

Chapter 18

ELTON'S INSIGHTS INTO
THE ECOLOGY OF ANT
INVASIONS: LESSONS
LEARNED AND LESSONS
STILL TO BE LEARNED

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18.1 INTRODUCTION

Charles Elton's (1958) classic book, *The Ecology of Invasions by Animals and Plants*, provides numerous case studies of biological invasions. Given the breadth of taxonomic coverage that appears in the book, it is not surprising that Elton would mention several ant species and use them to illuminate several different general points about invasions. With regard to the spread, impact and control (or, more likely, lack thereof) of some invasive ant species, Elton was usually prescient. Much has been learned about the spread and impact of invasive ant species since the publication of *The Ecology of Invasions by Animals and Plants*. In this chapter, we revisit and elaborate on some of the points that Elton raised about ant invasions. Our chapter is loosely organized around the chapter titles and key concepts of Elton's book. In 'The invaders' (section 18.2), we introduce some of the most notorious invasive ant species, with particular focus on the Argentine ant: the ant that Elton most frequently referred to and has since become one of the best studied invasive species (Pysek et al. 2008). In 'New food chains for old' (section 18.3), we discuss some of the diverse ramifications of invasion by the Argentine ant. In 'The balance between populations' (section 18.4), we highlight the effects of the Argentine ant on populations of native species and how those effects can be temporally and spatially dynamic. We also discuss the balance of populations between invasive ants and other ants in the native range of the invasive species. The section 'Ecological resistance and the role of disturbance' (section 18.5) addresses whether there are particular characteristics of communities or ecosystems that make them more or less susceptible to invasion. Finally, in the last section, 'Standing on Elton's shoulders', we suggest some possible avenues of research for the next 50 years of ant ecology.

18.2 THE INVADERS

More than 150 ant species have been introduced outside their native ranges, but not all of these species cause ecological or economic impact (McGlynn 1999). Five ant species – *Anoplolepis gracilipes* (yellow crazy ant), *Linepithema humile* (Argentine ant), *Pheidole megacephala* (big-headed ant), *Solenopsis invicta* (red imported fire ant) and *Wasmannia auropunctata* (little fire ant) – are among the 100 worst invasive species

(Lowe et al. 2000). Additionally, two of these species – *L. humile* at second and *S. invicta* at fourth – are among the four most studied invasive species (Pysek et al. 2008). Of these five notorious invasive ants, Elton mentioned only *L. humile* and *P. megacephala* in his book. However, this probably should not be held against him because at the time much less was known about the other species. E.O. Wilson's first publication on the distribution of *S. invicta* in the southern USA was less than 10 years old (Wilson 1951), and the scope of the ecological problems associated with *S. invicta* was not yet realized (Blu Buhs 2004). Similarly, information on *A. gracilipes* and *W. auropunctata* was largely relegated to the grey literature and regional taxonomic journals until the 1970s (Fabres & Brown 1978; Fluker & Beardsley 1970). *Pheidole megacephala* has continued to receive considerable research attention, especially in Australia (Hoffmann & Parr 2008; Lach & Thomas 2008) and islands in the South Pacific (Savage et al. 2009).

At the time of publication of Elton's book, *L. humile* was relatively well studied in its introduced range. In fact, the first records of *L. humile* are from the Atlantic island of Madeira between 1847 and 1858, pre-dating the type specimen collected in Argentina in 1866 (Wetterer & Wetterer 2006; Wetterer et al. 2009). The native range of the Argentine ant includes the Parana and Uruguay River drainage areas of Argentina, Brazil, Paraguay and Uruguay (Tsutsui et al. 2001; Wild 2004). *Linepithema humile* has become established in mild Mediterranean climates globally (for example California, Chile, the Mediterranean Coast of Europe, coastal Australia, parts of New Zealand, South Africa), and Wetterer et al. (2009) recently documented the occurrence of *L. humile* at over 2100 sites in 95 geographical areas (for example countries, states or islands) throughout the world (Fig. 18.1). Even in the 1950s, however, Elton recognized that the Argentine ant was a global pest:

'The Argentine ant has also spread to other countries in an explosive way. In South Africa and Australia there has been the same elimination of native ants. Australia both in the south and west was reached by 1939-1941, and a further bridgehead in New South Wales by 1951.'

Several studies have tracked the rate of invasion or range expansion by Argentine ants in their introduced

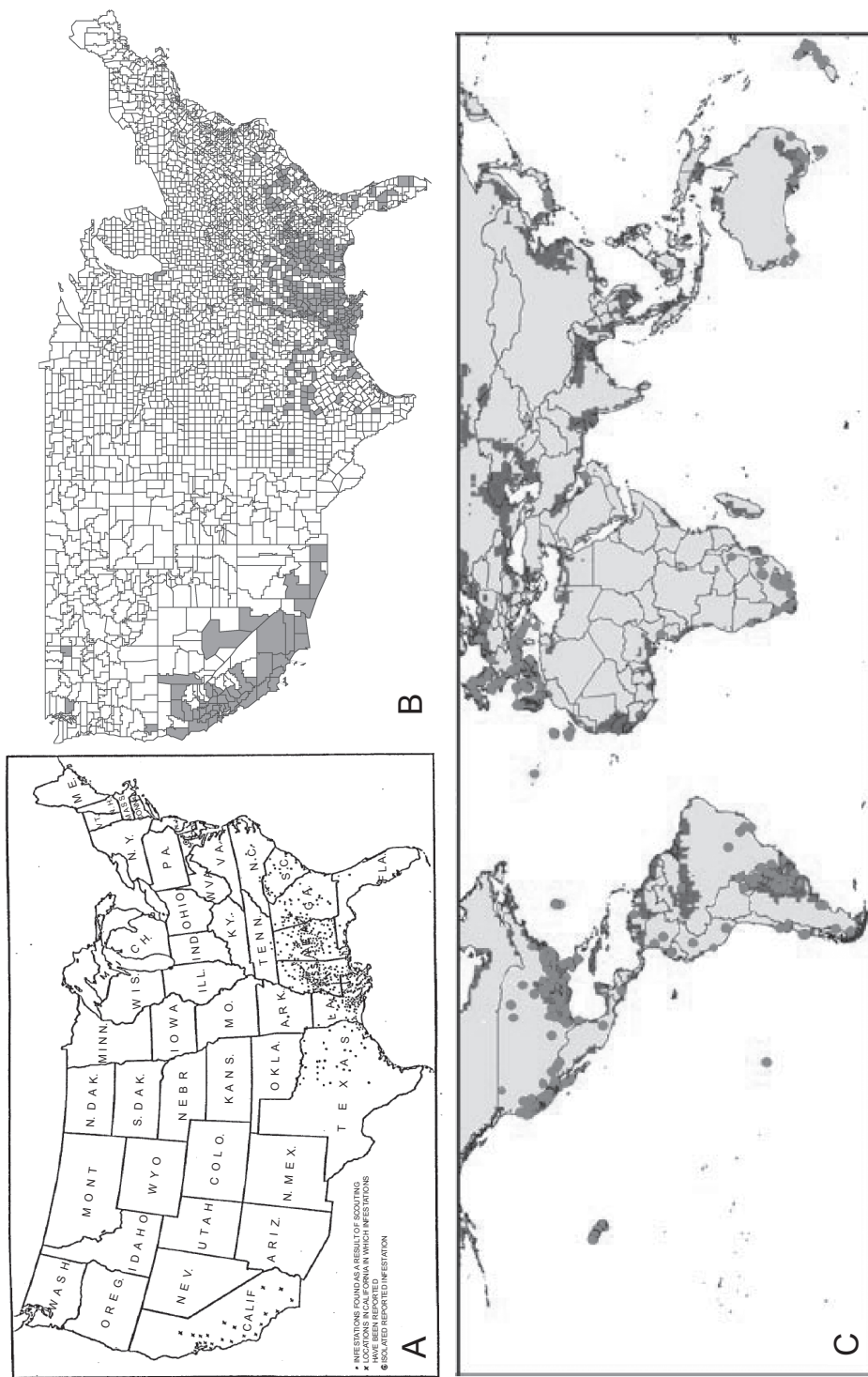


Fig. 18.1 The Argentine ant has become a model organism for spatial analyses of the occurrence and spread of invasive species. Sample figures from the Argentine ant's distribution in the USA (a, Elton 1958; b, Suarez et al. 2001) and globally (c, Roura-Pascual et al. 2004). Whether occurrence data were mapped as points on a map (a), associated with county level data (b) or globally geo-referenced (c), this information has been integral for both predicting regional patterns of spread through multiple dispersal processes (see, for example, Pitt et al. 2009) and for modelling how invasive species will change their distribution under different models of climate change (Roura-Pascual et al. 2004).

range (Suarez et al. 2001). At local spatial scales, the rate of spread of Argentine ants is quite slow (0–250 myr⁻¹) because colonies disperse by budding rather than by nuptial flights. However, at regional scales, Argentine ants move by human-assisted jump dispersal, resulting in rates of spread of several hundred kilometres per year (Suarez et al. 2001). Elton highlighted this scale-dependent rate of spread in Argentine ants, noting that

‘The Argentine ant is not, as a matter of fact, a very fast natural invader, for its nuptials take place almost entirely within the nest, and its movements by crawling would not take it more than a few hundred feet a year. It seems that transport in merchandise, especially by railway train, dispersed it so quickly within the United States.’

Long-term monitoring (see, for example, Holway 1998b; Heller et al. 2008b; Sanders et al. 2001) and historical data (Suarez et al. 2001) coupled with elegant experiments (Menke & Holway 2006) suggest that the rate of invasion, and perhaps ultimately the global distribution of Argentine ants, depends strongly on climate.

The impacts of *L. humile* on native biodiversity were also already clear at the time of Elton’s book. For example, Elton wrote of the Argentine ant:

‘Everywhere it multiplied immensely and invaded houses and gardens and orchards, eating food or – out-of-doors – other insects, also farming scale insects and aphids on various trees ... A conspicuous character of this fierce and numerous tropical ant is that it drives out native ants entirely.’

Research over the past 25 years has confirmed that almost everywhere it has become established, the Argentine ant has caused dramatic reductions in the diversity of ants, changed the relative abundance of other arthropods and altered the structure of communities (Ward 1987; Human & Gordon 1997; Holway 1998a; Sanders et al. 2003; Oliveras et al. 2005; Tillberg et al. 2007; Carpintero et al. 2007; Abril & Gomez 2009). For example, at a single site invaded by Argentine ants in southern California, the number of native ant species dropped from 23 to 2 over the course

of several years (Tillberg et al. 2007). Importantly, the impacts of *L. humile* on native diversity can occur almost immediately, and the effects of *L. humile* can cascade across the entire ecosystem by disrupting the co-evolved interactions among species (see Suarez & Case 2002; Lessard et al. 2009; Rodriguez-Cabal et al. 2009), something Elton devoted an entire chapter to called ‘New food-chains for old’.

18.3 NEW FOOD CHAINS FOR OLD

‘On the trees with ants, scale insects were on average five times as common; at the peak of the year 150 times. This was because the Argentine ants killed off many though not all of the natural enemies and parasites of the scales.’

Argentine ants, as well as many other invasive ant species, disrupt food webs and mutualistic interactions with plants and honey excreting hemipterans (see Lach 2003, 2007; O’Dowd et al. 2003; Savage et al. 2009). The ability of Argentine ants to exploit resources more efficiently than many native species may allow them to monopolize an important and relatively stable food resource: honeydew from hemipterans and extrafloral nectar from plants. Argentine ants have long been associated with high densities of honeydew-producing hemipterans, especially in agricultural and riparian systems (Newell & Barber 1913). More generally, there seems to be a growing appreciation that tapping into carbohydrate-rich honeydew fuels ant invasions (O’Dowd et al. 2003; Tillberg et al. 2007; Rowles & Silverman 2009), and Argentine ants are no exception in their ability to exploit hemipterans and extrafloral-nectar-bearing plants. Rowles and Silverman (2009) showed experimentally that access to carbohydrate-rich resources facilitated invasion of natural habitat by Argentine ants in North Carolina. The spread and impacts of other invasive ant species might also be exacerbated by their participation in mutualisms with hemipterans. For example, the yellow crazy ant (*Anoplolepis gracilipes*) has had dramatic effects on the flora and fauna of Christmas Island, in part because of its interactions with scale insects (O’Dowd et al. 2003). Invasion by red imported fire ant (*Solenopsis invicta*) may be facilitated by introduced species of mealybug in some parts of its range (Helms & Vinson 2002).

In addition to providing fuel for a work force, increased access to plant-based carbohydrates may also directly influence the growth and behaviour of invasive ants. In both Argentine ants (Grover et al. 2007) and fire ants (Helms & Vinson 2008) access to carbohydrates can increase colony sizes by up to 50%, primarily through worker longevity. Moreover, access to carbohydrates can increase levels of aggression and forger activity in Argentine ants (Grover et al. 2007). More research needs to be done to understand the role of mutualism in invasion dynamics generally (Traveset & Richardson, this volume). This is especially important for understanding ant invasions, given that ant-hemipteran interactions are ubiquitous in many systems.

Native ants provide numerous functions in ecosystems, and when they are displaced by Argentine ants, those functions, more often than not, are lost. A classic study from the fynbos in South Africa showed the potential consequences of invasion by *L. humile* for the plant species that relied on native ant species to disperse their seeds (Bond & Slingsby 1984). A recent review of the literature by Rodriguez-Cabal et al. (2009) found that, across all studies, sites with *L. humile* contained 92% fewer native seed dispersers than nearby sites without *L. humile*, and that the loss of native ant species had consequences: across all studies, sites with *L. humile* had 47% fewer seeds removed and seedling establishment was 76% lower. The effects of Argentine ants on seed-dispersal mutualisms are not always straightforward, however, and Argentine ants may favour seeds of some species over others (Rowles & O'Dowd 2009). Thus, for at least some plant species, Argentine ants may replace native ants as seed dispersers (Rowles & O'Dowd 2009).

Argentine ants affect more than just ants and the plants whose seeds the native ants disperse. They can also have indirect effects on vertebrate populations. In southern California, the Argentine ant has displaced numerous native ant species (Suarez et al. 1998; Tillberg et al. 2007), and this might have indirectly led to population declines of coastal horned lizards (Suarez et al. 2000; Suarez & Case 2002). Suarez et al. (2000) showed experimentally that when individual horned lizards are offered only *L. humile* as food, their growth rates decline precipitously. One compelling explanation for the decline in horned lizard populations is that *L. humile* displaces the native ants (mostly in the genus *Pogonomyrmex*), and it is these native ants that make up around 90% of the diet of coastal horned lizards. In

addition, continued habitat alteration in southern California has negative impacts on coastal horned lizards but positive effects on *L. humile* by making some sites more susceptible to invasion. Thus it appears that habitat alteration combined with invasion by *L. humile* could be responsible for declines in coastal horned lizard populations. There is also some evidence that Argentine ants affect bird populations as well (Pons et al. 2010).

18.4 THE BALANCE BETWEEN POPULATIONS

Though the impacts of Argentine ants on native species can be immediate, substantial and diverse, they are also temporally dynamic. That is, the impacts might dissipate over time and interact with abiotic conditions such as weather and climate (Heller et al. 2008b). Since 1993, Deborah Gordon's research group has monitored the distribution of the Argentine ant and native species in Jasper Ridge Biological Preserve in northern California. The data illustrate a couple of interesting points. First, and not surprisingly, sites with Argentine ants are species poor, for ants and other invertebrate taxa, relative to sites where Argentine ants have yet to invade (Human & Gordon 1997; Sanders et al. 2001). Second, though the number of ant species in a site can decrease dramatically upon the establishment by *L. humile*, there is a positive correlation between ant species richness and the number of years a site has been invaded (Heller et al. 2008b). That is, in areas where Argentine ants cannot maintain high densities, the negative effects of Argentine ants on diversity might decrease through time. Finally, there seem to be strong seasonal and abiotic effects on the distribution and range expansion of *L. humile* at Jasper Ridge: the distribution of *L. humile* increases in wet years and wet seasons and contracts during hot dry years and seasons (Human et al. 1998; Sanders et al. 2001; Heller et al. 2008b). One of the consequences of this seasonal ebb and flow of Argentine ants is that native species might rapidly colonize, or at least become more active, when Argentine ants retreat from a site (Sanders et al. 2001), something Elton (1958) pointed out:

'Just as soon as the Argentine ants begin to disappear, native ants invade the territory, and within a few years are as plentiful as ever.'

Elton suggested that the impact of the Argentine ant on native communities resulted from competitive displacement by interference:

'When there is a very clear verdict, as with the Argentine ant, that hard fighting has resulted in regular and catastrophic and general replacement of other species, including other ants, the case is complete: that is replacement through interference.'

Most studies of invasive ants (if not all ants generally) have focused on interference competition among species as the key determinant of community structure (Hölldobler & Wilson 1990; Holway et al. 2002a). However, both interference and exploitative competition occur in ant communities. The outcomes of interference interactions among species are likely determined by worker size (Fellers 1987), which species initiated the interaction (Human & Gordon 1999), or numerical advantages that depend recruitment ability or colony size. Exploitative competition, on the other hand, likely depends on both the ability of individual foragers to quickly and efficiently locate food resources, and the ability of recruits to retrieve the food resources once they are discovered (Fellers 1987; Holway 1999; Human & Gordon 1996).

Argentine ants interfere with native species (Way et al. 1997; Holway 1999; Human & Gordon 1999;). However, detailed behavioural observations on interactions among native ant species and Argentine ants indicate that the case for interference alone as a means of displacement is not as clear as Elton suggested. For example, Human & Gordon (1999) found that, under some conditions, Argentine ants were just as likely to retreat from native ants as native ants were from Argentine ants. Argentine ants were, however, more likely than native ants to behave aggressively toward other species. In a similar experiment, Holway (1999) found that, in head-to-head interactions, single Argentine ant workers experienced mixed success, but Argentine ant colonies were able to displace native ant species more often than not. Holway (1999) noted, 'The discrepancy between worker-level and colony-level interference ability suggests that numerical advantages are key to the Argentine ant's proficiency at interference competition.'

The numerical advantages conferred by a large colony size also increase the Argentine ant's exploita-

tive abilities. Several different studies have shown that Argentine ants are more proficient at finding and monopolizing resources than are native species (Human & Gordon 1996; Holway 1999). Taken together, the results of these studies indicate that Argentine ants might not adhere to an exploitation–interference trade-off that many native species are subject to. The basic idea of competitive tradeoffs, in ants at least, was first empirically tested by Fellers (1987). In a classic study, she found that, for a guild of native ant species, there was a negative relationship between interference ability and resource discovery rate. Holway (1999) was the first to show that Argentine ants, at least relative to the suite of native ant species with which they competed most directly, appeared to have broken the exploitation–interference trade-off and are proficient at both interference and exploitation. This competitive double blow, which is partly a product of behaviour, colony size and colony structure, undoubtedly confers a unique advantage to Argentine ants in their introduced range. In the native range of Argentine ants, however, several species are at least as proficient at securing resources as are Argentine ants (LeBrun et al. 2007). This might account for Elton's observation that the Argentine ant 'does not appear to be generally a pest of importance in [Argentina]'. LeBrun et al. (2007) argue that this release from competitive pressure might play an important role in the success of the Argentine ant in its introduced range.

So far, we have documented that the Argentine ant has had substantial impacts on biodiversity and the integrity of ecosystems outside its native range, as do many other invasive ant species (Holway et al. 2002a). But what else have we learned about the success of invasive ants by studying their native ranges? Elton was a strong proponent of studying invasive species in their native range in order to gain insights into what might make them invasive in their introduced ranges. It was perhaps not lost on Elton that most hypotheses suggested for the success of invasive species (for example escape from natural enemies, increased competitive ability, different competitive environment, pre-adapted to disturbance) require some comparison between native and introduced populations.

As pointed out above, Argentine ants experience different competitive environments in their native and introduced populations. This is not the only difference, however; Argentine ants also vary considerably in colony size among populations (Tsutsui et al. 2000;

Pedersen et al. 2006; Heller et al. 2008a; Vogel et al. 2009). Introduced populations of Argentine ants have long been known to have large 'supercolonies' where intraspecific aggression is absent among many spatially separate nests (Newell & Barber 1913). When ants do not exhibit any intraspecific aggression among nests over the scale of an entire population (for example the scale at which the potential for reproduction or competition can occur), that population is considered 'unicolonial' (Bourke & Franks 1995; Hölldobler & Wilson 1977). Nearly all introduced populations of Argentine ants are unicolonial and the only exceptions are a few rare cases where two enormous supercolonies come into contact with one another over large areas (Giraud et al. 2002; Thomas et al. 2006).

However, it was not until relatively recently that the spatial scale of supercolonies was examined in native populations (Suarez et al. 1999). Although Argentine ants also exist in polydomous supercolonies in their native Argentina, they are much smaller and many of them will co-exist in a single population (Pedersen et al. 2006; Tsutsui et al. 2000). Therefore, in contrast to introduced populations where intraspecific aggression almost never occurs, territorial behaviour is relatively common in native populations with dozens of intraspecifically aggressive supercolonies competing for resources.

It has been argued that intraspecific aggression among Argentine ant supercolonies can reduce their ability to monopolize resources, can influence colony growth (Holway et al. 1998) and result in massive mortality of workers at contact zones (Thomas et al. 2006). Unicoloniality may therefore contribute to ecological dominance by enhancing colonization ability, resource exploitation and interference interactions (Helanterä et al. 2009). Indeed, unicolonial colony structures have been documented or inferred for *Anoplolepis gracilipes*, *Linepithema humile*, *Pheidole megacephala*, *Solenopsis invicta* and *Wasmannia auropunctata*. What we do know about unicoloniality is based largely on studies of just a few species, and we still do not know answers to basic questions about the evolution of unicoloniality or how it is maintained in ecological time (Helanterä et al. 2009).

Ultimately, unicoloniality alone cannot account for the success of invasive species in general, or the Argentine ant specifically. As Elton pointed out, the interplay between traits of invaders and characteristics of recipient communities determines invasion success. For example, novel interactions between Argentine

ants and resident species in introduced populations may have allowed them to become successful invaders, and characteristics of communities might make them susceptible to invasion. We turn now to the interplay between invader and invaded community.

18.5 ECOLOGICAL RESISTANCE AND THE ROLE OF DISTURBANCE

Although there is little doubt that some characteristics of the Argentine ant make it a successful invader, much less is known about whether there are particular characteristics of ant communities that make them more or less susceptible to invasion. In the literature on non-ant invasive species, two characteristics have received the most research attention: ecological resistance and disturbance.

Elton noted that not all introduced species become highly invasive: 'there are enormously more invasions that never happen, or fail quite soon ... they meet resistance.' Elton also speculated on the nature of this 'resistance':

'... they will find themselves entering a highly complex community of different populations, they will search for breeding sites and find them occupied, for food that other species are already eating, for cover that other animals are sheltering in ... meeting ecological resistance.'

Ecological resistance is the notion that areas with high species richness should be more difficult to invade than areas with low species richness (Levine et al. 2004). Though this hypothesis (now often called the biotic resistance hypothesis or the diversity–invasibility hypothesis; Fridley, this volume) has been tested both observationally and experimentally, mostly in plant communities (Fridley et al. 2007), it has yet to be tested experimentally in ants. Observational studies of invasion by Argentine ants have not provided direct evidence that native ant diversity prevents or slows the spread of Argentine ants in California (Holway 1998b; Sanders et al. 2003; Carpintero et al. 2007; Roura-Pascual et al. 2009). However, it has been speculated that the species-rich ant communities in Australia, in which competitively dominant native ant species are often abundant, may offer resistance to ant invasions

(Majer 1994). The ideal experimental test of ecological resistance in ant communities would manipulate the number of ant species in a community and then add colonies of invasive species to those communities. To our knowledge, no one has yet tried this experiment, perhaps because of the logistical difficulties of manipulating intact ant communities and because it is ethically questionable to add invasive ant species to areas where they do not yet occur.

Many invasive species, including invasive ant species, often become established in disturbed sites. Most invasive ant species have also spread into relatively undisturbed sites: *Anoplolepis gracilipes* (O'Dowd et al. 2003; Hoffmann & Saul 2010), *Linepithema humile* (Holway 1999; Sanders et al. 2001; Krushelnycky et al. 2005a; Lach 2007), *Pheidole megacephala* (Hoffmann et al. 1999; Vanderwoude et al. 2000), *Solenopsis invicta* (Porter & Savignano 1990; Morris & Steigman 1993; Helms & Vinson 2001; Cook 2003; Stuble et al. 2009) and *Wasmannia auropunctata* (Clark et al. 1982; Walker 2006). Disentangling the combined and relative effects of disturbance and invasive species on native communities has only rarely been tested, even in observational studies. Holway (1998b) took advantage of 5 years of monitoring data on the spread of Argentine ants in riparian corridors to assess whether disturbance, native ant species richness (i.e. 'biotic resistance'), or stream flow (a measure of moisture availability) best predicted the spread of Argentine ants. Neither biotic resistance nor disturbance accounted for any of the variation in invasion rate. Stream flow alone accounted for 46% of the variation in invasion rate, supporting the notion that physiological tolerance plays an important role in the invasion dynamics of this species. Sanders et al. (2003) also found no relationship between species richness of native ants and probability of invasion by *L. humile* over a study lasting several years. Following up on Holway's observational study, Menke and colleagues (Menke & Holway 2006; Menke et al. 2007) experimentally manipulated moisture availability and the presence of native species. They found that moisture availability was more important than native ant community structure in explaining the invasion dynamics of *L. humile*, again strongly implicating a key role of climate on invasion processes.

Though there is evidence from other non-ant systems in support of the biotic resistance hypothesis (Fridley et al. 2007), there appears to be no evidence that native ant species richness acts as a deterrent to

ant invasions. Similarly, Argentine ants appear to invade both disturbed and undisturbed habitats, and no study so far has explicitly tested the hypothesis that disturbed habitats are more susceptible than undisturbed habitats to invasion. This suggests that disturbance alone cannot be used to predict a site's susceptibility to invasion.

Other factors are often correlated with invasion success, namely propagule pressure or propagule size (Simberloff 2010). However, there have been few tests of the role of propagule pressure or size in ant invasions. Recently, Sagata and Lester (2009) showed experimentally that neither propagule size (the size of the 'invading' colony) nor resource availability consistently predicted invasion success by *L. humile*. They went on to suggest that the ability of *L. humile* to modify its behaviour according to local conditions will all but rule out the ability to predict whether a site will be invaded, based simply on resource availability or characteristics of the native community at that site (Sagata & Lester 2009).

To summarize, it seems that three characteristics of Argentine ants, rather than biotic resistance or disturbance, drive invasions by *L. humile*: unicoloniality, their competitive ability and their behavioural flexibility. Those three factors, coupled with appropriate climatic conditions of a site (for example neither too dry nor too cold), seem to account for the success and failure of Argentine ant invasions.

18.6 STANDING ON ELTON'S SHOULDERS

Elton focused on the Argentine ant, because it was (and still is) the best-studied invasive ant species (Pysek et al. 2008). In this chapter, we have also focused on the Argentine ant, but clearly numerous other ant species pose serious threats to biodiversity and the functioning of ecosystems, and much remains to be learned even about those well-studied species like the Argentine ant and the red imported fire ant. Additionally, in the 50 years since the publication of *The Ecology of Invasion by Animals and Plants*, ant ecologists, like all ecologists, have built on what Elton wrote about, in part because of the continued evolution of technological tools that have allowed us to ask questions about the chemical ecology and population genetics of invading populations (Brandt et al. 2009; Vogel et al. 2010), trophic dynamics during invasion

(Tillberg et al. 2007) and the ability to predict global distribution of invasive ants in response to climate change (Roura-Pascual et al. 2004). Here, we highlight what we think are the most substantial advances since the publication of Elton's book and suggest a few areas of future research on the ecology of ant invasions.

Much remains to be learned about the role of positive interactions in invasions (Richardson et al. 2000), and especially for invasive ant species. In some cases, invasive ants may simply replace native ants as mutualists, but in other cases important functions might be lost (Rodríguez-Cabal et al. 2009). And, unfortunately, most studies that have examined whether invasive ant species disrupt mutualisms have focused almost entirely on the Argentine ant (Rodríguez-Cabal et al. 2009). Clearly more work, on more invasive species, needs to be done. Stable isotope analyses (see, for example, Tillberg et al. 2007) will likely play an important role in examining the role of invasive species in new food chains and as mutualists.

Climate clearly influences the distribution of many invasive ant species. This leads to a question that Elton did not raise, but is now at the forefront of considerable research: how will climate change affect the distribution of Argentine ants and other invasive ant species at global scales and perhaps mediate their impact on native biodiversity? In general, environmental niche models suggest that the Argentine ant has the potential for further spread into central Madagascar, Taiwan, southeast Asia, high-elevation Ethiopia and Yemen, and numerous oceanic islands are likely at risk of future establishment (Roura-Pascual et al. 2004; Hartley et al. 2006). Environmental niche modelling can be an important tool for conservation practitioners, but they could be improved by incorporating information on dispersal (see, for example, Roura-Pascual et al. 2009) and ecological interactions with other species, as well as evolutionary responses to changing climates (Fitzpatrick et al. 2007). For example, the outcome of interactions between Argentine ants and native species can depend on environmental temperature (Holway et al. 2002b), but understanding how climatic change will modify interspecific interactions, drive evolutionary responses of both native and invasive species, and ultimately mediate the impact of invasive species is a pressing challenge (Dukes & Mooney 1999; Araujó & Rahbek 2006).

Linepithema humile and *Solenopsis invicta* are the best studied invasive ant species (and perhaps the best

studied ant species), and the ever-evolving population genetics toolkit has uncovered many surprising and important characteristics of the population structure of both species in their native and invasive ranges (see, for example, Tsutsui et al. 2000). The other major invasive ant species – *Anoplolepis longicornis*, *Pheidole megacephala* and *Wasmannia auropunctata* – have received some research attention, but not nearly as much as *L. humile* or *S. invicta*. The paucity of information on many other exotic and invasive species is troubling (for example *Doleromyrma darwiniana*, *Lasius neglectus*, *Monomorium pharoensis*, *Monomorium sydneyense*, *Myrmica rubra*, *Pachycondyla chinensis*, *Paratrechina longicornis*, *Paratrechina fulva*, *Pheidole obscurithorax*, *Technomyrmex albipes*, *Tetramorium tsushimae*, *Ochetellus glaber* and several species in the genus *Cardiocondyla*). Unfortunately, what we have learned about *S. invicta* and *L. humile* has been too little too late: they are both responsible for dramatic alterations in native communities. Perhaps by devoting some research effort towards understanding the behaviour and ecology of these other species *before* they become invasive will help minimize or eliminate their potential impacts on biodiversity.

Controlling, or even eradicating, populations of exotic species is a lucrative business and a focus of continued research (Myers et al. 2000). This is especially true for invasive ant species (see Silverman & Brightwell 2008). Though there have been some successful eradications and efforts at controlling spread and impact – *A. gracilipes* on Christmas Island (Green & O'Dowd 2009) and *W. auropunctata* on smaller islands in the Galapagos archipelago (Causton et al. 2005) – much remains to be learned, from both the successes and the colossal failures (for example *S. invicta* in the southeastern USA). For example, what are the traits of species that make them more or less susceptible to eradication and control? Are there particular environmental or ecological conditions that mitigate control efforts? Our view is that ant ecologists studying invasive species should also contribute at least some research effort to improving the ability to control the spread and impact of invasive ant species (see, for example, Krushelnicky et al. 2005b).

Elton was prescient in realizing the importance of studying invaders within native populations to understand what makes them successful. Since Elton's publication, the Argentine ant has received more research attention in its native range than any other invasive ant species, and perhaps more than many other

invasive species. The insights gained from these studies are numerous and have highlighted some of the mechanisms that might contribute to its success as an invasive species. However, by comparison, we know very little about the biology of other invasive ants in their native ranges (except perhaps *S. invicta* and more recently *W. auropunctata*). And for most introduced ant species, we still have not even identified from where introduced populations originate. However, for the well-studied species like *L. humile*, recent and ongoing research in nearly all parts of its introduced range offer exciting, but largely untapped, opportunities for comparative studies of the impact of this globally important species.

It is abundantly clear that invasive species are a leading cause of population- and species-level extinctions (Clavero & Garcia-Berthou 2005), and that invasive species can dramatically alter the structure and function of ecosystems (Kurlle et al. 2008). In the absence of experimental introductions or removal of invasive species over extensive regions, longitudinal studies of ant communities pre- and post-invasion will help elucidate the consequences of ant invasions on native biodiversity and the functioning of ecosystems (see, for example, Tillberg et al. 2007; Heller et al. 2008b; Hoffmann & Parr 2008). Nevertheless, the consequences of ant invasions, across trophic levels, taxa and for a variety of ecosystem processes are often severe (Holway et al. 2002a). Though the general public's awareness of the impacts of invasive ant species on human health and agriculture has grown substantially in the 50 years since the publication of Elton's book, those who care about the threats that invasive species pose must be vigilant and ensure that, from time to time, we get out of the ivory tower to inform the public and policy makers about the threats that invasive ant species pose, much like Charles Elton did more than 50 years ago.

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