INVASIVE ANTS

Invasive species, those species that demonstrate ecological, environmental, or economic impacts (Colautti and Richardson 2009), are now widely recognized as one of the primary threats to biodiversity and the functioning of ecosystems, and invasion ecology has become a discipline in its own right. Though invasive ants currently comprise <1% of all known ant species, the contribution of these species to understanding ant ecology is disproportional to their number.

Invasive ants represent an opportunity to apply everything we currently know about ants to a rapidly growing problem. Fundamental to understanding invasive ants is a comprehensive appreciation of the life cycles, social structures, and ecological roles of invasive ants in the context of the environment and evolutionary processes. Indeed, the study of invasive ants has led to opportunities for exploring new (or at least newly rediscovered) lines of inquiry that apply to ant ecology more broadly: How is social structure related to dominance? What ecological or environmental factors keep dominant ants in check? And how important is evolutionary history in shaping interactions with other organisms? Moreover, invasive ants grab the spotlight of public attention like few native insects; handled in the right manner, public concern about pest species can be a stepping stone for educating the public more broadly about the importance of insects and human impacts on them.

The chapters here build on the foundations of global diversity and biogeography, and community and population ecology provided earlier in the book. The first two chapters delve into processes mediating invasion success. Chapter 13 describes the variation in modes of dispersal observed in invasive ants. Suarez, McGlynn, and Tsutsui then take a close look at the biogeography and phylogeny of introduced ants in a search for patterns of which ants become invasive. Chapter 14 explores the question of invasion success at the community and population ecology levels. Krushelnycky, Holway, and LeBrun first examine factors that affect local spread, including biotic interactions, abiotic conditions, and habitat disturbance, before discussing causes of success including competitive displacement and predation, abundance, unicoloniality, generalist habits, ecological release, and genetic changes.

The final two chapters concern the impacts and management of invasive ants. Chapter 15 summarizes the consequences of ant invasions on native ants and other invertebrates, vertebrates, plants, and soil. Lach and Hooper-Bùi call for long-term and experimental approaches, and more attention paid to indirect effects, evolutionary adaptations for coexistence, and the potential for manipulating invasions to mitigate their harm. Finally, Chapter 16 provides a brief historical overview of the techniques used in ant management programmes, and highlights lessons learned from successful and unsuccessful eradication attempts. Hoffmann, Abbott, and Davis outline a management approach incorporating pest risk analysis, public education, data collection, cost–benefit analysis, decision-making, treatment, and monitoring, and call for a more proactive approach to invasive ant management.

Throughout Part IV, authors adhere to the definitions of Holway *et al*. (2002a) in distinguishing the term 'invasive' denoting impact, from terms that refer to origin (alien, exotic, non-native, and tramp). However, today's tramp ant may be tomorrow's invasive ant. As noted across the chapters,

much of the information we have to date about the ecology of invasive ants derives from just two species: the red imported fire ant, *Solenopsis invicta* and the Argentine ant, *Linepithema humile*. Other ants may follow a different pathway to becoming invasive and researchers should remain open to finding new patterns to explain their success and impacts. We still have much to learn.

Chapter 13

Biogeographic and Taxonomic Patterns of Introduced Ants

Andrew V. Suarez, Terrence P. McGlynn, and Neil D. Tsutsui

13.1 Introduction

One of the many goals of invasion biology is the identification of factors that determine whether a species will establish successfully in a new environment and that predict whether a newly introduced species has the potential to become highly invasive. Most research in this area has focused on species-specific attributes that may convey ecological success. However, insights into these processes can also come from examining broad biogeographic and taxonomic patterns of introduction.

Introduced ants are an appropriate group for such an approach. Of the approximately 12,500 described species of ants, over 200 have established populations outside of their native ranges (McGlynn 1999b). Of these, many have become highly destructive invaders, and five (the Argentine ant *Linepithema humile*, the big-headed ant *Pheidole megacephala*, the yellow crazy ant *Anoplolepis gracilipes*, the little fire ant *Wasmannia auropunctata*, and the red imported fire ant, *Solenopsis invicta*; see Plate 14) are currently listed among the world's 100 worst invasive species (Lowe 2000). In addition to being economically costly in both urban and agricultural areas, invasive ants can greatly modify ecosystems by reducing native ant diversity, displacing other arthropods, negatively affecting vertebrate populations, and disrupting ant–plant mutualisms (see Chapter 15). Although hundreds of ant species have become established outside of their native ranges, most research has concentrated on the biology of only a few species (including those

mentioned above). Despite clear insights gained from this approach, single-species treatments do not provide information on (*a*) patterns of ant species movements into new areas, (*b*) biogeographic patterns of invasion including the identification of regions that may either produce many invaders or be particularly prone to invasion, and (*c*) systematic perspectives on the evolutionary correlates of success. In this chapter, we address these three issues by first comparing natural versus anthropogenic means of dispersal in ants. We then examine broad-scale biogeographic and taxonomic patterns in ant invasions, and conclude by suggesting some areas of future research.

13.2 Patterns of dispersal in ants

13.2.1 Natural patterns of dispersal

Dispersal is a fundamentally important life-history characteristic of all organisms. The frequency, timing, and distance of successful dispersal determine the ability of species to colonize new areas and, in some cases, the survival of geographically isolated populations. Moreover, gene flow among populations via dispersal is a key determinant of their underlying genetic structures. In most organisms, dispersal distance distributions are 'leptokurtic' in shape – most new individuals settle relatively near where they originated but a few may disperse longer distances (Case 2000; Kot *et al*. 1996). However, patterns of dispersal can vary substantially among organisms, depending on a multitude of

intrinsic and extrinsic factors including the mode of dispersal, nutrition, social structure, competition, and predation (Shigesada and Kawasaki 1997).

Normally, ant colony structure and social organization are intimately related to patterns of dispersal (reviewed in Bourke and Franks 1995; Hölldobler and Wilson 1990; Wilson 1971). In many ants, reproduction occurs via the production of winged alates that mate away from their natal nests. In contrast to species that undergo mating flights, virgin queens of other species mate within their natal nest with males that have been produced locally, from within the same colony, or from nearby colonies. This type of reproductive behaviour is particularly prominent in invasive ants (Passera 1994; Chapter 14), and ants with intranidal mating are expected to be genetically homogeneous within colonies, but highly genetically differentiated across colony boundaries, even at relatively small spatial scales (Pedersen *et al*. 2006).

In many cases, colony reproduction in species with intranidal mating can occur via dependent colony foundation, or colony budding (see Chapter 9). Budding occurs when a subset of a colony's population (tens to thousands of workers, one to hundreds of queens) disperses away on foot to a new location and becomes established as a separate colony elsewhere. Examples of species that reproduce by colony budding include many of the most widespread and damaging invasive ants, such as *A. gracilipes*, *L. humile*, *P. megacephala*, *W. auropunctata*, *Monomorium floricola*, *M. pharaonis*, *Tapinoma melanocephalum*, and the polygyne form of *S. invicta* (reviewed in Holway *et al*. 2002a and Wilson 1971).

During the spring, male and female alates are produced within *L. humile* colonies, as occurs in many species of ants. Although the female alates possess well-formed wings, curiously, they cannot, or do not fly and mate in their natal nest almost immediately after eclosion. Males, on the other hand, are clearly able to fly and, under appropriate conditions, large numbers of males can be observed aggregating at nest entrances and departing on the wing. These observations are confirmed by the presence of male Argentine ants at lights and in pitfall traps placed hundreds of metres from the nearest Argentine ant colony (A. Suarez, unpub-

lished data). However, it is unknown if these dispersing males ever successfully enter other colonies and mate. Colony budding in *M. pharaonis* is reviewed in detail by Wilson (1971), and this description closely matches the reproductive patterns displayed by *L. humile*.

13.2.2 Variation in modes of dispersal, an example with *S. invicta*

While many introduced ants are polygynous and reproduce primarily by dependent colony foundation (see Chapter 14), this is not the case with monogyne populations of the red imported fire ant, *Solenopsis invicta* (reviewed in Tschinkel 2006). Under suitable conditions (warmth, high humidity, low wind), most often in the spring, mature monogyne colonies of *S. invicta* release reproductive males and, a short time later, the reproductive females. The reproductives fly to great heights of 50–100m (Markin *et al*. 1971), find each other via behaviours that are unknown, and mate. Newly mated queens may then descend immediately to the ground or fly some distance, typically downwind, before landing. New colonies may be founded by individual queens (haplometrotically) or by groups of queens (pleometrotically) (see Chapter 9), but the latter revert to the monogyne form when the first workers emerge and kill all but one of the foundresses (Tschinkel and Howard 1983). Various studies by George Markin and colleagues (reviewed in Tschinkel 2006) have estimated that dispersal distances are typically on the order of hundreds of meters or, occasionally, a few kilometres. Although nuptial flights can also occur in the introduced polygyne form of *S. invicta*, they typically occur closer to the ground (2–3 m elevation) and the newly mated queens do not seem to disperse as far as monogyne queens do. Moreover, polygyne *S. invicta* colonies may also disperse by dependent foundation.

These differences in mating and dispersal between monogyne and polygyne forms of *S. invicta* are reflected in the genetic structure of these ants in their introduced range (Shoemaker *et al*. 2006). Because newly mated monogyne queens travel much farther during nuptial flights, local genetic

differentiation at maternally inherited mitochondrial loci is low or absent. Polygyne populations, on the other hand, are characterized by high levels of mitochondrial differentiation at relatively small spatial scales. At nuclear loci, however, substantial genetic differentiation is absent at a local scale for both forms because males may disperse more widely, and males from monogyne colonies can mate with queens from polygyne colonies, thus eroding genetic differences between the social forms. These population genetic differences between social forms are also evident at large spatial scales – pronounced mitochondrial differentiation, but at levels equivalent to that seen between sympatric populations, and very low levels of nuclear genetic differentiation (Shoemaker *et al*. 2006). At this larger spatial scale, genetic homogeneity, particularly at nuclear loci, likely arises in large part from the anthropogenic transport of *S. invicta* among spatially distant sites. These transfers increase the overall levels of realized gene flow among regions, thus eroding genetic differences among them.

13.2.3 Anthropogenic patterns of dispersal

Left to their own devices, ants are surprisingly poor long-distance dispersers and colonizers. As noted by Wilson (1971), prior to the advent of human-assisted dispersal, ants (as well as many other taxa) were unable to colonize many mid-Atlantic and distant Pacific Islands (see Chapter 2). Similarly, the pioneering island biogeographic studies of Simberloff and Wilson (1969) found that following the removal of arthropods from mangrove islands in the Florida Keys, ants were among the last arthropod taxa to recolonize. For invasive ants, the limited long-range (e.g. intercontinental or transoceanic) dispersal and colonization abilities of ants have been overcome by inadvertent human-assisted transport. In Hawaii, for example, there are no native ants, but about 50 ant species currently occur there, all introduced by human activities primarily in the mid-twentieth century (Krushelnycky *et al*. 2005b).

The large-scale anthropogenic dispersal of invasive ants is, in many cases, facilitated by their nesting habits and reproductive strategies. Many of these species do not construct elaborately excavated nests, but nest in superficial and/or ephemeral sites such as root masses or leaf litter, under stones, and in logs and plant debris. Moreover, many of these species are highly peripatetic, quickly absconding from sites as they become abiotically unsuitable (too dry, too wet, too hot) and colonizing new nesting sites. When coupled with human commerce and habitat alteration, these nesting habits translate into frequent human-mediated dispersal, as propagules colonize objects destined for transport to a new location. For example, ants transported to the United States and New Zealand are associated with a wide variety of commerce, but a majority of ants have been detected on plant material (Table 13.1; Suarez *et al*. 2005a; Ward *et al*. 2006). This likely reflects both the nesting habits of ants transported by humans, as well as the inspection policies of regulatory agencies that are biased towards plants and plant products.

Because many ant invaders are highly polygynous, individual colony fragments have a high probability of containing at least one fertile queen, thus increasing the likelihood of propagule viability. For example, laboratory colony fragments consisting of a single queen with as few as ten workers can be reproductively viable for *L. humile* and *P. megacephala* (Chang 1985; Hee *et al*. 2000). It is also possible that queens are not even necessary for establishment of some invasive ants. In the Argentine ant, for example, haploid eggs are present within colonies year-round; propagules containing only workers and brood can potentially establish new populations through the production of new queens and males followed by intranidal mating (Aron 2001).

New populations of invasive ants may be introduced from a single native source, multiple native sources, or from other previously established populations in other parts of the introduced range. Disentangling the history of ant invasions can therefore be quite difficult, but insight has been attained for some species by using genetic data (e.g. *L. humile*, Corin *et al*. 2007b; Tsutsui *et al*. 2001; *W. auropunctata*, Mikheyev and Mueller 2007; *S. invicta*, Caldera *et al*. 2008; *A. gracilipes*, Abbott *et al*. 2007). One useful example is the invasive little fire ant (*W. auropunctata*), which is native to large

Table 13.1 Commerce on which ants are transported to New Zealand (NZ) and the United States (USA). Data from Suarez *et al*. (2005a) and Ward *et al*. (2006). It should be noted that these data are heavily influenced by inspection policies that may favour the quarantine of plant material.

Commodity	% of Records	
	NZ	USA
Ornamental Plants		60
Fresh Produce	47	14
Shipping Containers	22	3
Personal Items	16	1
Vehicle	11	1
Timber	4	4
Other*		17

*Including soil and other plant materials.

portions of Central and South America. Phylogenetic analyses show that native populations fall into two major clades (Mikheyev and Mueller 2007); one is primarily distributed throughout Central America and the Caribbean, while the other is distributed throughout mainland South America (although some Brazilian populations fall in both clades). Introduced populations are also distributed across these two clades, indicating that multiple propagules have originated from different parts of the native range and have become established in different parts of the introduced range (Mikheyev and Mueller 2007).

The Argentine ant is another well-studied example. The spread of this invader occurs via two discrete modes: (*a*) dependent colony foundation, by which colonies advance at the rate of tens to a few hundred metres per year (Holway 1998b; Sanders *et al*. 2001) and (*b*) human-mediated jump-dispersal, which results in rates of dispersal three to four orders of magnitudes higher than by budding (Suarez *et al*. 2001). Current evidence suggests that some introduced populations may trace their ancestry back to different source populations in the native range. For example, some populations of *L. humile* from South Africa, Hawaii, and California are genetically distinct from other introduced populations, in terms of both allele identity and frequency at microsatellite loci (Tsutsui *et al*. 2001). However, the immediate source of most introduced populations is likely another previously established population (Corin *et al*. 2007b). In the southeastern United States, for example, almost

every steamboat arriving at New Orleans and Baton Rouge in 1916 was infested with Argentine ants, as were many ports and rail stations (Barber 1916). Although Argentine ants are inherently slow dispersers (Holway 1998b; Sanders *et al*. 2001), through close association with humans they spread rapidly and discontinuously throughout the twentieth century, establishing themselves in at least 23 states in the United States and 35 countries worldwide (Roura-Pascual 2004; Suarez *et al*. 2001; Wetterer and Wetterer 2006).

13.3 Biogeographic patterns of ant invasions

13.3.1 Origins and exchange of introduced ants

Records of faunal exchange and invasions of ants date back to the European colonial era (Wilson 2005). Though many species of ants have been moved around the world, and new species continue to become established, only a small fraction of transported ants have become invasive (McGlynn 1999b; Suarez *et al*. 2005a). Biogeographic patterns in ant introductions show a number of clear trends (Figure 13.1). Like many other taxa, ants typically become established when introduced to a region different than from where they originated (Williamson 1996). Oceanic islands, with depauperate or absent ant faunas, have received the greatest number of introduced ant species by far. The tropical and subtropical
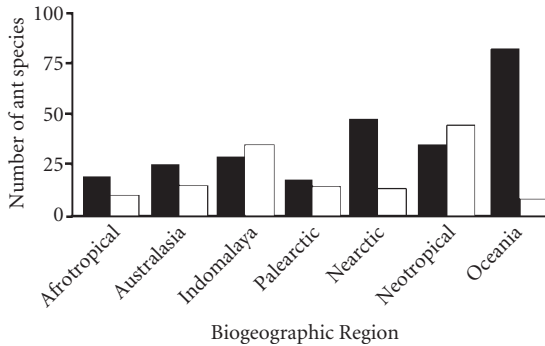
Figure 13.1 The number of introduced ants that have either become established in (black bars) or have originated from (open bars) each major biogeographic region (data from McGlynn 1999b). Notably the Oriental and Neotropical regions have exported more species than they have received. However, it should be noted that this pattern could be biased due to variation in sampling effort and taxonomic knowledge of the ant faunas among regions (Rackzkowski and Wenzel 2008).

regions of Australia host a number of invasions, but few invaders have been derived from the exceptionally diverse native ant fauna of this region. Likewise, North America has received many foreign ants, though ants originating from North America have apparently not established populations anywhere other than in Hawaii (McGlynn 1999b). The single region that has produced the greatest number of invaders appears to be South America. Palearctic and Indomalaya regions, according to existing records, have produced and received equivalent numbers of invaders. Currently, too little is known about the status of ant invasions in Africa (particularly north of South Africa) to meaningfully comment.

Because ant taxonomy and sampling are biased across regions (e.g. Dunn *et al*. 2007d; Raczkowski and Wenzel 2008), it is not clear how much inference can be made about these patterns at this point. The origin of multiple invasive species in central South America suggests either patterns of trade that are conducive for transporting ants, or that environmental conditions there may favour the evolution of species with a tendency for invasiveness. Behavioural experiments on interspecific competition in this region suggest high rates of general behavioural dominance and competitive interactions among ants (LeBrun *et al*. 2007). More-

over, a number of successfully introduced ants are native to and occur sympatrically in the seasonally inundated floodplains of the major rivers systems of northeastern Argentina, southern Paraguay, and Brazil including *L. humile, S. invicta, S. richteri, W. auropunctata, Brachymyrmex patagonicus*, and *Pheidole obscurithorax* (LeBrun *et al*. 2007; Wild 2007a; Table 13.2). It is possible that the adaptation to disturbance in the form of flooding, coupled with the species-rich and competitive environment may select for characteristics that allow species to do well in anthropogenically disturbed areas. The identification of other areas with similar characteristics (e.g. highly competitive environment (Andersen 1997) and natural disturbance regimes), coupled with better knowledge of the native ranges of introduced ants, is still needed to determine if specific regions can act as crucibles for creating potential invaders.

Since the latter half of the twentieth century, there are no examples of new, widespread (e.g. across many biogeographic regions), highly invasive ant species, even though this era has seen a major expansion in global trade that typically facilitates the emergence of invasions (Hulme 2003; Perrings 2005). However, it should be noted that many species not previously recognized as highly invasive (including *Monomorium pharaonis, M. destructor*, and *Paratrechina longicornis*) have become threats on many oceanic islands since the Second World War. The major invasive species established prior to the midpoint of the twentieth century predominately originated from tropical or subtropical climates (Table 13.2) (McGlynn 1999b). In contrast, it is possible that in the last 25 years or so, a new class of invasive ant is emerging with the potential to eventually become as widespread as some of the aforementioned species with tropical or subtropical origins. These include species that are temperate in origin, and that predominately invade other temperate climates (Table 13.2). For example, *Lasius neglectus*, likely native to eastern Europe, has emerged as an invader in temperate Europe. In North America, *Myrmica rubra* (also from Europe) is expanding its range in the northeastern United States. Two species from Japan, *Pachycondyla chinensis* and *Tetramorium tsushimae*, are spreading throughout the east coast of North America and the midwestern United States, respectively.

Table 13.2 The first six species listed below represent the most significant invasive ants, in terms of distribution, density, and damage to invaded environments, according to Holway *et al*. (2002a). All were invasive prior to 1900, except *S. invicta* which was first detected as an invader in the 1920s by W. S. Creighton (Wilson 1951). The bottom four species are more recently documented as exhibiting characteristics consistent with other highly invasive ant species and are largely from temperate climates.

Species	Origin
Anoplolepis gracilipes	Sub-Saharan Africa or tropical Asia
Linepithema humile	Central South America
Pheidole megacephala	Sub-Saharan Africa
Solenopsis geminata	Tropical Central and South America
Solenopsis invicta	Tropical and subtropical South America
Wasmannia auropunctata	Tropical Central and South America
Lasius neglectus	Probably Turkey (Seifert 2000, Cremer et al. 2008)
Myrmica rubra	Palearctic North Temperate Zone (Groden *et al*. 2005)
Pachycondyla chinensis	North Temperate to subtropical Asia (Nelder *et al*. 2006)
Tetramorium tsushimae	North Temperate China and Japan (Steiner *et al*. 2006)

Further evidence for this trend comes from the southern hemisphere, where approximately 20 species from temperate Australia have been detected in New Zealand (Ward *et al*. 2006). It remains to be seen how widespread these predominantly temperate species will become.

There is no overt explanation for the temporal disjunction between the emergence of tropical invasive ants and temperate invasive ants. Contemporary patterns of global commerce do not seem to be able to explain the emergence of temperate invaders. There is also a clearly documented time lag of several decades for two of the new invasive species: *P. chinensis* has been in North America for at least 70 years (Smith 1934) and *M. rubra* was introduced at least a century ago (Wheeler 1908). Furthermore, another temperate species, *Tetramorium caespitum*, which is native to Europe, has expanded its range throughout North America during the past 100 or more years, although it is not often considered 'invasive' (Steiner *et al*. 2007).

13.3.2 Using modeling approaches to understand biogeographic patterns of invasion

Species distribution models can be powerful tools for evaluating the potential for spread of invasive ants within and among geographic regions. Distribution models try to predict areas with suitable climate for the establishment or spread of species based either upon occurrence data from their native range, or other introduced populations (correlative approach), or by incorporating direct measurements of a species' response to environmental conditions (eco-physiological approach) (Pearson and Dawson 2003; Roura-Pascual and Suarez 2008).

Correlative approaches have been recently utilized for predicting the potential distribution for a number of introduced ant species including *S. invicta*, *L. humile*, and *T. caespitum* (Fitzpatrick *et al*. 2007; Hartley *et al*. 2006; Roura-Pascual 2006; Steiner *et al*. 2006b; Ward 2007a). Climate models have also been used to examine the potential distribution of ants in the face of global climate change. Scenarios that envision future increases in average global temperature generally predict an expansion of the ranges of invasive ants (Fitzpatrick *et al*. 2007; Roura-Pascual 2004; Zavaleta and Royval 2002).

In contrast to correlative (climate matching) approaches, eco-physiological distribution models base their predictions on direct measures of a species' response, in terms of growth, persistence, or reproduction, for example, to particular abiotic conditions, such as temperature and moisture (Helmuth *et al*. 2005). This approach has been applied to predict the distribution of red imported fire ants at a variety of spatial scales by examining temperature dependent colony growth and alate production (Morrison *et al*. 2004; Sutherst and Maywald

2005; Xiong *et al*. 2008). Similarly, degree-day models for colony growth of Argentine ants, based on development rates in relation to temperature, have been used to assess their potential for spread throughout New Zealand (Hartley and Lester 2003) and Hawaii (Krushelnycky *et al*. 2005a).

These modelling approaches do have some limitations. The geographic range of a species is not simply determined by abiotic suitability, but is determined by a variety of factors and processes that are often scale dependent (Wiens 1989). These are not often included in distribution models, and include fine-scale variation in abiotic conditions driven by anthropogenic disturbance (rather than climate), biotic interactions, dispersal capacity, and adaptability of the species (Roura-Pascual and Suarez 2008). Human-mediated disturbance and fine-scale changes in abiotic conditions due to land-use practices may be particularly important in determining the occurrence of introduced ants (King and Tschinkel 2006; Menke and Holway 2006) and need to be incorporated directly into modelling efforts (Menke *et al*. 2007). Despite these limitations, distribution modelling is a powerful tool for guiding monitoring efforts to help prevent the establishment of new populations of invasive species, and for identifying donor and recipient areas with similar climates that may be at high risk for new introductions.

13.4 Taxonomic patterns of invasion success

13.4.1 Taxonomic patterns of ant transportation across biogeographic regions

Most research on ant invasions has been conducted on a few widespread and highly invasive species. However, efforts to identify mechanisms of success or to establish a baseline of information that can be used to prevent future invaders hinges upon an informed understanding of the identity of species that are being transported – that is, the pool of species that have had the opportunity to become established. Only with this information can we make quantitative assessments of the characteristics that distinguish successful versus unsuccessful invaders.

A few studies have used historical records to identify the ant species that are most frequently transported by human commerce across biogeographic regions. Suarez *et al*. (2005a) found a high diversity of ants being transported by humans in the middle of the twentieth century. Identification of ants from roughly 400 separate interceptions in quarantine in the United States from 1920s to the 1970s revealed 232 species from 58 genera. Of this pool of potential invaders, only 28 species from 17 genera now occur as established non-native species in the continental United States. Moreover, the most commonly encountered ants in quarantine (species with five or more records: *Azteca* sp., *Cardiocondyla wroughtoni*, *Campanotus planatus*, *Linepithema iniquum*, *Monomorium pharaonis*, *Pseudomyrmex ferrugineus*, and *Tetramorium simillimum*) have either not become established, or are not considered among the most widespread and invasive ants in North America. Thus, these data suggest that the particular species that become the most successful invaders are not necessarily the same species that humans transport across biogeographic regions most frequently.

On the other hand, studies in different regions have reported a different pattern: the most frequently introduced species are also the most likely to establish. In New Zealand, for example, Lester (2005) found that a notoriously adept invader, *P. megacephala*, was the most frequently intercepted species, at an average of 17.67 interceptions per year.

There are several possible explanations for the different patterns reported in the United States and New Zealand. On one hand, differences in commerce and trade routes between the two countries may produce opportunities for different species to be sampled and transported (but see Table 13.1). Alternatively, the differences could reflect the different time periods examined by the studies. For example, between the periods of 1966–82 and 1997–2003, the interception rate for ants arriving in New Zealand differed across time: the interception rate for 13 species more than doubled while the interception rate for 12 other species was reduced by half. This suggests that the species pool may be homogenizing through time, perhaps as ports and other areas acting as sources for the

Table 13.3 Taxonomic composition of ants intercepted in ports of entry (POE) in New Zealand (from Ward *et al.* 2006) and the United States (from Suarez *et al.* 2005a), and of global ant species (from Bolton 1995b).

Subfamily	POE records (%)		Established (%)		Ant species (%)
	NZ	US	NZ	US	Global
Myrmecinae	36	47	54	52	48
Formicinae	30	22	7	22	27
Dolichoderinae	17	11	18	6	6
Ponerimorphs[*]	13	11	21	18	14
Pseudomyrmecinae	1	7	0	1	2
Dorylinae	1	1	0	0	1

[*]Includes taxa in the subfamilies Ponerinae and Ectatomminae.

transport of ants become dominated by fewer, ecologically dominant ant species. Future work on interception records of ants that examines temporal trends in occurrence data over long periods (e.g. 100+ years), or that contrast records within versus among regions, will be very valuable for addressing issues relating to opportunity and invasion success.

The taxonomic similarity (at the subfamily level) between ants intercepted at quarantine and ants generally suggests that ants with the opportunity to become established may be drawn from the species pool haphazardly (Table 13.3). More data are needed, however, to determine if taxonomic patterns will be evident at other levels (e.g. genera), and if taxonomic patterns are indicative of ecological characteristics that may promote success at other stages of invasions (e.g. establishment and spread). Using interception data as the basis for the examination of characteristics that promote invasion success or failure will be significant for illuminating mechanisms of success (Commonwealth of Australia 2006; Lester 2005; Suarez *et al.* 2005a). For example, many traits relating to diet, nesting habitats, and colony structure have been implicated in the success of invasive ants (see Chapter 14). How these traits interact with opportunity and propagule pressure to influence establishment remains unresolved, and provides a strong justification for the monitoring of interception data in a more scientific manner and also for the study of the basic natural history of ants generally.

13.4.2 Taxonomic/systematic patterns of success

Many characteristics, including high competitive ability, polygyny, dependent colony foundation, and a unicolonial colony structure have been suggested to promote invasion success in ants. A general description of these traits is covered in Chapter 14. However, in contrast to work conducted on invasive plants and birds (e.g. Grotkopp *et al.* 2002; Lockwood 1999), we know very little about taxonomic or phylogenetic patterns in the origin of invasiveness. While some biogeographic patterns are beginning to emerge, it is clear that success in terms of establishment and spread in new areas can emerge independent of phylogeny (McGlynn 1999b). For example, the five most invasive ant species come from the three most speciose subfamilies (Myrmecinae, Dolichoderinae, and Formicinae). Moreover, while the bulk of invasive species are in the subfamily Myrmicinae, this is not disproportionate to the species richness of this subfamily relative to other ants (McGlynn 1999b). When considering the taxonomic distribution of successfully introduced ants, we find a similar pattern to that described for ants being transported by humans above (McGlynn 1999b) (Table 13.4). Specifically, ants become established roughly proportional to how many species there are at the subfamily level. Whether this holds at other taxonomic levels (e.g. genera) remains to be seen.

A powerful approach for understanding taxonomic patterns of introduced species and uncovering the characteristics that promote invasiveness

Table 13.4 The number of ant species that have successfully established populations outside their native range and the total number of described species, by subfamily. Only subfamilies with at least one known introduced ant species are included. Data from McGlynn (1999a) and Bolton (1995b) and may not include recently discovered introduced species.

Subfamily	Number of known introduced species	Number of described species
Cerapachyinae	1 (0.7%)	198 (2.1%)
Dolichoderinae	11 (7.5%)	554 (5.8%)
Formicinae	39 (26.5%)	2,458 (25.8%)
Myrmeciinae	1 (0.7%)	89 (0.9%)
Myrmcinae	71 (48.3%)	4,377 (45.9%)
Ponerinae	23 (15.6%)	1,299 (13.6%)
Pseudomyrmicinae	1 (0.7%)	197 (2.1%)

will be to compare successful versus unsuccessful invaders in a phylogenetic context. For example, invasive ants are often unicolonial (see Chapters 10 and 14), and are also often among the smallest members of their genus (McGlynn 1999a). Mapping out these and other ecological characters onto generic level phylogenies will shed light as to which characteristics best predict the success of introduced species (see Grotkopp *et al*. 2002 for an example with pines). This approach will be particularly informative if done in conjunction with information gathered in interception data (Lester 2005; Suarez *et al*. 2005a; Ward *et al*. 2006). For example, using ants detected in quarantine in the United States, Suarez *et al*. (2005a) found 4 species of *Linepithema* and 13 species of *Pseudomyrmex*, yet only one from each genus (*humile* and *gracilis*, respectively) has become established outside of greenhouses. A phylogenic approach will shed light as to which characteristics may promote association with humans generally (if shared by all imported species) versus those that promote invasiveness (those unique to *L. humile* or *P. gracilis*).

Other genera for which a phylogenetic approach will be powerful for uncovering mechanisms of invasion success include those in which many species have become successfully introduced. For example, the Myrmecine genera *Cardiocondyla, Monomorium, Pheidole, Solenopsis*, and *Tetramorium* all have at least three successfully introduced species plus others that are moved around by humans but have not yet been recorded as established outside their native range (McGlynn 1999b; Suarez *et al*. 2005a). A careful, phylogenetically corrected comparison of natural history traits and biogeography of species within these genera will greatly increase our understanding of the factors that contribute to a species ability to become transported by humans, establish new populations, and spread.

13.5 Future directions

Two of the primary goals of invasion biology are predicting and preventing the future establishment of invasive species. Some of the recent research on invasive ants reviewed here suggests clear ways by which these goals may be accomplished. For example, continued and enhanced vigilance must be maintained as a first line of defence. This should involve a thorough examination of high-risk commercial items (such as living plants), and inspection programs should explicitly include sufficient flexibility to respond and adapt to changing situations. Although we recognize that the economic consequences of temporarily halting imports of problematic items are often unpalatable, federal and state agencies must be encouraged to adopt an assertive, forward-leaning stance when facing high-risk situations (see Box 13.1 for a description of New Zealand's risk management). Clearly, the economic consequences of introducing new invaders outweigh the short-term losses that may result from appropriate cautionary measures. This heightened vigilance should also be coupled with scientifically based data collection. For example, while a majority of ants detected in quarantine are intercepted on plant material, this may simply reflect the fact that plants are the most heavily scrutinized commodity.

Box 13.1 Preventing the international spread of invasive ants through implementation of offshore biosecurity risk management policy
Simon O'Connor and Grant P. Weston

Government biosecurity agencies are typically responsible for creating and enforcing policies to prevent the introduction or contain the spread of unwanted organisms. Invasive alien ants provide unique challenges to this process for many reasons. Ants contaminate an infinite range of commodities and are incredibly adaptable across a wide range of environments, which subsequently increases their chances of establishing in new places. Additionally, their reproductive strategies allow rapid nest maturity and efficient population expansion. Increased international trade has allowed the ranges of many invasive alien ant species to increase, and the sea cargo pathway presents a particularly high risk for the introduction of ants (Figure 13.1.1). For example, two of the three *Solenopis invicta* incursions eradicated in New Zealand were linked to contaminated cargo in imported sea containers. This dictates the need for biosecurity agencies to utilize innovative pre-border systems to prevent the entry of invasive ant species.

Figure 13.1.2 The supply-chain environment. Lightly shaded boxes are areas where initial contamination or re-contamination opportunities exist; the darkest shaded box represents the optimal control point for implementation of remedial and prophylactic biosecurity actions (i.e. critical control point).
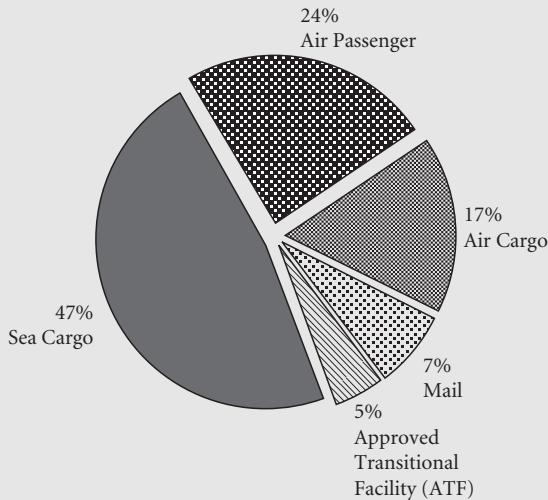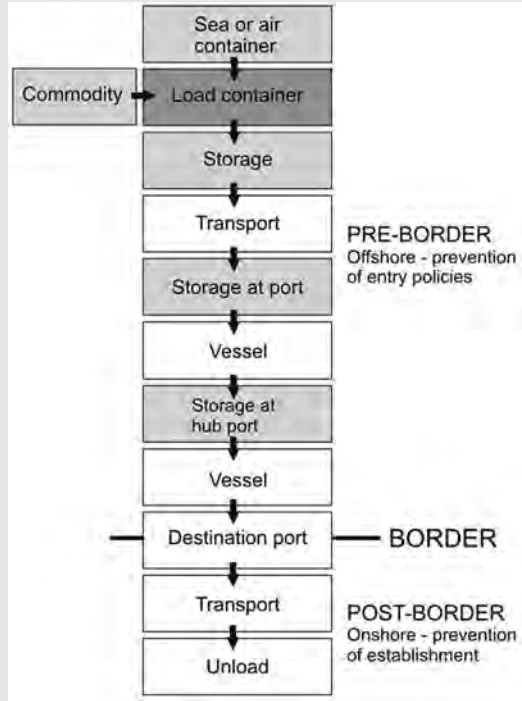

Figure 13.1.1 New Zealand intercept data demonstrating varied pathway use by ants. Approved Transitional Facilities are areas where imported containers and cargo are inspected by Quarantine Inspectors or importers, who have received basic biosecurity training. All ants detected were identified for a seven-month period. Data from Ministry of Agriculture and Forestry, Biosecurity New Zealand.

Pathway contamination rates are likely to be a function of the number and length of contamination opportunities, the ant species and densities present at the source localities (e.g. container load and storage points), and attractants present within the container/commodity, such as suitable nest sites or food sources. A holistic supply-chain environment examination is therefore required, considering contamination likelihood at each opportunity (Figure 13.1.2). In reality, contamination can occur at any point on the supply chain, but is highest where containers remain undisturbed for extended periods and in direct contact with the ground. Effective offshore policies are documented in the International Standards for Phytosanitary Measures (ISPM, FAO 2006), but are rarely used for invasive ants. By utilizing the detailed guidelines in the appropriate ISPM

continues

Box 13.1 continued

standards and ant specific control methodologies, practical improvements in offshore risk management can be achieved as the following case study demonstrates.

Practical offshore risk management: a New Zealand case study

During 2003, New Zealand biosecurity officials became aware of multiple invasive alien ant incursions linked to a single import pathway: sea cargo. These incursions were traced back to three Melanesian ports utilized by one shipping line. Invasive ant contamination rates of empty sea containers on this pathway peaked at 17% of inbound containers. The high associated incursion response costs were being borne by the New Zealand taxpayer. Using site-based evaluations (ISPM No.6), it was determined that container origin ports had high densities of invasive ants and high species diversity (ISPM No. 8). There was also ample habitat and food to sustain populations, as well as multiple opportunities to enter sea containers prior to arrival in New Zealand. New Zealand's biosecurity agency entered into a collaborative risk-management agreement with the shipping line which saw the development and implementation of an offshore based sea container hygiene system (ISPM No. 24) at each of the three ports.

New Zealand biosecurity officials set maximum contamination limits for industry to meet, which provided the mechanism to measure system performance. Integrated pest-management programmes were designed and implemented by an ant-control specialist. The results dramatically reduced port-based ant populations via toxic baiting programmes and habitat reduction. Once containers were cleaned, re-contamination opportunities were also reduced to maintain cleanliness (ISPM No. 10) through the use of dedicated ant free storage areas. In addition, a prophylactic residual insecticide band was applied to all potential ant re-entry points on the cleaned containers to reduce the likelihood of recontamination of future supply chain points (ISPM No.14) where ant-control strategies were unlikely to be used. To gauge system performance, all containers were subsequently inspected by biosecurity staff in New Zealand (ISPM No. 23) over an initial 3-month period, and results fed back to industry partners. Following on from the initial successful three month trial period, a container hygiene system audit regime was implemented to ensure all components of the system were maintained. The resulting feedback systems (ISPM No. 13) facilitated continuous improvement, and ant contamination rates dropped from a recorded high of 17% to less than 0.2%, and commonly 0%. The success of this approach has resulted in the rollout of this system to other high risk import container ports in the Pacific.

Data should be collected at ports of entry to quantify the taxonomy, vectors of transport, and ports of departure for ants reaching international borders. At a minimum, long-term, well-curated sampling of quarantine specimens should be prioritized. These samples will provide invaluable insights into the dynamics of human-mediated transport through time and space.

Our ability to predict and prevent future invasions will be strengthened by a variety of predictive modelling approaches. Much good work has already been performed, but the development and application of new tools and approaches will provide in-

creasingly precise and accurate insights into the future. For example, distribution models that examine the contribution of multiple mechanisms simultaneously (abiotic conditions, biotic factors including taxonomic similarity and species diversity, and exchange rates of commerce) are needed to identify geographic regions that are at a high risk of invasion, and to determine which species are most likely to be problematic in many regions. Climate matching can also be used to identify regions connected by trade that may be at a high risk for faunal exchange and determine if invaders have more commonality in geographic origin than in phylogenetic origin. This

would suggest that invasion success may be tied to the evolution of characteristics related to geography (e.g. the presence of natural disturbances such as flooding) rather than life history characters constrained by phylogeny. In contrast, phylogenetic approaches can provide important insights into the mechanisms that contribute to why some species become invasive, yet related species do not.

Finally, our knowledge of the biology of introduced ants is restricted to a few 'well-studied' species. There are huge numbers of ants being moved around by humans that we know virtually nothing about, and it remains to be seen if generalizations about the spread and success of invasive ants will hold once others are studied in more detail. In fact, we have not even identified the native range for many invasive ants. Careful behavioural, ecological, and genetic studies of invasive ants in their native range are essential for understanding their success elsewhere. Are there particular selective regimes that groom some species to become invaders? What are the particular traits involved? How many different ways are there to become an invader? Studies that place this information in a comparative and explicitly phylogenetic context may be particularly insightful.

13.6 Summary

While research on biological invasions is often species-specific, insight into the mechanisms of in- vasion success can also come from broad biogeographic or taxonomic perspectives. Invasive ants have natural and anthropogenic modes of dispersal, which strongly influence genetic relatedness within a population. Ant introductions are taxonomically diverse; however, certain biogeographic regions are over-represented as either donors or recipients of introduced ants. While invasive ants have historically come from tropical and subtropical climates, contemporary invaders are also emerging from temperate regions. Future research needs to concentrate on the many rarely studied introduced ants to determine if current patterns are general, and to understand the relative importance of taxonomy versus biogeography in predicting future potential invaders and areas most likely to be invaded.

Acknowledgements