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*,
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> 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

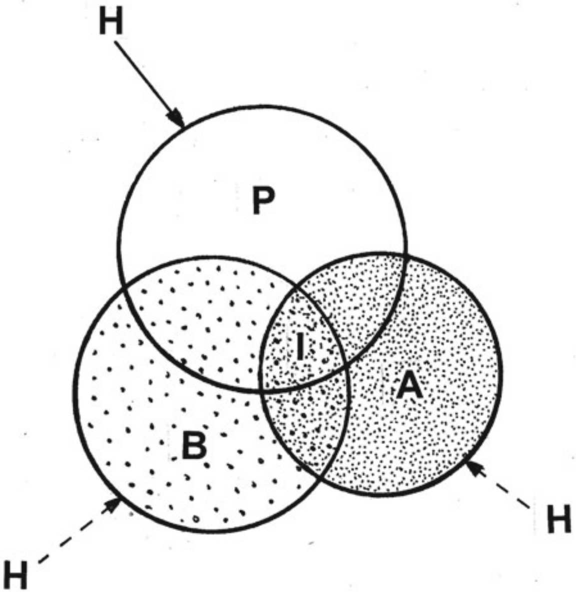

Fig. 3.1 Propagule pressure. Schematic diagram to illustrate how propagule pressure (*P*), abiotic characteristics (*A*) and biotic characteristics (*B*) interact to drive invasion (*I*, which occurs when the above three interact), and how humans may modify each factor (*H*). The strength and extent 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

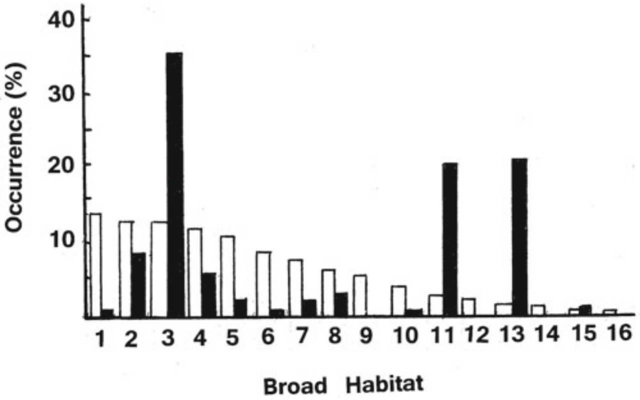

Fig. 3.2 Habitat distributions of alien (*black bars*) and native (*open bars*) plant species across the broad habitat types found in five study regions in England. The regions, each of 3600 Km^2, encompassed northern, southern, eastern, western and central areas, and data are based on the New Atlas 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 countryside (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-

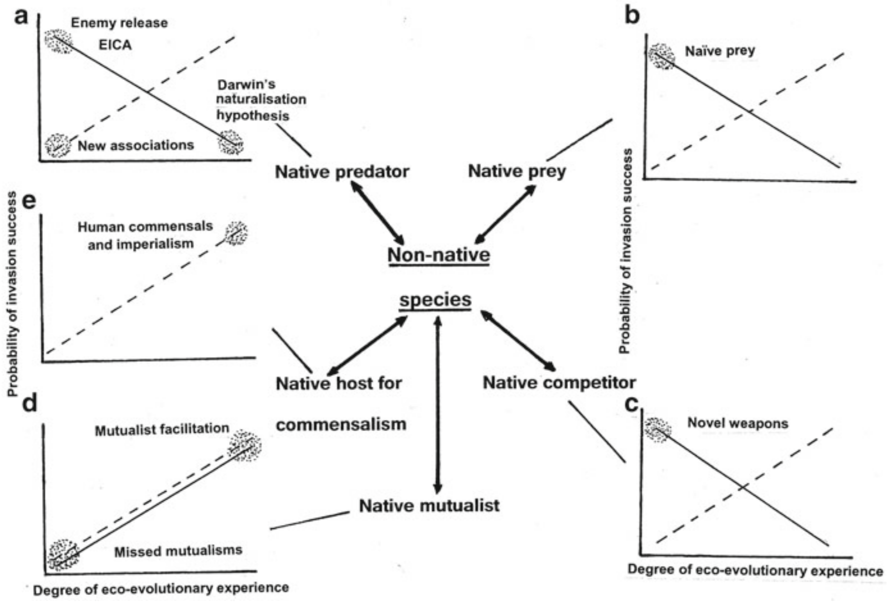

Fig. 3.3 Five hypothetical scenarios on the influences of eco-evolutionary experience in non-native (*dashed line*) and native species (*solid line*) on probability of invasion success, according to the kind of ecological interaction. Interactions are: (**a**, **b**) predator-prey; (**c**) competition; (**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

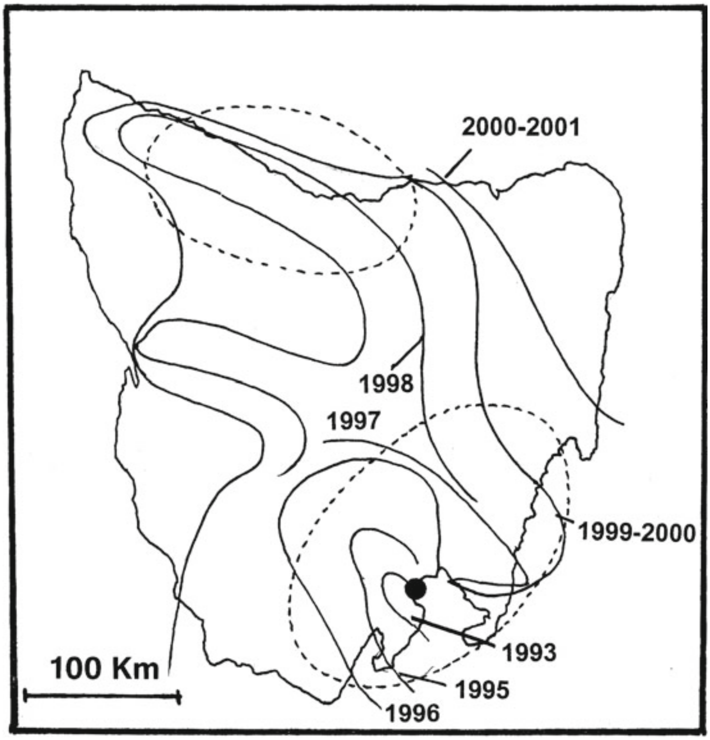

Fig. 3.4 Outline map of Tasmania to indicate range expansion of the bumble bee *Bombus terrestris*, plotted from historical records from its arrival (first sighting in Hobart 1992, site shown by *black spot*) to summer 2000–2001. Different *year numbers* indicate records in new areas for time indicated;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

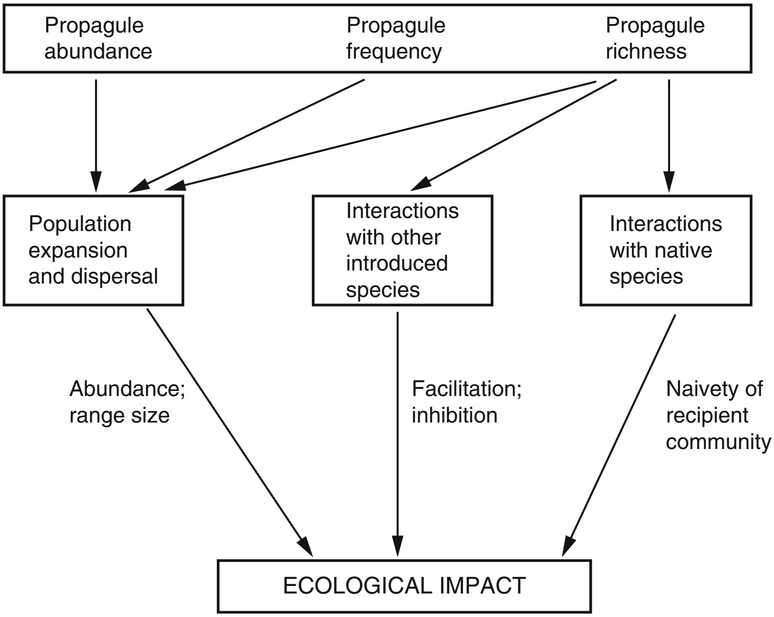

Fig. 3.5 The interactions between three components of propagule pressure (propagule abundance, frequency and richness) and the population-level and community-level processes that mediate impacts of introduced species. Major processes are blocked in the centre row and some specific mediating factors or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