Invasion Processes and Causes of Success

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14.1 Introduction

Biological invasions represent communities in flux. Although stasis is never the rule in nature, biological interactions in communities usually occur within a framework of shared ecological and evolutionary history. Consequently, biological invasions represent unique opportunities to study dynamics that can otherwise be difficult to observe (Elton 1958). Invasive ants are excellent organisms with which to pursue this goal, in part because ants as a group play a variety of important ecological roles within biological communities (Hölldobler and Wilson 1990). Ant invasions hold much potential for improving an understanding of ecological processes in general, as well as of interactions more specific to myrmecology. For instance, the dynamics that exist during ant invasions may reveal the traits that promote behavioural or ecological dominance. Furthermore, highly successful invasive ant species are often less conspicuous in their native ranges, so identification of the factors responsible for their greater prominence in introduced areas can provide insight into the more typical workings of ant communities, may highlight intrinsic differences between communities that have formed in separate biogeographic regions, and may suggest possible methods of control. Understanding ant invasion processes and causes of success thus has both basic and applied relevance.

Human activities have introduced many ant species to new biogeographic regions (McGlynn 1999b; Chapter 13). While most introduced ant species have limited success in spreading away from the human-modified habitats in which they usually first arrive, a subset can invade nearby, or even distant, undisturbed natural habitats. This distinction is not always hard and fast, as virtually all species exhibit different degrees of invasiveness and ecological dominance in different locales, and sometimes even under similar conditions in the same locale (e.g. Abbott *et al*. 2007). Notwithstanding, the following species are the most consistent in their ability to penetrate natural ecosystems and affect the composition or abundance of native species within them (Holway *et al*. 2002a): the Argentine ant (*Linepithema humile*), the red imported fire ant (*Solenopsis invicta*), the tropical fire ant (*S. geminata*), the big-headed ant (*Pheidole megacephala*), the little fire ant (*Wasmannia auropunctata*), and the yellow crazy ant (*Anoplolepis gracilipes*) (see Plate 14). We focus on these species because of their pronounced invasive tendencies, and also because they have been studied the most intensively, especially with regard to the factors that control spread and underlie dominance. In fact, the majority of our knowledge on these topics comes from studies on just two species: *S. invicta* and *L. humile*. This represents both a major weakness and a clear avenue for progress in the field, pointing to a need for more complete information on the ecologies of other invasive ant species, as well as their close relatives that fail to become invasive (Chapter 13; see also Section 14.4). This limitation must be acknowledged at the outset, as it impinges on our under-

standing of which causal factors are important only in particular cases, and which form more general patterns central to invasive ant success.

Chapter 13 described how ants are introduced to new areas: which species are likely to be transported, the pathways by which this occurs, and where they are likely to establish. In this chapter, we address patterns of invasion at the community scale, examining the invasion process after the point of establishment. This is the spatial scale at which invading colonies interact with a finite set of resident ant colonies and are affected by abiotic factors that vary over metres or tens of metres. This viewpoint complements the regional and global perspectives of Chapter 13, and together these two chapters provide an integrated picture of the invasion process and the forces that mediate it.

14.2 Invasion processes: the determinants of local patterns of spread

Once an invasive ant species establishes in a new area, what factors determine how quickly and in which directions it will spread? Embedded within this overarching question is a host of related questions. To what extent do biotic interactions influence patterns of spread? Do different invasive ants rely on a common set of environmental factors to spread into ecosystems? Do invasive ants require anthropogenic disturbance to invade, or are the frequent associations between disturbance and invader presence more often correlative?

There exist two broad modes of dispersal among ants (Chapter 9). The more common (independent colony foundation) is usually characterized by flighted dispersal of newly mated queens and males, and is typical of species that possess monogyne, discrete, and mutually antagonistic colonies. In contrast to this arrangement, in a minority of ant species generally, but in a majority of invasive ants (Hölldobler and Wilson 1977), colony foundation or expansion is dependent, and mated queens disperse from their natal nests on foot with retinues of workers and establish new nests nearby (Holway *et al*. 2002a; Passera 1994). Invasive ants thus typically form networks of mutually tolerant, polygynous colonies that are collectively termed supercolonies (see Box 14.1). The major exceptions

to this rule are *Solenopsis invicta* and *Solenopsis geminata*, which possess both monogyne and polygyne forms (Tschinkel 2006). In *S. invicta*, the multicolonial monogyne form founds new colonies independently through mating flights, while the polygyne form can disperse both on the ground (dependently) and via mating flights (independently), although dependent dispersal appears to be the more successful mode among polygyne fire ants (Tschinkel 2006). In addition, the polygynous *A. gracilipes* engages in mating flights as well as dependent dispersal, but flying dispersal events and independent colony founding are believed to occur rarely (Abbott 2006).

Dispersal through mating flights and independent colony founding results in a different pattern of spread from that of dependent dispersal. For example, monogyne *S. invicta* queens can found new colonies 1.6 km or more from their natal colonies, although they usually fly much shorter distances (Markin *et al*. 1971), and this mode of dispersal can produce a highly scattered, discontinuous distribution. Similarly, small isolated supercolonies of *Anoplolepis gracilipes* on Christmas Island, Indian Ocean, may be formed by flying queens (Abbott 2006). Dependent dispersal, in contrast, usually proceeds at rates of tens to several hundreds of metres per year (Holway *et al*. 2002a; however, propagules may sometimes disperse long distances when moved by humans or water, Suarez *et al*. 2001; Walker 2006; Walsh *et al*. 2004), and often produces a clean separation of invaded from uninvaded areas. Because invasive ants generally spread locally through dependent dispersal, we focus here on spatially continuous expansion of supercolonies into surrounding uninvaded areas. Such patterns resemble classic examples of diffusive spread (e.g. Elton 1958) that have inspired the modelling efforts of mathematical biologists for decades (Shigesada and Kawasaki 1997). In this regard, ant invasions offer rare opportunities to examine the factors that control spatial spread.

Environmental factors interact in complex ways to influence patterns of ant invasion. While acknowledging that none of these factors act in isolation, we first discuss how biotic interactions can either repel or encourage the local spread of invasive ants. We then examine how physical

Box 14.1 The ecological consequences of cooperative behaviour among workers from different nests
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Unicoloniality, or the absence of behavioural boundaries among nests within a population, is considered a key trait of many invasive ant species (see Section 14.3.2.1). Unicoloniality and monodomous, multicoloniality, in which colonies occupy a single nest and are mutually intolerant, represent opposite extremes of a continuous gradient in social organization, characterized by increasing exchange of individuals among nests. Along this gradient, key transitions in social behaviour allow for heightened levels of internest cooperation and confer specific ecological advantages (see Chapter 10 for discussion on colony structure).

An ecologically critical transition occurs when intraspecific aggression declines to the point that neighbouring colonies within populations cease behaving aggressively towards one another. The potential evolutionary forces leading to this change may be diverse (Giraud *et al*. 2002; Steiner *et al*. 2007; Tsutsui *et al*. 2000), but the ecological consequences are similar. Colonies cease to engage in intraspecific interference competition and territorial contests. The greatly reduced costs of competition that result are thought to allow for higher local worker density and, as a result, to enhance interspecific competitive ability and ecological dominance (see citations in Section 14.3.2.1). *Myrmica rubra*, introduced into the northeastern United States, exhibits low-intensity intraspecific aggression that increases over short distances within local sites, but nevertheless forms large, continuous, and dense populations of colonies that closely resemble supercolonies (Garnas *et al*. 2007). Colonies within such populations do not engage in obvious intraspecific interference competition. Further along the gradient are populations of polygyne *Solenopsis invicta* in the southern United States, in which workers from different nests are mutually non-aggressive, but only limited exchange of workers or queens occurs among nests. These societies are best characterized as semi-permeable. Queens and workers within nests are

unrelated, suggesting that inter-nest movement occurs. However, queen number, allele frequencies, and worker mass exhibit nest specific signatures, indicating the existence of boundaries preventing the free exchange of workers (summarized in Goodisman *et al*. 2007). These functional colony boundaries ensure that intraspecific competition is not entirely absent. In these populations, workers recruiting to a large food item tend to belong to only one nest in the neighbourhood, typically the closest. In fact, the degree to which resources are monopolized is significantly greater than would be expected, based upon the relative distances of the nests from the food resource (Weeks *et al*. 2004). Thus, a weak form of intraspecific exploitative competition may operate, and because nests do not commonly intermix, colonies may restrict each other's movements.

The next possible level of colony integration is the free exchange of workers, but not queens, among nests. *Formica exsecta*, a non-invasive ant, provides an example of a species in which adult workers mix freely among nests, but queens do not (Kümmerli and Keller 2007). Examining the genetics and behaviour of the workers, these populations appear unicolonial, but this social organization maintains a multi-colonial genetic structure within the immature workers and queens. Emergent ecological benefits of this particular social structure have not been explored, but newly established nests could potentially suffer lower mortality rates given their ability to grow rapidly. This might confer advantages to new nests in environments where survival requires large numbers, thereby favouring populations exhibiting this trait. This form of social organization has not been documented for an invasive ant species.

A final critical shift in social organization occurs when queens and workers mix among nests: nest fusion. If nest fusion is sufficiently common, all genetic and functional boundaries between colonies disappear and populations become fully unicolonial (Suarez *et al*.

continues

Box 14.1 continued

2008; Vasquez and Silverman 2008). Known examples of invasive ants in this category include *Linepithema humile* and *Wasmannia auropunctata*, and this arrangement is also strongly suggested for some populations of *Anoplolepis gracilipes* and *Pheidole megacephala* (see Section 14.3.2.3). Ecologically, nest fusion allows for functional integration across large spatial scales. If nests can fuse, then space is no longer pre-empted, making fine-scale adjustments between worker density and resource availability or microhabitat suitability possible. During times of abiotic stress, nests can form large aggregations in potentially limited suitable microsites. Large aggregations of ants can maintain environmental homeostasis more easily, regulating temperature and humidity within the nest. During less stressful times of year, nests can disperse through the environment and track resource pulses. The invasive *L. humile*, and non-invasive

Formica truncorum, provide examples of species that excel at this opportunistic use of space (Elias *et al*. 2005; Heller and Gordon 2006). These two very distinct taxa both evolved in environments that select for the ability to exploit patches of space that are only ephemerally available. *F. truncorum*, a boreal species, migrates seasonally between its large winter nests and its dispersed summer nest sites on productive rocky outcrops, while *L. humile* evolved in the seasonally inundated floodplain of the Paraná River, and must be able to exploit dry ground as it appears and recedes. Many of the species with populations that lack intraspecific aggression but are not fully unicolonial, such as polygyne fire ants and some species of northern European *Formica*, require elaborate nest structures that are costly to construct. These may make colonies inherently less mobile, and thus reduce the opportunity for and ecological benefits of nest fusion.

conditions and disturbance influence invasibility, and how different factors can interact.

14.2.1 Biotic interactions

Given that 'the biggest enemies of ants are often other ants' (Hölldobler and Wilson 1990), interspecific competition from resident ants may repel invasive ants, or at least curb the rate at which invasive ants penetrate ecosystems. Few data are available to rigorously test this prediction. In northern California, the spread of Argentine ant supercolonies in riparian corridors over a 4-year period was independent of the number of native ant species present (Figure 14.1a; Holway 1998b), evidence inconsistent with the biotic resistance hypothesis (Elton 1958). Further research on another California system, however, revealed that under suitable abiotic conditions, Argentine ants invade sites to a greater extent when native ants are removed, compared to when they remain present (Menke *et al*. 2007). This latter result indicates that native ants can slow the advance of supercolonies. Extending

this idea to a biogeographic scale, one might predict that regions with highly competitive ant faunas may be especially resistant to invasion. For instance, competition from Australia's dominant dolichoderines has been offered as a potential explanation for the apparent inability of invasive ants to easily spread beyond human-modified habitats on that continent (Andersen 1997; Majer 1994; see also Way *et al*. 1997 for a potential European example). Although no studies to date have tested whether the presence of dominant Australian ants, such as *Iridomyrmex* spp., can prevent the expansion of invasive ant supercolonies, several studies have recently examined their effects on Argentine ant activity and competitive ability (Rowles and O'Dowd 2007; Thomas and Holway 2005; Walters and Mackay 2005). Results of these studies have been mixed, but on balance suggest that biotic resistance interacts with abiotic conditions to limit Argentine ant competitive success in some habitats, and therefore possibly also its distribution in these areas. In mesic to wet forested ecosystems, to which it is well adapted, *Pheidole megacephala* invades in spite of

competition from Australian ants (Hoffmann *et al*. 1999; Vanderwoude *et al*. 2000), but like the Argentine ant may be less able to do so in drier areas. More research is needed to clarify the importance of competitive resistance in influencing invasion patterns in regions with highly diverse ant faunas, like Australia.

While biotic resistance from competitors may discourage the spread of invasive ants, reciprocally positive interactions may act to encourage their spread. Ants participate in an astonishing array of mutualistic associations with other organisms (Hölldobler and Wilson 1990), but the commonly formed associations between invasive ants and honeydew-producing insects (especially Hemiptera) seem especially likely to contribute to ecological success. Although research suggests that these opportunistic mutualisms promote higher densities of invasive ants than would be possible if the ants were primarily acting as predators (see 14.3.2.2), it is unknown to what degree the distribution and density of honeydew-producing insects influences patterns of invasive ant spread (Helms and Vinson 2002). These interactions are of more general interest as well, because mutualisms may encourage the spread of a wide range of introduced species. Examples of potential facilitation and mutualism between two or more introduced species have been increasingly reported in recent years (Simberloff 2006).

14.2.2 Abiotic conditions

The abiotic environment can strongly limit the activity and local abundance of invasive ants. As small-bodied insects, ants are highly vulnerable to temperature stress and desiccation (Hölldobler and Wilson 1990). Risks associated with exposure are especially acute for foraging workers, which must journey away from the safety of their nests, and which lack winged flight. With respect to ant invasions, abiotic factors can dictate patterns of invasion at multiple spatial scales (Menke *et al*. 2007). At small scales, the amoeba-like spread of ant supercolonies may be strongly influenced by abiotic suitability – with rainfall (or soil moisture) often invoked as a key factor. In seasonally dry California, for example, Argentine ants advance in riparian corridors along perennial streams, but not
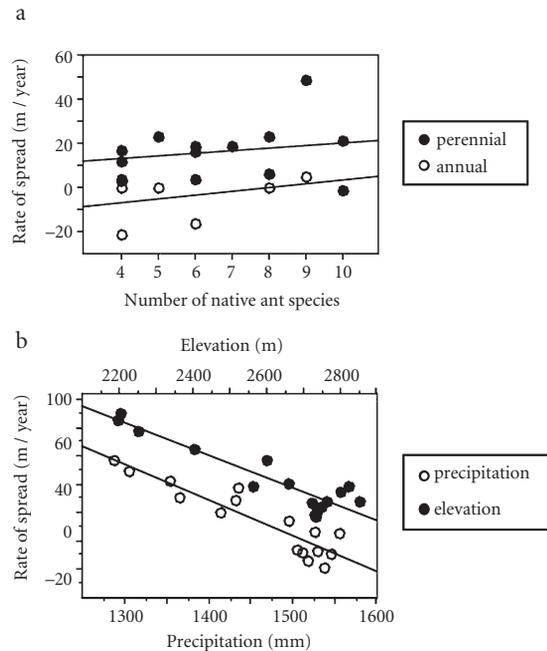
Figure 14.1 (*a*) Mean annual rate of spread of Argentine ants versus the number of native ant species in 20 riparian corridors in northern California. Over a 4-year period (1993–7), *Linepithema humile* spread more quickly at sites along perennial streams than it did at sites along intermittent streams (multiple regression: $t = 3.36$, $df = 17$, $p < 0.01$). Rate of spread was independent of native ant diversity 100 m ahead of the initial location of each invasion front ($t = 1.03$, $df = 17$, $p > 0.05$). (*b*) Mean annual rate of spread of Argentine ants versus elevation and precipitation in two spatially disjunct populations in Haleakala National Park, Maui, Hawaiian Islands. For the population in which spread is measured as a function of precipitation, the 16-data points represent net rates of outward spread between 1980 and 1997 along equally spaced radial lines (22.5° apart) emanating from a central point. For the population in which spread is measured as a function of elevation, the 16-data points are similar measures of outward spread between 1982 and 1997.

intermittent streams (Figure 14.1a; Holway 1998b), suggesting that the ability of this species to invade seasonally dry areas may be largely controlled by whether or not soils remain moist enough during the summer drought. This hypothesis is corroborated by observational studies that report positive correlations between rainfall and local patterns of Argentine ant abundance or rates of spread

(DiGirolamo and Fox 2006; Heller *et al.* 2008; Holway and Suarez 2006), field experiments that use irrigation to encourage the spread of *L. humile* (Menke *et al.* 2007; Menke and Holway 2006), and physiological studies showing that Argentine ants lose water more rapidly compared to native ants (Schilman *et al.* 2005). In arid locales, heat stress is also usually a factor during parts of the day, and Argentine ants are less capable of withstanding high temperatures compared to native ant species from arid ecosystems in both California (Holway *et al.* 2002b) and Australia (Walters and Mackay 2004). In both regions, a combination of hot and dry conditions appears important in preventing spread into xeric habitats from more suitable, and often anthropogenically modified, adjacent areas (Holway *et al.* 2002b; Thomas and Holway 2005; Walters and Mackay 2003a; 2004).

At the other end of the climatic spectrum, cold and wet conditions can also influence local patterns of ant invasion. In a montane shrubland habitat in Hawai'i, for example, both high elevation and abundant rainfall appear to have influenced long-term rates and spatial patterns of spread of *L. humile* (Krushelnycky *et al.* 2005a). In this system, areas with higher rainfall support a more dense vegetative ground cover, which reduces soil temperatures (S. Hartley and P. Krushelnycky, unpublished data). Lower temperatures thus appear to prevent Argentine ant spread into more windward, wetter habitat (Figure 14.1b). At the same time, the rate of spread of a nearby but separate unicolonial population of *L. humile* is strongly negatively correlated with elevation (Figure 14.1b), which also directly influences soil temperature. Similarly, low temperatures are likely responsible for limiting regional Argentine ant distributions in New Zealand (Hartley and Lester 2003). On a local scale, the distance of Argentine ant spread into New Zealand's natural areas from adjacent human-modified sites is much greater in open-canopy habitat than in closed-canopy habitat, probably because of higher ground temperatures in open sites (Ward and Harris 2005).

Seasonal patterns of invasion by Argentine ants are also largely tied to abiotic conditions. Nest clusters spread out as worker numbers increase during the warmer and drier parts of the year, at least in non-arid habitats (Heller *et al.* 2006; Newell and Barber 1913). This translates into overall expansion at the supercolony level during summer and fall, as well as some contraction in winter and spring in some locales (Heller *et al.* 2006; Krushelnycky *et al.* 2004; Sanders *et al.* 2001).

While rates and spatial patterns of spread of dependently dispersing supercolonies can be measured in a straightforward manner, identifying the factors that affect spread for species that disperse primarily by mating flights and independent colony founding is more difficult because of the complex spatial patterns that result. Nonetheless, abiotic factors can strongly influence patterns of establishment for invasive ants that colonize by mating flights, as in the case of monogyne *S. invicta* in Florida that proliferates in forest openings and in areas with moist soils (Tschinkel 1988b). In fact, *S. invicta* is generally absent from closed-canopy forests throughout the southeastern United States (e.g. Zettler *et al.* 2004), perhaps because thermal conditions in these environments are not consistently above the threshold for colony growth (Porter 1988), or because founding queens may have lower success in shaded forest habitats (McInnes 1994).

14.2.3 The role of disturbance

One factor likely to be of general relevance with respect to where ants invade is disturbance. Introduced ants commonly (but not exclusively) occur in anthropogenically disturbed environments (King and Porter 2007; Passera 1994). Although a distinction should be made between disturbances that directly result from human activity and those that do not, the causal relationship between disturbance and invasion success may be unrelated to the source of the perturbation. We view disturbance here as defined by Krebs (2000): any discrete event that disrupts community structure and changes available resources, substrate availability, or the physical environment. For ants, classes of disturbance that may often promote invasibility include flooding, soil perturbation, and the removal of trees. The clearest insights into how these factors affect invasibility will come from field manipulations that incorporate disturbance as an

experimental treatment and that consider not only the effects of disturbance on the invader but also on resident ants. Disturbance may directly abet invaders that are predisposed to benefit from it. In addition, disturbance may indirectly promote invaders by negatively affecting native taxa, thus facilitating spread into recently impoverished communities (Diamond and Case 1986). The effects of disturbance, therefore, may commonly result from an interaction of biotic and abiotic factors.

The central role of anthropogenic disturbance in the success of monogyne red imported fire ants in the southeastern United States has been clarified in a series of studies by Walter Tschinkel and colleagues. Observational studies in northern Florida illustrate that *S. invicta* prefers open, recently disturbed areas (e.g. roadsides), whereas the putatively native *S. geminata* occupies less exposed sites with some canopy cover (McInnes 1994; Tschinkel 1988b, 2006). To identify the mechanisms underlying this pattern of invasion, King and Tschinkel (2006) and King and Tschinkel (2008) carried out manipulative experiments in Florida, adding or removing monogyne *S. invicta* colonies from study plots and physically altering some plots to emulate disturbances favoured by *S. invicta*. This body of work revealed – somewhat surprisingly – that the mixed assemblage of native and introduced ants present in the vicinity of plots in human-made pastures were unaffected by partial *S. invicta* removal (King and Tschinkel 2006). Conversely, the experimental establishment of *S. invicta* in natural forest plots was aided substantially by physical disturbance, while native ants were negatively affected by both the experimental additional of fire ants and disturbance (King and Tschinkel 2008). Taken together, these findings indicate that the spread of monogyne *S. invicta* in Florida may be driven largely by human-induced modifications to the landscape that simultaneously affect native ants.

However, disturbance may not be a necessary prerequisite for monogyne fire ant invasion in all systems. In a Texas savanna, monogyne *S. invicta* invaded a grassland habitat that had experienced no anthropogenic disturbance for at least 15 years prior to the arrival of red imported fire ants (Helms and Vinson 2001). In agreement with the results from Florida, there was no evidence that this invasion substantially affected native ant populations. In contrast, polygyne *S. invicta* invasions in Texas clearly depress native ant diversity (Morris and Steigman 1993; Porter and Savignano 1990), although in some systems local diversity has recovered (Morrison 2002b; see Section 14.4). Interestingly, Plowes *et al*. (2007) recently described a fine-scale distribution pattern similar to the disturbance-dependent invasion of Florida and the southeast United States in central Texas: in an urban landscape, *S. invicta* was common in open, recently cleared sites, whereas *S. geminata* persisted in historic neighbourhoods with mature shade trees. However, in the surrounding undeveloped matrix, all open habitats were invaded by polygyne red imported fire ants, regardless of disturbance history. Moreover, while polygyne *S. invicta* also thrives in deforested habitats, it has spread from these areas into naturally open and undisturbed habitats, such as prairies (Morris and Steigman 1993). This raises the question of whether a scarcity of unaltered naturally open and undisturbed habitats throughout the southeastern United States may be largely responsible for the close association of *S. invicta* with disturbed sites in this region.

The invasion of California by the Argentine ant has also been well studied, and offers an interesting comparison with that of the red imported fire ant. Like *S. invicta*, Argentine ants thrive in environments disturbed by humans. In southern California, for example, GIS analyses demonstrate the close association between *L. humile* and human-modified environments at the landscape scale (Menke *et al*. 2007). This positive relationship results in large part from two factors: (*a*) the Argentine ant's inherent dispersal limitations (Suarez *et al*. 2001), which keep this species from quickly spreading out from urban source populations, and (*b*) the tendency for it to benefit from irrigation (Menke and Holway 2006), which reflects its requirements for adequate levels of soil moisture. However, where moisture is naturally higher, Argentine ants readily invade, and in so doing displace a wide variety of native ants (Holway 1998a; b; Human and Gordon 1996; Ward 1987). Argentine ants become especially prolific in riparian woodlands of California (Holway 1998b, 2005) – perhaps unsurprising, given that they thrive in this habitat

in Argentina. Thus, although *L. humile* benefits from certain aspects of human activity, it does not depend on these modifications to invade. Moreover, the kinds of disturbances (e.g. clearing of trees, soil disturbance) that promote the spread of *S. invicta* (Tschinkel 1988b; Zettler *et al*. 2004) fail to encourage *L. humile* in California unless they are accompanied by inputs of water. For example, anthropogenic degradation of riparian woodlands does not affect the rate at which Argentine ants spread in this habitat, nor does it influence native ant diversity or abundance (Holway 1998b).

One striking commonality of recent experimental work on *L. humile* and *S. invicta* concerns the importance of abiotic factors in the establishment and spread of these ants in North America. Native ants either interact weakly (monogyne *S. invicta*: King and Tschinkel 2006) or fail to repel (polygyne *S. invicta*: Porter and Savignano 1990; *L. humile*: Holway 1998b) invaders, and as a consequence the distribution of *L. humile* and *S. invicta* is largely dictated by physical conditions, which are altered to varying degrees by human activity. The local patterns of distribution of these two ant species in North America largely mirror their microhabitat selection in South America: Argentine ants most commonly inhabit floodplain woodlands or wetland habitats with emergent vegetation, whereas *S. invicta* is more common in open pastures and grasslands (LeBrun *et al*. 2007). These fine-scale habitat preferences are reflected in the spectacular success of *S. invicta* in the southeastern United States following landscape-level deforestation of this region (Tschinkel 2006). Likewise, the profligate use of water in seasonally dry coastal California opens up large areas to invasion that would otherwise be unsuitable to *L. humile* (Menke *et al*. 2007).

Despite the frequent connection between disturbance and ant invasions, it is apparent that, like *L. humile* and polygyne *S. invicta* in North America, most, if not all other invasive ant species are capable of spreading from human-modified habitats into largely undisturbed natural areas if the abiotic conditions are suitable. Examples of this phenomenon include *W. auropunctata* (Clark *et al*. 1982; Le Breton *et al*. 2003; Walker 2006), *A. gracilipes* (Abbott 2006; Hill *et al*. 2003), *P. megacephala*

(Heterick 1997; Hoffmann and Parr 2008; Wetterer 2002), as well as *L. humile* in other parts of the world (Bond and Slingsby 1984; Krushelnycky *et al*. 2005a; Oliveras *et al*. 2005a; Ward and Harris 2005).

14.3 Causes of success

In cases where invasive ants do manage to spread into natural areas supporting native ant communities, they often displace a majority of native ant species in the process (Holway *et al*. 2002a; Chapter 15). This is a remarkable feat, in view of the fact that ant communities typically represent a diverse array of species employing a variety of life histories and competitive strategies. Monogyne populations of *S. invicta* in disturbed habitats of the southeastern United States may be notable exceptions to this pattern, in that their invasions in these areas may not greatly suppress colonies of many other ant species (Helms and Vinson 2001; King and Tschinkel 2006; Morrison and Porter 2003). But for other instances in which invasive ants have excluded the vast majority of native ant species, the question remains: how do they accomplish this and what characteristics account for this unusual ability?

14.3.1 Competitive displacement and predation

Coexistence among native ant species in intact communities is accomplished through a variety of mechanisms (Hölldobler and Wilson 1990; Chapter 5). For systems not structured by disturbance, coexistence among species that compete for similar food resources under similar abiotic conditions can be mediated, in part, by a foraging strategy trade-off between resource discovery and resource dominance (Davidson 1998; Feener 2000; Feener *et al*. 2008; Fellers 1987; Holway 1999; LeBrun and Feener 2007). Some species excel at rapidly finding and retrieving food (superior exploitation ability), while other species are slower at discovery but excel at displacing those species that arrived sooner through behavioural dominance (superior interference ability). There are few studies that have managed to elucidate the competitive dynamics between invasive ants and native ant communities at contact zones where displacement is actively

occurring. Most information on this process comes from studies of Argentine ant invasions in California. In two different ecosystems, researchers found that Argentine ants were more likely to find baits, located and recruited to baits more quickly, and foraged over a greater part of the day than did native ants (Holway 1999; Human and Gordon 1996). Because of an omnivorous diet, Argentine ants also likely competed for food resources with a wide range of native species. Once they located baits, Argentine ants recruited more workers, persisted longer than native ants, and were more frequently aggressive towards native ants than vice versa. Thus, through pre-emption and displacement, *L. humile* controlled a majority of available baits in the contact zones. Similar results have recently been reported for an Argentine ant invasion front in Spain (Carpintero *et al*. 2007; Carpintero and Reyes-López 2008), although subtle differences appear to exist in the prevalence and effects of Argentine ant aggression in these three invaded communities.

These studies suggest that Argentine ants come to dominate the ant communities they invade by consistently excelling at both exploitation and interference competition (Figure 14.2). This presumably allows them to monopolize a majority of available resources at the leading edges of their expanding populations, and in the process to displace a majority of the resident native ant species. While such detailed studies of the competitive dynamics of invasions in progress are not available for most other invasive ant species, at least a few of them appear to possess similar abilities. For instance, *W. auropunctata* foraged 24 h a day and displaced other ants from a large majority of baits in contact zones at the edges of its range in the Galápagos (Clark *et al*. 1982). In areas where *S. invicta* still co-occurs with *S. geminata* in its native range in the southern United States, *S. invicta* has been found to retrieve more food (Morrison 1999) and to forage over a wider range of temperatures and humidities (Wuellner and Saunders 2003) compared to *S. geminata*. Similarly, in a recently invaded field in the southern United States, colonies of hybrid imported fire ants (*S. invicta* × *Solenopis richteri*) discovered and recruited to baits more quickly than did native ants, and also retained
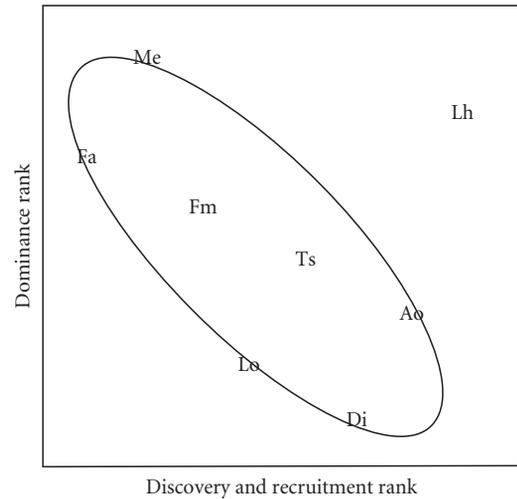
Figure 14.2 For ant assemblages of northern California riparian woodlands, an interspecific trade-off exists between the abilities of species to discover food resources versus their ability to dominate them. The invasive Argentine ant (Lh) does not conform to this relationship because it is highly successful at both discovery and dominance. Remaining ant species abbreviations are as follows: Ao = *Aphaenogaster occidentalis*, Di = *Dorymyrmex insanus*, Fa = *Formica aerata*, Fm = *Formica moki*, Lo = *Liometopum occidentale*, Me = *Monomorium ergatogyna*, Ts = *Tapinoma sessile*. (Modified from Holway 1999 and Feener 2000)

control of more baits after several hours (Gibbons and Simberloff 2005).

The aggressive behaviour of invasive ant species is not limited to the acquisition of food. Nest raiding of heterospecific colonies has been reported for *L. humile* (Carpintero and Reyes-López 2008; Fluker and Beardsley 1970; Rowles and O'Dowd 2007; Zee and Holway 2006), polygyne *S. invicta* (Hook and Porter 1990) and *P. megacephala* (Dejean *et al*. 2008), and although difficult to observe, this behaviour may be common. In fact, nest raiding may be the primary way in which colonies of some species are displaced (or destroyed). This is likely to be the case for species, such as harvester ants, that have little overlap with invasive ants in resource use but nevertheless disappear from invaded areas (Plate 15; Erickson 1971; Hook and Porter 1990; Human *et al*. 1998; Zee and Holway 2006). It is often unclear to what degree raided adults and brood are taken for prey, and therefore this

behaviour may sometimes represent interference competition (Hook and Porter 1990), predation (Carpintero and Reyes-López 2008), or both (Zee and Holway 2006). Aggression directed at dispersing queen foundresses is likely important in preventing the re-establishment of native colonies within the territories of invasive ants (Human and Gordon 1996).

14.3.2 The advantages of numbers

But how, exactly, do invasive ant species excel in these competitive or predatory abilities? A number of studies have shown that invasive ants are not particularly successful in one-on-one competition with native ants (e.g. Buczkowski and Bennett 2007; Holway 1999; Holway and Case 2001). Instead, most evidence indicates that invasive ants derive their superior competitive abilities from higher numbers (Buczkowski and Bennett 2007; Carpintero and Reyes-López 2008; Holway 1999; Holway and Case 2001; Human and Gordon 1996; Human and Gordon 1999; Morrison 2000; Rowles and O'Dowd 2007; Tremper 1976; Walters and Mackay 2005). Numerical asymmetries commonly determine competitive outcomes in ants generally (Hölldobler and Wilson 1990), and these asymmetries can be taken to extraordinary levels in the case of invasive ants. Invasive ant colonies are not only larger than competing native colonies, they can sometimes attain such high abundances that they greatly exceed in number or biomass all of the native ant species, combined, in the communities they invade (Hoffmann and Parr 2008; Holway 1999; Human and Gordon 1997; Morris and Steigman 1993; Porter and Savignano 1990). These elevated densities are not only the key to their success against native ants, but are also the underlying cause for many of their other ecological and economic impacts (Holway *et al*. 2002a). Explanations for this phenomenon, reviewed here, have been the topic of much research.

14.3.2.1 Unicoloniality
Unicoloniality is shared among most (but not all) invasive ant species (Holway *et al*. 2002a; Passera 1994; see Box 14.1). While unicoloniality is not unique to invasive ant species, some *Formica*, for

example, form expansive supercolonies (Bourke and Franks 1995; Hölldobler and Wilson 1990), unicoloniality has attained its most dramatic form among certain invasive ants. Introduced populations of *L. humile* and *W. auropunctata* can form vast supercolonies and occupy disjunct sites over hundreds of square kilometres (Corin *et al*. 2007a; Giraud *et al*. 2002; Le Breton *et al*. 2004; Tsutsui *et al*. 2000). Within such supercolonies, workers from different nests generally behave towards one another as if they were nestmates, even when the workers originate from distant locations. It is worth noting that this is not always the case, and in some situations multiple supercolonies of much smaller size occur in a region or locality (Abbott *et al*. 2007; Buczkowski *et al*. 2004; Sunamura *et al*. 2007). Although the sizes of supercolonies can vary, unicoloniality appears to consistently promote high densities of ants. Why is this the case?

At a local scale, the absence of intraspecific aggression can have profound consequences. Because aggression in ants is often strongest among conspecific colonies (Hölldobler and Wilson 1990), species that lack intraspecific aggression avoid large costs associated with territoriality. The polygyne forms of *S. invicta* and *S. geminata*, for example, while not considered strictly unicolonial, are believed to maintain higher nest densities and worker biomass compared to those of the monogyne forms (MacKay *et al*. 1990; Macom and Porter 1996) in part because of reduced intraspecific aggression. Argentine ants provide an additional example. Over most of their range in California, Argentine ants show little or no hostility to one another (Tsutsui *et al*. 2000), but where genetically differentiated supercolonies contact one another the story is entirely different. Battles between supercolonies at points of contact are frequent, prolonged and intense, and can result in considerable worker mortality (Thomas *et al*. 2006). The potential for this type of aggression to limit colony growth and competitive ability can be readily studied in the laboratory. Compared to non-aggressive pairs of experimental colonies collected from the same supercolonies, mutually antagonistic pairs have lower rates of worker foraging and food retrieval, higher worker mortality, and reduced productivity (Holway and Suarez 2004; Holway *et al*. 1998). In the laboratory, such costs also impinge

on interspecific competitive ability. In a similar study, colonies of *Forelius mccooki* experienced greater worker mortality and lower egg production when reared with non-aggressive pairs of Argentine ants than they did when reared with intraspecifically aggressive pairs (Holway and Suarez 2004). Dramatically, two-thirds of *F. mccooki* colonies matched with cooperative *L. humile* colony pairs were killed outright, while none of those matched with mutually antagonistic *L. humile* colony pairs died. Although conducted in a simplified laboratory setting, these experiments on *L. humile* illustrate in principle not only how the absence of intraspecific aggression can lead to higher abundances of invasive ants, but also how it should translate into strong competitive advantages against native ants.

The breakdown of intraspecific territoriality within supercolonies can result in extremely high nest densities. After most heterospecific ant colonies have been displaced, invasive ants have all suitable nesting sites at their disposal. This allows them to saturate the environment and more thoroughly monopolize food resources, undoubtedly boosting densities further. Numerous studies have shown that within supercolonies (i.e. away from invasion fronts), invasive ant species are highly effective at food exploitation. Through higher local forager densities, often combined with a more rapid foraging tempo, they have been found to cover ground more quickly when foraging compared to assemblages of native ants (*L. humile*: Oliveras et al. 2005a), to find food faster compared to native ants (*L. humile*: Gómez and Oliveras 2003; Holway 1999; polygyne *S. invicta*: Porter and Savignano 1990; *P. megacephala* and *A. gracilipes*: Ward and Beggs 2007), and to find more of it (*L. humile*: Human and Gordon 1996; polygyne *S. invicta*: Porter and Savignano 1990; *W. auropunctata*: Le Breton et al. 2005; *P. megacephala*: Dejean et al. 2007b; Ward and Beggs 2007; *A. gracilipes*: Ward and Beggs 2007). In other situations, comparisons of performance with native ant species are unavailable, but data nevertheless indicate a thorough acquisition of offered food baits (Lester and Tavite 2004; Sarty et al. 2007; Vanderwoude et al. 2000).

This same absence of territoriality within supercolony boundaries also allows for flexibility in nesting arrangements. Instead of being subjected to the limitations of central-place foraging strategies, invasive ants that are unicolonial may more commonly employ dispersed central-place foraging as a result of their polydomy (Holway and Case 2000). Under this arrangement, food, workers, brood, and queens can be shifted among nests, and new nests can be constructed, to counteract spatial heterogeneity in available resources, and minimize energy expended in food retrieval and distribution (Holway and Case 2000; Newell and Barber 1913; Silverman and Nsimba 2000). Similarly, ants with this colony structure move their nests in order to take advantage of favourable abiotic conditions (Heller et al. 2006; Markin 1970b; Newell and Barber 1913). Such strategies are largely unavailable to multicolonial species, which would often need to usurp another colony in order to move. Despite the absence of territoriality in polygyne *S. invicta*, relatedness among workers within and across mounds indicates a general lack of exchange of workers or queens among nests (Goodisman et al. 2007; Ross 1993), revealing that it does not share this ecological advantage with fully unicolonial species (see Box 14.1).

14.3.2.2 Generalist habits

As a subset of the broader group of tramp species, invasive ant species typically have loose nesting requirements (Holway et al. 2002a). This allows them to establish nests in a wide variety of sites and reinforces the trend towards high nest density within supercolony boundaries (e.g. *P. megacephala* in Tonga, Wetterer 2002; *W. auropunctata* in New Caledonia, Le Breton et al. 2005; *L. humile* in California, Heller 2004; *A. gracilipes* in the Seychelles, Haines and Haines 1978a and on Christmas Island, Abbott 2005).

A broad diet also characterizes most invasive ant species (Holway et al. 2002a), and this trait enables a more complete use of available resources. However, it appears that a particular aspect of omnivory is especially important, namely the heavy use of liquid carbohydrate resources. Plant exudates and insect honeydew play a vital role in the energy budgets of many ant species, but may be of particular importance for ecologically dominant species that attain high densities and maintain high levels of activity (Davidson 1998; Davidson et al. 2003;

Chapters 6 and 7). It is therefore not surprising that strong associations with honeydew-producing insects have been reported for all of the major invasive ant species (Lach 2003; Ness and Bronstein 2004). For *S. invicta* in eastern Texas, up to half of the colony energy requirements may be supplied by hemipteran honeydew, most of which comes from an introduced mealybug (Helms and Vinson 2002). The exploitation of abundant and cheap carbohydrate-based fuel may be unsurpassed on Christmas Island in the Indian Ocean, where facultative mutualisms with possibly introduced honeydew-producing Hemiptera appear to contribute importantly to the extraordinary density and frenetic activity of *A. gracilipes* that currently exists there (Abbott 2005; Abbott and Green 2007; O'Dowd *et al*. 2003).

Besides boosting invasive ant abundances, liquid exudates may also influence behaviour. In the case of *L. humile*, carbohydrate deprivation reduces aggression and activity (Grover *et al*. 2007). It remains to be seen whether this is true of other invasive ants, or whether different species employ somewhat different strategies in achieving ecological dominance. For instance, despite heavy use of liquid exudates (Clark *et al*. 1982; Le Breton *et al*. 2005), *W. auropunctata* does not usually engage in high-tempo foraging and scouting activity. Instead, it seems to rely on an especially high saturation of the environment with its nests. This species therefore manages to locate and recruit to food quickly (Le Breton *et al*. 2005) despite the slow movement of its workers. In addition to disparities among ants, each invasive species may use plant-based exudates differently depending on site-specific variation and time since introduction. Such flexibility in resource use has recently been demonstrated for *L. humile* (Tillberg *et al*. 2007), and could be partially responsible for differences in density or behaviour among sites.

14.3.2.3 Ecological release and genetic changes

The characteristics discussed above explain how invasive ants achieve their remarkable dominance in introduced areas. However, they do not adequately address the important question of why invasive ants are able to employ these mechanisms to such greater effect in their introduced ranges than in their native ranges, where they typically coexist

with many other ant species (Feener *et al*. 2008; Heller 2004; LeBrun *et al*. 2007; Porter *et al*. 1997; Suarez *et al*. 1999; Tennant 1994). For most ant invasions, ecological success likely results from the joint action of multiple causal factors, and a key challenge is to develop a clearer understanding of the relative importance of each factor and how they interact.

A common explanation to account for the success of invasive species involves escape from natural enemies (Mack *et al*. 2000), whereby an invader gains a competitive advantage over natives by leaving behind its suite of specialized pathogens, predators, and parasites in its native range, while its new competitors must still contend with theirs. *S. invicta* has until recently faced only a handful of pathogen and parasite species in North America, compared to several dozen in its South American homeland (Porter *et al*. 1997). Phorid flies, which parasitize adult worker ants, provide an example of one such enemy. Phorids modify interspecific competitive outcomes in ants through differential effects on worker behaviour (Feener 2000). Phorids are typically host-specific and often associate with dominant ants. When present, the disruption phorids create through their attempts to oviposit can substantially diminish the behavioural dominance and foraging efficiency of the beleaguered species, including *S. invicta* in its native range (Feener *et al*. 2008; Orr *et al*. 1995; Porter *et al*. 1995). In fact, the potential importance of these effects forms the basis of recent biological control programs that have introduced phorid flies into the southeastern United States in an attempt to suppress the dominance of *S. invicta* over native species. Where *S. invicta* co-occurs with *S. geminata*, for instance, it can forage unmolested day and night, while diurnal foraging by *S. geminata* is reduced when its own phorid parasitoids are present (Morrison 1999). However, the strength of phorid fly impacts on behavioural dominance appears to be community-dependent (Feener *et al*. 2008), and so far there is no evidence that introduced phorid populations have succeeded in suppressing populations of *S. invicta* (Morrison and Porter 2005). The importance of escape from pathogens, parasitoids, and predators is unknown in the case of other invasive ant species, because no such natural enemies have so far been

identified. More attention should be directed towards this goal.

Ecological release, and thus greater dominance, of invasive ants in their introduced ranges could also result from a less competitive environment, mediated chiefly by the rigour of the new ant communities that are faced (Buren *et al*. 1974; Heller 2004). For *S. invicta, L. humile*, and *W. auropunctata*, ant communities in their native ranges in South America are typically more species rich than are those in various areas around the world where they have been introduced (e.g. compare: Clark *et al*. 1982; Tennant 1994; Heller 2004; Human and Gordon 1996; Le Breton *et al*. 2005; Suarez *et al*. 1999; Ward and Harris 2005; reviewed in Carpintero and Reyes-López 2008; Feener *et al*. 2008; LeBrun *et al*. 2007; Tschinkel 2006). This imbalance is most acute for oceanic islands, where many introduced ant species often occur and native ant faunas are often depauperate. Both *S. invicta* and *L. humile* experience strong interspecific competition within the diverse ant communities in their native ranges – including from each other where they are sympatric – and this competition shapes local distributions and patterns of dominance (LeBrun *et al*. 2007). Other species in these communities exhibit greater behavioural dominance, or are more efficient at resource location, and therefore attain some degree of ecological dominance even in the presence of *S. invicta* and *L. humile*. The lower-diversity ant communities in many invaded regions appear unable to offer this type of resistance. But what about cases where invasive ants have completely displaced highly diverse ant communities in undisturbed ecosystems, such as *W. auropunctata* in western equatorial African forests (Walker 2006) and *P. megacephala* in both open forests and monsoonal rain forests in Australia (Hoffmann *et al*. 1999; Vanderwoude *et al*. 2000)? Because the invaders are not entering species-poor communities in these examples, it would suggest that factors other than competitive release are operating. On the other hand, the competitive strength of an ant community may be only loosely tied to the number of species present, and could, for example, vary systematically among communities that evolved in different biogeographic regions (LeBrun *et al*. 2007; Suarez *et al*. 2008; Chapter 13). If true, simple comparisons between the diversity of an invader's source community and those of

introduction sites may not accurately predict whether competitive release is occurring. Much remains to be learned in this area.

A final factor potentially involved in the greater ecological dominance and increased size of invasive ant supercolonies concerns genetic changes that take place during and after introduction. This idea has been studied in greatest detail with the Argentine ant and postulates that reduced genetic variation, resulting from bottlenecks during founding events, has led to a diminished ability to discriminate between nestmates and non-nestmates within introduced populations (Tsutsui *et al*. 2000). Giraud *et al*. (2002) suggest that losses in discriminatory ability arose primarily after establishment through differential selection against uncommon recognition alleles. In either case, the resultant reduction in intraspecific aggression may have contributed to the formation of the massive Argentine ant supercolonies found in a variety of introduced areas. In addition, reduced genetic diversity may play a role in maintaining or expanding the size of introduced supercolonies by mediating patterns of asymmetric aggression among different supercolonies, with lower diversity supercolonies exhibiting greater agonistic behaviour towards higher diversity supercolonies than vice versa (Tsutsui *et al*. 2003). It is clear, however, that the vast supercolonies in some introduced areas are also the product of widespread transportation of a small number of founder colonies. The relative importance of these and other factors is still uncertain. Colony-structure variation occurs in native populations of Argentine ants, and includes localized supercolonies, but these are typically orders of magnitude smaller than those in introduced areas (Heller 2004; Holway and Suarez 2004; Suarez *et al*. 1999; Tsutsui *et al*. 2000 Pedersen *et al*. 2006). Smaller supercolonies are more likely to experience intraspecific competition from neighbouring supercolonies, and this may be part of the reason that Argentine ants are less ecologically dominant in their native range (Suarez *et al*. 2008).

Differences in genetic diversity between native and introduced populations also exist for *S. invicta* and *W. auropunctata*. In the case of *S. invicta*, genetic bottlenecks during introduction to the United States have resulted in changes in the sex determination

system, with the frequent production of sterile dip-loid males in polygyne populations (Ross 1993). However, this reduced genetic diversity is not linked to polygyny. Instead, polygyny appears to be determined at a single genomic region marked by the locus *Gp-9* in both introduced and native populations of *S. invicta* and its close relatives (Krieger and Ross 2002; Ross and Keller 1998), although differences exist between native and introduced populations in the number of queens per nest and patterns of relatedness within nests (Ross *et al.* 1996). Like some introduced populations of *L. humile*, *W. auropunctata* in New Caledonia has also passed through a severe genetic bottleneck, and there are large differences in the sizes of its supercolonies between native and introduced ranges (Foucaud *et al.* 2006). Unlike other ants, however, both introduced and some native populations of *W. auropunctata* reproduce predominantly clonally (in both queens and males; Fournier *et al.* 2005), and it appears that these clonal populations have arisen from normal, sexually reproducing populations in less disturbed parts of the native range (Foucaud *et al.* 2007). It remains to be determined how this variation in genetic diversity among populations relates to ecological dominance. In some cases, connections between genetic differences and ant density may be difficult to elucidate. For example, Abbott *et al.* (2007) documented two genetic haplotypes of *A. gracilipes* that are both unicolonial, but that attain strikingly different densities and levels of ecological dominance on the atolls of Tokelau. It is as yet unknown to what degree variation in the habitats occupied by each haplotype might contribute to this difference. In general, genetic differences between native and introduced populations strongly relate to patterns of human translocation, and genetic bottlenecks that occur from one introduced population to another or through human-mediated introduction events within the native range have the potential to confound the native versus introduced range dichotomy.

14.4 Future directions

Major gaps in our knowledge remain at each stage of the invasion process. At the earliest stage, the dynamics of establishment and initial persistence have received relatively little attention. How do small incipient colonies survive long enough and displace enough competing colonies to begin forming the supercolonies that subsequently make them so dominant? In some cases it appears that invasive ant supercolonies have managed to establish, survive, and grow in largely undisturbed natural habitats supporting diverse ant faunas (e.g. Vanderwoude *et al.* 2000), suggesting that they must possess fairly strong competitive abilities even at low densities. The most compelling evidence for such abilities comes from colony-introduction experiments. When single relatively small colonies (500 to 1,500 workers) of *L. humile* have been placed in the field among native Californian ants, these have often been found to be successful at winning control of baits (Holway 1999; Human and Gordon 1996). In Australia, however, results from similar experiments have been mixed. Small Argentine ant colonies were found to always win control of baits when facing colonies of *Iridomyrmex bicknelli* and two other native species in one community (Rowles and O'Dowd 2007), but even substantially larger colonies (5,000 workers) of *L. humile* were unable to displace *Iridomyrmex* 'rufoniger' from baits in another community (Walters and Mackay 2005). In cases where small Argentine ant colonies succeeded against resident ant colonies, they appeared to do so by recruiting higher numbers of workers to offered baits, frequently exhibiting aggression towards heterospecific workers, and raiding the nests of nearby competing colonies. Similar experiments have not been performed for other invasive ant species, but would seem to hold promise for illuminating key mechanisms involved in this early phase of the invasion process. Moreover, because they can remove much of the numerical imbalance that exists between native colonies and well-established invasive supercolonies, small colony-introduction experiments also have the potential to shed light on the question of possible asymmetries in inherent competitive abilities between species that originated in different biogeographic regions.

Important questions persist about dynamics that continue after establishment. For instance, while the heavy use of carbohydrate resources by invasive ants has long been recognized, it is unclear whether particular ant species require the presence

of certain types of honeydew-producing mutualists to spread into some habitats, or to become dominant in some communities. Likewise, it would be useful to know whether invasive ants typically rely on introduced mutualists, or instead whether there are enough native mutualists in most communities to meet their carbohydrate needs. Another area of interest concerns mechanisms of coexistence with invasive ants on the part of native ants. It is often reported that a few resident ant species can persist with invaders, but the ways in which they do this need to be tested more explicitly (e.g. Sarty *et al.* 2006, 2007; Ward 1987).

Longer-term dynamics are also of great interest, but not well studied. For example, the remarkably high densities of nests and workers measured in some invasions may exist above carrying capacity and thus be unsustainable. In one case study, the initial invasion of Brackenridge Field Station in central Texas by polygyne *S. invicta* resulted in the local displacement of native ants and many non-ant arthropods, with the severity of these impacts positively related to fire ant density (Porter and Savignano 1990). Over the subsequent decade, however, the initially high numbers of *S. invicta* declined to the point that native ants re-colonised the site and effects on non-ant arthropods became difficult to discern (Morrison 2002). In other cases, long-term studies have documented that other invasive ant species can remain abundant over time and continue to suppress native ants (Heller *et al.* 2008; Hoffmann and Parr 2008; Holway 1995; Tillberg *et al.* 2007; Walker 2006). In yet another pattern, some ant species may be present at low densities for many decades before suddenly becoming very abundant and invasive (Groden *et al.* 2005; O'Dowd *et al.* 2003). As for invasions generally (Simberloff and Gibbons 2004), the mechanisms underlying long-term changes in density of invasive ants can be hard to pinpoint (Krushelnycky *et al.* 2005a; Morrison 2002b), but making progress in this area is important. Increasingly, global climate change needs to be considered in studies of long-term population dynamics (Heller *et al.* 2008; Morrison *et al.* 2005; Roura-Pascual 2004).

Finally, as mentioned in the introduction of this chapter, a major barrier to understanding general causes of success among invasive ants is the currently small sample size. We have accumulated considerable knowledge about a few ant species, but still know little about others. For example, *Technomyrmex albipes, Paratrechina fulva*, and *P. longicornis* can attain high densities in some situations (Wetterer *et al.* 1999; Zenner-Polania 1994 Holway *et al.* 2002a), but little is known about the dynamics of these cases. Several other species, including *Lasius neglectus, Myrmica rubra*, and *Tetramorium tsushimae* have been recognized as invasive, or have become the subjects of research only relatively recently (e.g. Espadaler and Rey 2001; Groden *et al.* 2005; Steiner *et al.* 2006b). Additionally, a number of species have long been regarded as urban pests (e.g. *Monomorium pharaonis, Monomorium destructor*, and *Tapinoma melanocephalum*, Vander Meer *et al.* 1990; Williams 1994), and while these often appear to share some of the biological traits possessed by the species discussed throughout this chapter, the processes and mechanisms by which they achieve their success have not been sufficiently studied.

Further examination of the most common and widespread invasive ants is needed, but research on these additional ant species should also be highly informative. For example, both *L. neglectus* and *M. rubra* exhibit many characteristics common to invasive ants, including polygyny, polydomy, and an apparent ability to form large, continuous, high density aggregations of nests that spread out from anthropogenic habitats into surrounding more natural habitats (Espadaler *et al.* 2007; Groden *et al.* 2005). However, *L. neglectus* is of interest because, while it is unicolonial and has rapidly spread via human transportation like other invasive ant species (Ugelvig *et al.* 2008), its queens are morphologically and physiologically intermediate between those of typically monogynous, claustral-founding species that undergo mating flights and those of most invasive ant species, which are typically polygynous and undergo dependent-colony founding (Espadaler and Rey 2001). Laboratory colonies of *L. neglectus* can be initiated by independent queens, and while there is currently little evidence that winged dispersal by solitary queens occurs under natural conditions, the retention of traits associated with independent colony founding may provide physiological advantages that enhance invasion

success (Espadaler and Rey 2001). Meanwhile, *M. rubra* is unusual in that it forms large, dense populations of colonies that resemble supercolonies despite the presence of intraspecific aggression (Garnas *et al*. 2007). Apparently, aggression among nearby colonies is relatively subdued and does not prevent coexistence. These two more recently invasive species thus emphasize the fact that considerable variation exists among invasive ants. Their cases, as well as others, need to be further explored to gain a more complete picture of the factors that can lead to invasiveness. Moreover, these factors should be systematically compared between invasive ant species and their non-invasive relatives, as has been done for other taxa (e.g. Rejmánek and Richardson 1996), to strengthen inferences about their causal roles.

14.5 Summary

The nature of the current global economy all but ensures that introduced ants will continue to be transported to new regions of the world, and that they will initiate new invasions upon reaching some of these locales. A comprehensive understanding of the causal factors that promote invasiveness, as well as the mechanisms that mediate the invasion process, should assist in developing a predictive capacity about which species are likely to become invasive in which habitats. Comparisons among invasive ant species studied to date indicate that most appear to be pre-adapted to some degree for periodic disturbance, and most are either unicolonial or exhibit a reduction in inter-nest aggression. They can form relatively large colonies, even within their native ranges, and employ abundant active and generalist workers. When invasive ants meet suitable abiotic conditions within introduced ranges, native ant communities have shown little ability to stop their spread, although longer-term dynamics may follow various trajectories. The characteristics of several common invasive ant species in their native ranges are still not known, and much remains to be learned about a number of other species. Current conclusions, therefore, may be biased. Even if most invasive ant species appear to share a common group of behavioural traits, they may have arrived at this condition in different ways. As an example, recent research has revealed that the genetic mechanisms underlying unicoloniality, or at least polygyny and the breakdown of intraspecific territoriality, appear to be different for *L. humile, S. invicta* and *W. auropunctata*. Among other topics, future research should seek to understand how multiple strategies, genetic pathways, and ecological factors combine to create the emergent property of invasiveness in ants.