive, these changes are unified through impacts of any invasive species being a result of range size, average abundance over that range, and per capita (or per unit biomass) impact – so that significance to any native species reflects the size of the native population or scarcity of the native resources as affected by climate change (Fig. 10.1).

Most discussion of range changes with climate has focused more on details of individual species rather than aspects of 'invasion' and impacts in the extended, previously unoccupied area. A major exception is the importance of 'climate matching', using CLIMEX or some other model in seeking and introducing classical biological control agents (Chap. 6), exercises that clearly endorsed that climate tolerance and suitability is essential to establishment success. However, the four general conclusions on insect conservation in a changing climate made by Wilson et al. (2007) (Table 10.3) all raise issues of very wide concern. Not least, and as recognised widely by others, the contrast in responses between generalist and specialist taxa parallels some characteristics of 'more invasive' versus 'less invasive'

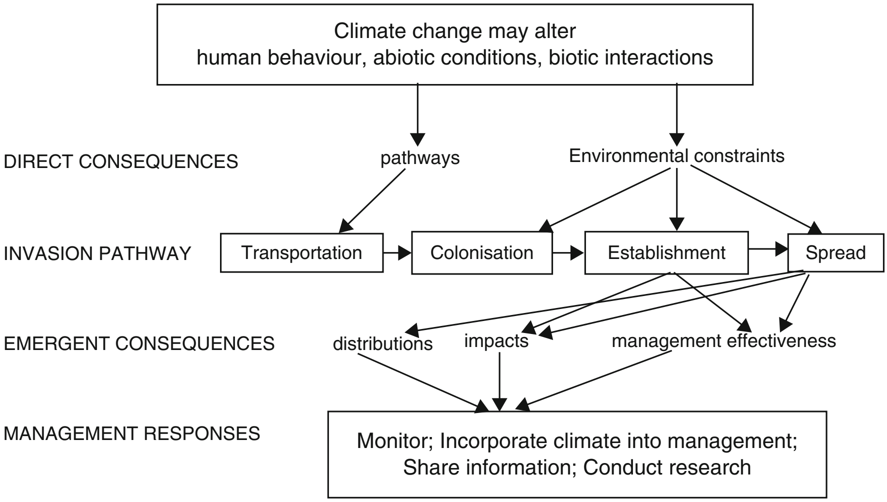

Fig. 10.1 Relationships between invasion pathway and the five consequences (see text) for invasive species under climate change (Based on Hellmann et al. 2008)

Table 10.3 The four general conclusions relevant to insect conservation in a changing climate, as listed and discussed by Wilson et al. (2007)

1. Climate change disproportionately threatens species with small or isolated populations or distribution sizes, narrow habitat requirements (or narrow distribution of resources in space or time) and poor dispersal abilities
2. Priority conservation management may be required in habitats or regions whose biodiversity is particularly sensitive to the effects of climate change
3. At regional scale, landscape-scale habitat management of reserve networks and the wider environment will be important both to maintain current populations of species and to increase their likelihood of colonising locations or habitats that become more favourable
4. The maintenance of habitat heterogeneity at local and landscape scales may favour species' persistence: (1) habitat associations of species change with climate over time and over geographical range, so that provision of a variety of habitats/mutualists allows species to exploit conditions that are the most favoured at a particular time; (2) habitat heterogeneity may act as a buffer against extreme conditions, allowing populations to survive when other places become unfavourable

species in other contexts. Wilson et al. noted that widespread generalist species at their cool range margins commonly expand their distributions, whilst localised ecologically specialised species and those at their warm margins have declined. Promoting landscape heterogeneity may both assist colonisations of newly-favourable areas and conserve the species elsewhere. Climate change is most likely to increase threats to those specialised or restricted species that are already of conservation concern.

Ecological influences of climate change, examined in a pioneering book by Dennis (1993), reflect the complexity of understanding the mechanisms and processes that underlie how an insect may adapt as its 'comfort zone' changes. New physical and biological environments, changed resource supply, enforced novel interactions, likely changed phenology and risks of lost synchrony with food supplies, and many other factors intervene. Imposed continued range modifications, however, are inevitable for many taxa. Species' responses encompass biogeographical, phenological, physiological, behavioural and genetic changes, each with implications for the fitness and survival of the individual species and the ecosystems it either enters or leaves – and one common difference from many 'traditional invasives' is that part of an occupied distribution may be vacated, a circumstance that might facilitate establishment of further invaders there.

Britain has proved an ideal arena in which to explore such changes, for reasons that largely parallel other initiatives in advancing insect conservation within that fauna. Those reasons include (1) broadly, all species are named and identifiable, with popular diurnal groups of Lepidoptera and Odonata extremely well documented in relation to many other places; (2) for most, a strong historical record of species incidences and distributions over at least a century, often more, provides clear baseline information against which change may be appraised; (3) the development of recording schemes based on standard mapping units (10×10 km^2) and to which numerous volunteer naturalists contribute records to centrally coordinated data bases (such as the United Kingdom Biological Records Centre), with standardised methodology allowing for strong quantitative inferences (Pollard and Yates 1993) and through which evidence of seasonal and abundance changes can also be assessed; and (4) a limited fauna contains many species on the northward fringe of their European range, in a region with room for them to expand northward into areas known to be unoccupied previously, so constituting a dynamic frontier for changes as climate warming occurs. Recent discussions confirm the widespread reality of changes, with extent, rates and species-specific responses all variable. The changing status of Odonata in Britain shows arrival of several novel species in recent years, some with their major distribution in the Mediterranean regions of southern Europe (Parr 2010). The pattern for *Anax parthenope* (Aeschnidae) recorded by Parr illustrates the more general pattern of (1) initial unsubstantiated record in the mid-1980s; (2) substantiated record in 1996; (3) annual records thereafter accumulating to several hundred individuals over the next decade or so, most of them migrants but with record of successful breeding; and (4) record numbers seen in 2006, with oviposition at at least five sites, as a clear colonist that has continued to thrive. Many species are currently undergoing range changes, mostly expanding to the north and west, and parallel phenological changes are evident, with emergence earlier in the season.

Mason et al. (2015) concluded that, self-evidently, resource and wider habitat suitability and availability are critical in an expanding range, but it is often unclear how other range-determining factors – such as natural enemies and competing species – influence differences observed between broader taxonomic groups. Closely related species can differ greatly in their responses to different aspects of climate change and linkages to key resources. Local rates of change produce idiosyncratic responses that may link with abundance and habitat availability, but most impacts of gradually range-expanding species are unknown, with most studies exploring rates

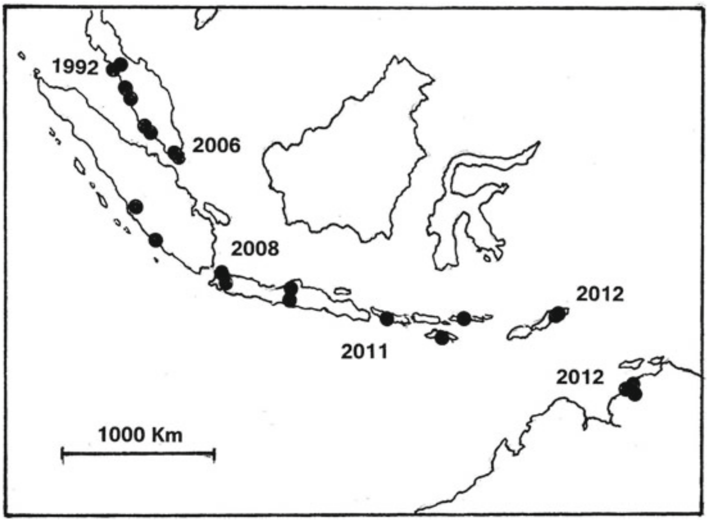

Fig. 10.2 The changing distribution of the butterfly *Acraea terpsicore* in south-east Asia and reflecting its invasion of northern Australia, indicating known locations (*black spots*) and years of first detection from Malaysia to Australia (Braby et al. 2014)

and extent of changes, rather than possible invasive impacts and resultant faunal changes. It can be difficult to distinguish relative roles of climate and habitat changes in such expanding ranges that clearly occur along possible climatic gradients.

The Tawny coster butterfly (*Acraea terpsicore*, Nymphalidae) was first recorded in Australia in April 2012, and has spread rapidly (Braby et al. 2014). Native to lowland areas of India and Sri Lanka, the butterfly has become widely distributed in much of south east Asia, thence in Indonesia and subsequently arriving in northern Australia; this progressive range expansion is summarised in Fig. 10.2. As with *Danaus plexippus* (p. 41), the mechanisms of this expansion are not wholly clear, and Braby et al. indicated at least three possible hypotheses as (1) accidental recent introduction to IndoChina from India; (2) natural expansion from India to colonise Thailand via Myanmar; and (3) it has always existed there but in low numbers, and has become more abundant as the degraded habitats favoured by larval food plants, have increased. Braby et al. suggested that this habitat modification may be a key influence, not least because the most frequented environments in Australia are highly modified open areas, including disturbed grassland and degraded savanna woodland. That biotope form, together with climatic suitability, are key features for the predicted future spread of *A. terpsicore* in Australia, to potentially occupy much of northern Australia and some north eastern coastal areas of Queensland.

The recent extensive spread of the Yellow-legged hornet (*Vespa velutina*, p. 40) in Europe is likely to increase markedly as climates increase in suitability (Barbet-Massin et al. 2013), mainly into parts of central and eastern Europe. In those regions, increased hornet predation on honeybees and other pollinators (such as Syrphidae) could become a serious concern. Barbet-Massin et al. emphasised that bee-keeping activities could become under severe threat in this expanded hornet range, with considerable disruption to plant-pollinator interactions.

Use of models to predict climatic changes and their influences on distributions of invasive species has developed rapidly, and with increasing sophistication, as a tool in anticipating management needs, with finer details reflecting the methodology used in extrapolation. Thus, two studies on the Australian Bronze bug (*Thaumastocoris peregrinus*, Thaumastocoridae) using different climate modelling schemes (CLIMEX: Saavedra et al. 2015; WorldClim 1.3: Montemajor et al. 2015) both forecast considerable future spread of the bug, largely in association with *Eucalyptus* plantations, but with some differences in detail of likely intensity of invasion across the largely overlapping predicted ranges. Many such models involve predictions of a suitable 'bioclimatic envelope', but many are based on uniform increases of temperature or precipitation levels, which may render them over-simplistic (Mika and Newman 2010).

10.3 Moving Species Deliberately

Natural modifications to range due to climate change are generally a very gradual process. Deliberately moving insects is a recognised component of species conservation, most commonly in the form of 'translocations' to enhance small populations or to re-introduce species to restored secure sites within their native range. The process can be very complex, and decisions over numbers, stages, season, and methods needed to maximise chances of success parallel those inherent for introducing classical biological control agents – but, most commonly from the basis that the species' biology is reasonably well understood, and that the operation is taking place within its current or recently historical range (New 2009). The context is fundamentally 'non-alien', but similar conservation considerations have led directly to more distant movements based on 'assisted migration' for insects (notably, some butterflies), expanding the principles of conventional translocations, to move species to places outside their historical distribution range, where they function essentially as aliens introduced into novel environments that are anticipated to increase their chances of survival as currently occupied areas become unsuitable because of climate changes. For some species confined to small or isolated vulnerable habitat patches and that are unable to track landscape changes themselves, this may be the only viable conservation option, but may not always be possible, not least because of regulatory restrictions (Shirey and Lamberti 2010). One proposed case tacitly raised the issue of defining 'historical range', with considerations of the feasibility of bringing back to Britain two species of butterflies that became extinct there early in the twentieth century (so are not part of the current fauna), but have remained in mainland Europe and where they are currently declining (Carroll et al. 2009). That case could provide valuable experience for later assisted migrations of other European butterflies, never known to be resident in Britain, to follow (Thomas 2011). Increased understanding through both climate modelling outcomes for relatively local transfers (Carroll et al. 2009) and experimental transfers (Willis et al. 2009) of butterflies in Britain illustrate many of the consequences that must be considered for geographically wider exercises.

Such assisted movements, however, could lead to new problems if the focal species becomes invasive or significantly outcompetes previously resident species in their newly expanded range (Mueller and Hellmann 2008). That risk may generally be small, but could occur at various scales – from relatively short-range to intercontinental transfers. As Mueller and Hellmann put it ‘Assisted migration is a drastic solution to a pressing problem’, with some opinion that any such operation has potential for some disruption to the receiving systems, as for any ‘proper’ invading species. In general, success rates for insect translocations, of any sort, are low – a feature suggested to reflect a combination of inadequate awareness of species’ biology and selection of release sites (Heikkinen et al. 2015). As in more typical invasions, factors such as propagule pressure and receiving site quality may be critical, with a key practical consideration being whether to spread a limited number of foundation individuals across several new sites or focus on a single site with a larger innoculative population. In either context, prior enhancement of critical resources is likely to be beneficial both in facilitating establishment and enabling population increase and subsequent spread across the new landscape.

Assisted migrations, and indeed other translocations, have potential to separate co-dependent or mutualistic species (Moir et al. 2012). Whilst presence of suitable host plants for insect herbivores is an obvious need, hosts for associated parasitoids with unknown wider host ranges may not be so, as wider constituents of the relevant community. The focal species itself is clearly the primary focus of any assisted migration exercise, with the complications of changes to multitrophic interactions often neglected – in many cases necessarily so through lack of knowledge. Monitoring and evaluation is a clear need. The wider perspective of consequences and strategies generated by the dual considerations of individual species wellbeing and restoration of ecological process as motivations for assisted migration (Lunt et al. 2013) may be assessed in relation to three contrasting approaches (Fig. 10.3). The most familiar context for insects (and most other taxa) is of a species threatened by climate change being moved to one or more recipient sites where survival is predicted to be higher as conditions change, and the taxon sustained for the future. For ecosystem processes, one or more taxa are transferred to a recipient site to sustain or restore a process or function that has declined with climate change or loss of provisionary species. The two outcomes may be achieved together if transfer of a threatened species also restores declining ecosystem services in the receiving site. These options have been termed ‘push’, ‘pull’ and combined ‘push and pull’, respectively (Lunt et al. 2013). Expectations of ecological impacts from any imported species could also constitute some acceptance of risk. However, those same ecological benefits, enhancing a wide range of processes and taxa, may also grant them priority over single threatened species conservation if costs are similar and the risks considered acceptable.

Other contexts for ‘moving species’ occur, and can create controversy. Much commercial apiary in Australia, for example, depends on migratory bee-keeping,

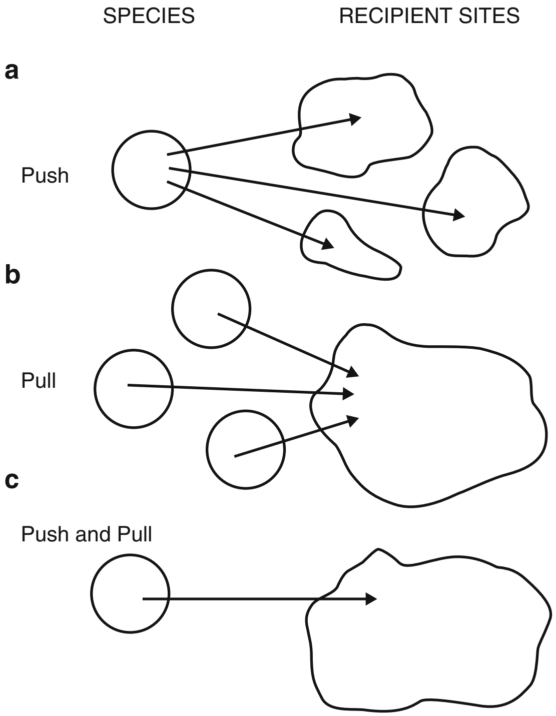

Fig. 10.3 Three forms of assisted colonisation: (**a**) specific species assisted colonisation: a specified taxon threatened with decline under climate change is moved ('pushed') into one or more receiving sites where future persistence is predicted to be high; (**b**) ecological replacement assisted colonisation: one or more taxa are relocated ('pulled') to a specific receiving site to maintain or restore and ecosystem process/function that is declining there due to climate change; (**c**) assisted colonisation used to 'push' a threatened taxon into a receiving site, but this also restores and ecosystem process/function that is declining due to climate change, so achieving the joint outcomes anticipated from the previous two options, so 'push and pull'. Primary motivations are concerns for the source species (**a**), receiving site (**b**) or both (**c**) (After Lunt et al. 2013)

through which hives are shifted to track seasonal nectar supplies. Because of denudation of many natural landscapes for agriculture, pressures have increased to site hives in national parks and other areas where native flora continue to thrive and these pressures have provoked strong dissension between bee-keepers whose livelihoods depend on assured nectar supplies and conservationists who see the intrusion of aggressive alien honey bees likely to induce competition with native pollinator species harboured in those reserve areas whose existence is founded in a conservation role. The arguments are complex (Paton 1996), but regulations in each relevant State impose considerable restrictions on unfettered access, through licensing only limited sites within protected areas. As the New South Wales National Parks and Wildlife Service (2002) commented 'The impact of bees may need to be considered in areas of identified critical habitat or threatened species or communities', and relocation of hives to more suitable areas undertaken should known threatened species be susceptible to activities of foraging honey bees.

10.4 Information

Earlier chapters have exemplified widespread uncertainties over all stages of alien species invasiveness and of the impacts of many alien species in the receiving environments. Whilst the impacts of some are indeed clear, and salutary warnings of harm to native insects that might befall from other alien species, documenting and monitoring the trajectories and effects of a wider array of invasive plants and animals is a key conservation need, in providing fundamental information to managers. Gathering and summarising information on invasive species, and making that information available through centralised databases is a continuing need and key component of monitoring and managing those species, with each phase of prevention, surveillance and response, and control and eradication drawing on such information. As with the British 'Great Britain Non-Native Species Information Portal' discussed by Roy et al. (2014), inventory can increase awareness of the impacts of invasive species, indicate their relative presence and impacts in different biotopes, and contribute to the chronological and biological knowledge that enables those roles to be clarified and, where necessary, countered. Britain's long history of biological monitoring imparts that scheme considerable reality and, at the end of 2011, insects were clearly the most numerous invasive animal group (344 species), although still well behind higher plants (1376 species), a significant component of the total 1958 established non-native species recorded.

Widespread lack of knowledge generates uncertainty, and has led to statements such as 'Uncertainty is at the root of the precautionary principle, not theory' (Prins and Gordon 1914a), in urging protection for Australia against invasive species because 'we do not know whether we will lose wonderful native species if alien species are allowed to invade'. Although insects are not conventionally recognised amongst the 'wonderful native species' (except by entomologists!), many are indeed amongst the most vulnerable native taxa to many alien invaders. The sentiment expressed by Prins and Gordon extends far beyond Australia, to embrace ecologically specialised endemic species of many parts of the world.

10.5 Concluding Comment

The seemingly endless taxonomic and ecological variety of alien species renders any suggestions on their overall impacts on native insects tentative, and perhaps superficial and naïve. Many aliens, viewed initially as disruptive threats, may prove to be critical supplementary resources augmenting or replacing those already lost to transformations such as urbanisation (New 2015), in areas where the roles of even a few alien species can appear pervasive. Each alien species that invades a new environment may potentially affect the dynamics of the receptor community, influence the composition of local food webs, and induce losses of native species. However, because many such changes are context-specific and site-dependent, predicting outcomes is highly unreliable.

Thus, the significance of use of many of the diverse non-native plants by native insects in urban 'green spaces' is very difficult to interpret. Their use as food by larval Lepidoptera, discussed by Burghardt et al. (2010), does not itself clarify whether those alien plants are the 'ecological equivalents' of native species they have replaced in local food webs – and several studies cited earlier demonstrate the differing levels of consumer fitness that may ensue. The thesis advanced by Burghardt et al., based on studies of the Lepidoptera of Delaware (United States) and noted for urban landscapes by New (2015), reflected the relevance of taxonomic relationships between alien and native plants: Lepidoptera laid eggs and larvae fed on congeneric alien plants (which may be linked by common chemical features) more often than on alien plants not related to native hosts. However, there is little doubt that continued adoption of alien host plants by native insect herbivores (1) contributes to homogenisation of faunas (for butterflies, demonstrated by Graves and Shapiro 2003), and (2) may facilitate invasions of additional plant and consumer species. Shifts within local food webs are augmented by increasing numbers of alien species – leading to increased expressions of concern for ecologically specialised native insects, most fundamentally (1) herbivores existing in small localised populations (or metapopulations) that become increasingly vulnerable to losses of their restricted natural hosts, or to the competitive impacts of adaptable native species on those hosts, and (2) the changed prey or hosts of natural enemies, whether these are deliberately or accidentally presented.

Highly anthropogenic environments are traditionally considered those most vulnerable to alien species invasions – and are those in which such species come most readily to notice, and where their impacts are most obvious and best documented. However, few – if any – more natural terrestrial or freshwater environments have escaped some level of alteration from, especially, invasive insects or plants, and the interactions between these – with both each other and higher level alien or native consumers and in some cases leading to considerable wider impacts on native communities and ecological processes. In short, alien invasive organisms are universal, inevitable and many are essentially harbingers of permanent changes, often to the detriment of native biota in the invaded environments. Conservation of native insects, many of the species signalled as high priority, ecologically specialised and vulnerable to the onslaughts of more adaptable generalists (typified by many invasive species), inevitably confronts alien influences at both individual species and wider community levels. Most concerns from invasive aliens arise from more generalised species, for which vagaries in outcomes from individual circumstances are largely irrelevant in view of their pervasive adaptability – and from which chances of adverse or undesirable non-target impacts are greatest, often augmented by good dispersal powers and large numbers of invaders.

The lessons from pest management and allied ‘applied’ disciplines involving alien species furnish much of the scientific understanding on which practical conservation actions can be founded, and alien species’ impacts on native insects understood and countered. Whilst many direct impacts are intuitively obvious, although commonly far more difficult to quantify, the complexities of many more indirect effects, such as changes to complex native food webs, are more insidious and can often be only inferred. Suppression or eradication of invasive aliens is advocated commonly but, again, can pose complexities – such as introductions of further aliens (biological control agents) with likely or possible further harmful effects. Whilst many concerns over such practices have been raised, and ‘general rules’ to assure safety pursued sincerely and diligently, the great differences between impacts of the same species in different receiving environments and between different species in the same or similar environments ensure that some element of risk may remain, or be perceived. ‘Threat’ from alien invasive species is a very widespread supposition. In concert with direct losses and changes to habitats and erosion of critical resources needed by specialised native insects, alien insects and plants (in particular) are frequently associated with such disruptions as facilitating environments for those invasives are progressively created. The twin features of habitat change and invasive alien species are major contributors to accelerating onset of the Anthropocene. The overviews in this book of some key themes relevant to insect conservation reflect the complex and pervasive processes that attend invasions by alien species and their parts in leading toward biotic homogenisation accompanying the largely unheralded losses of numerous insect species and associated disruptions of intricate and long-coevolved ecological dependencies.

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