

seedlings does influence neighboring siblings. The use of silenced plants to establish the allelopathic potential of a chemical would be an indispensable tool for putative allelopathic crops such as *Sorghum bicolor*.

ALLELOPATHY AND PLANT INVASIONS

Allelopathy has been investigated as a probable cause of invasion success of nonnatives. However, the traditional approach that examines nonnatives in the same way as other native plants also suspected of allelopathic activities was taken. Ragan Callaway and colleagues at the University of Montana compared allelopathic effects of exotic invasives on species from their native and invaded communities, which provides stronger evidence than the traditional approach for whether or not allelopathy actually contributes to invasive success. The term “novel weapons hypothesis” was proposed to describe the general effects of *Centaurea* species, and chemicals contained in their root exudates, which were more effective against species in invaded regions than against related species in native regions. *Centaurea diffusa* and *C. maculosa* roots exude 8-hydroxyquinoline and (\pm)-catechin, respectively, in both their native lands in Eurasia and in their naturalized ranges, but in some experiments, these chemicals inhibited North American species more than Eurasian species. Some of this work, however, was criticized due to inadequate methodology for soil extraction and conflicting data on recovery of catechin from *C. maculosa* soils. This may be the result of climatic and edaphic variation that creates a great deal of conditionality, which influences the exudation and availability of chemicals in soil.

CONCLUSION

A better knowledge of the biochemical pathways (enzymes and genes) involved in the production of putative allelochemicals, their accumulation and transport to the soil, and the potential in vivo interactions of these compounds will provide the physiological basis for improved understanding of the role of allelopathy in both agricultural and natural ecosystems. Allelopathy is a conditional and species-specific effect, and the term “allelopathy” may be misleading unless this conditionality is addressed. In addition to investigating the roles of allelochemicals at population level, there is a need to explore temporary versus long-term ecological changes caused by allelochemicals, and to define changes at population and community levels. Allelopathy needs to be conceptualized and investigated in terms of soil chemical ecology, which can further allelopathy research and reduce some of the less fruitful controversy surrounding this science.

SEE ALSO THE FOLLOWING ARTICLES

Competition, Plant / Novel Weapons Hypothesis / Seed Ecology / Vegetative Propagation

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AMPHIBIANS

SEE REPTILES AND AMPHIBIANS

ANTS

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Five of the world’s 100 worst invasive species (see Appendix) are ants, although ants make up only a minuscule fraction of the Earth’s biodiversity. There are over 12,000 described ant species, yet in some places, it is possible to spend entire days (if not entire field seasons) studying the ant fauna without seeing any native ants. Almost without fail, when populations of invasive ant species become established, they dramatically affect populations of native ants, other arthropods, and in some cases populations of vertebrates and plant communities.

INVASIVE ANT SPECIES

Approximately 150 ant species have become established outside of their native ranges, but not all of them have become invasive—that is, have established in and disrupted native ecosystems outside of their native range.

The five most widespread and problematic invasive ant species are *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).

Though these species are globally widespread and recognized as pests, tremendous variation exists in how much is known about each. There are over 1,300 publications about *S. invicta*, 467 about *L. humile*, 116 about *P. megacephala*, and 85 about *W. auropunctata*, but only 33 about *A. gracilipes*. This article will, by necessity, focus on species for which adequate information is available. But that is not to deny that many other potentially problematic species might threaten native communities and ecosystems, or at least become pests, in their introduced ranges.

NATIVE AND INTRODUCED RANGES

Introduced invasive ants originate in both the Old and New Worlds. With few exceptions (e.g., *Myrmica rubra*), most introduced invasive species have originated in the southern hemisphere. Of the five most widespread species, three are South American: *Linepithema humile*, *Solenopsis invicta*, and *Wasmannia auropunctata*. While the native ranges of *L. humile* and *S. invicta* include Argentina, Uruguay, and Paraguay, *W. auropunctata* occurs from Argentina north to Central America, and the origins of invasive populations are still unclear. *Pheidole megacephala* and *Anoplolepis gracilipes* originated in Africa (or Asia for *A. gracilipes*).

These species now occur on most continents and many isolated oceanic islands. The introduced range of *A. gracilipes* includes southern Africa, southern Asia, the Caribbean, and several islands in the Indian and Pacific oceans. *Linepithema humile* has become established in mild Mediterranean climates globally (e.g., California, the Mediterranean coast of Europe, coastal Australia, parts of New Zealand). *Solenopsis invicta* became established in the southern United States in the 1930s and has since spread as far west as Texas and California and as far north as Maryland and Delaware in the United States. It has also been detected in China, New Zealand, Hawaii, Australia, Malaysia, and Taiwan. *Pheidole megacephala* is from southern Africa, and it now occurs in many of the world's temperate and tropical regions. *Wasmannia auropunctata* has been introduced to parts of Africa, North and South America, and Israel, as well as to islands in the Caribbean and the Pacific Ocean (New Caledonia, Vanuatu, Tahiti, Galapagos, Hawaii, and the Solomon Islands).

Most research on invasive ant species has occurred in the introduced ranges of the species (with one exception;

more is known about *Myrmica rubra* in its native range than in its introduced range). This paucity of research is unfortunate because studying species in their native ranges might reveal important differences in the behavior, life histories, population biology, and ecology of invasive species that could help explain the success of invasive ant species in their introduced ranges. Of course, the native ranges of some invasive species remain unknown, and it is often difficult to do fieldwork in remote locations. However, several recent studies, especially with *L. humile*, have shown that the population genetic structure, competitive interactions with the rest of the ant community, and trophic ecology can differ dramatically between native and introduced ranges. These differences have illuminated, at least for this species, some of the mechanisms that might account for its success as an invasive species.

Modeling the Potential Introduced Range of Invasive Species from the Native Range

Environmental niche models aim to predict the potential introduced ranges of invasive ant species based on information about environmental conditions in their native ranges. The general approach of environmental niche modeling is to obtain information on climatic conditions in the native range of the species and then to find locations with the same, or at least similar, conditions in other parts of the globe. Places outside the native ranges with similar environmental conditions to those in the native range are considered susceptible to invasion. However, this approach generally ignores three important facts. First, both biotic and abiotic factors limit the distributions of ant species, and most environmental niche models are not equipped to include the influence of factors such as competition or disturbance. Second, in order to model the potential range of an introduced species, the species must be at equilibrium with climate in its native range. That is, it has to occur everywhere it possibly can, at least as determined by climatic conditions, and it has to have been sampled well enough in its native range to know where it occurs and where it is absent. And third, species evolve and undergo niche shifts. If either evolution or niche shifts occur, perhaps because of genetic bottlenecks common to many invasions, then the environmental niche models will fail to predict accurately the potential ranges of introduced ant species.

Several recent studies have modeled the potential invasive range of *Solenopsis invicta* in North America based on its apparent distribution in its native range. However, the models frequently fail. That is, in some cases, the predicted invasive range is substantially smaller than the actual range

of *S. invicta*. But in other cases, the models undoubtedly overestimate the potential range of *S. invicta* in North America. For example, it is highly unlikely that *S. invicta* will become established in Canada or points northward, though some models have predicted such a scenario.

Species Traits That Might Correlate with Success

One early goal of invasion biology was to identify traits of particular species that might promote their success as invaders. Most investigators would argue that searching for traits alone as a key to invasion success oversimplifies the issue—that the interplay between the traits of the invader and the characteristics of the native community and environment, along with the opportunity to invade, are the key determinants of invasion success. The same is likely true for invasive ants, but are any life history traits shared among the most successful invasive ant species?

TROPHIC ECOLOGY The five worst invasive ant species are all omnivores. They prey on small arthropods, scavenge dead animals, and tend hemipterans for their carbohydrate-rich secretions. But many, if not most, ant species are omnivorous, so omnivory alone cannot account for the success of invasive species. There is some evidence that the ability of some invasive species to exploit hemipterans more efficiently than do native ant species might fuel their success.

Stable isotope analyses have proven useful in characterizing diets of many native and nonnative ant species. Although more studies are needed, recent evidence suggests that the diet of invasive ant species, at least for *Linepithema humile*, may be more flexible than that of native ant species. Such dietary flexibility could promote invasion success by allowing invasive ants to exploit a wide variety of food resources in order to use the most abundant or nutrient-rich resources.

BODY SIZE Body size is an important life history trait for most species. In ants, body size spans several orders of magnitude, both among species and even within the same colony of a single species. Edward O. Wilson was among the first to argue that within-colony variation in body size, or polymorphism, might allow workers to specialize and thereby increase colony efficiency. Is there evidence that the most successful invasive species are polymorphic? Some are (*Solenopsis invicta*, *S. geminata*, and *Pheidole megacephala*), but others (*Linepithema humile*, *Anoplolepis gracilipes*, *Wasmannia auropunctata*) are not. Similarly, many noninvasive species exhibit extreme polymorphism, so polymorphism alone cannot account for invasion success.

It has been argued that successful invasive species are smaller than native species in the communities in which they invade, or are smaller than congeners that are not invasive. Indeed, some invasive ant species are small relative to noninvasive ants and to native species in the communities they invade. But many are not. *Anoplolepis gracilipes*, for example, can be over 5 mm in length. Additionally, previous global analyses of body size of invasive ants did not consider polymorphic species (e.g., *Pheidole megacephala*, *Solenopsis invicta*, *Solenopsis geminata*). Whether body size is an important predictor of invasion success remains an open question.

COMPETITIVE ABILITY Some ant species are notoriously good at quickly discovering food resources, but those species are often quickly displaced by more aggressive species. Other species are good at displacing competitors from resources but slow to discover resources. Thus, a tradeoff exists: some species are good at discovering resources, but others are good at displacing their competitors from resources, and few species excel at both. These dominance–discovery tradeoffs might promote coexistence in native ant communities. But the ability to break the tradeoff—to be able both to discover resources faster than your competitors and to displace competitors once they do discover the resources—could be an important aspect of invasion success for some invasive species. In fact, many invasive ant species do seem to break this tradeoff. When an ephemeral resource becomes available, invasive ant species are likely to discover it before any native ant species does, to recruit nestmates to the resource in higher numbers than native species, and to initiate aggressive interactions before native ant species do. The ability to excel at both exploitative and interference competition undoubtedly confers a competitive advantage on invasive ant species.

It might be that invasive ants not only engage in competition with native species but also prey on them. Distinguishing between competition and predation among ants is challenging. For example, when a group of *L. humile* workers is seen dismembering a worker of a native ant species, is that competition or predation? However, there are some clear-cut instances of predation. For instance, both *Linepithema humile* and *Solenopsis invicta* are known to raid nests of native ant species, where they aggressively attack and kill workers and remove brood (Fig. 1). In actuality, some combination of predation and superior competitive ability probably accounts for the success of invasive ant species. It would be interesting to know more about the relative effects of exploitative competition,



FIGURE 1 *Linepithema humile* workers attacking a *Pogonomyrmex subdentatus* worker near Davis, California. (Photograph courtesy of Alex Wild.)

interference competition, and predation by invasive ants on native ant biodiversity.

COLONY SIZE One reason some invasive ants may be able to break the dominance–discovery tradeoff and successfully engage in colony raids of other species is that they tend to have large colonies. Because colonies are large, invasive ant species can invest in scouts (workers that search for food resources), recruit in high numbers, and overwhelm native species in interference interactions for food resources.

But this begs a question: how do colonies of invasive species become large when they presumably begin with, at most, a few queens and workers? One intriguing potential mechanism is that colonies of invasive species may become large because they are unicolonial. Unicoloniality is the condition in which colonies consist of connected networks of nests and exchange workers freely among nests. Because nests exchange workers and presumably do not compete with one another, colonies are free to invest all of their energy in interspecific competition rather than intraspecific competition. Unicoloniality can confer ecological dominance by enhancing colonization ability or resource exploitation. It can also shift the outcome of interference interactions. Indeed, unicolonial colony structures have been documented or inferred for *Anoplolepis gracillipes*, *Linepithema humile*, *Pheidole megacephala*, *Solenopsis invicta*, and *Wasmannia auropunctata*.

Most research on unicoloniality in invasive species has been on the Argentine ant, *Linepithema humile*. Early work suggested that the Argentine ant perhaps passed through a genetic bottleneck upon introduction in California, and so as the species expanded its range, nests over large areas remained highly related, and intraspecific aggression was absent over large areas, resulting in the formation of expansive “supercolonies.” As a result of

a lack of intraspecific aggression at the population level, Argentine ants are free to focus entirely on interspecific competition. In contrast, the biology of the Argentine ant appears different in the native range; colonies are often aggressive toward one another within populations (e.g., scales of tens to hundreds of meters), which could explain why the Argentine ant is not as ecologically dominant in its native range. More recent work, however, has documented variation in the scale at which intraspecific aggression occurs in Argentine ants in both their introduced and native ranges, so while unicoloniality is the norm in introduced populations, expansive supercolonies extending hundreds of meters still occur in native populations. Research on other unicolonial invasive ant species has shown that most exhibit variation in the degree of intraspecific aggression, particularly between native and introduced ranges, and that introduced populations may often result from multiple introductions from the native range. Together, detailed studies of Argentine ants in their native and introduced ranges and a handful of studies on other invasive species suggest that unicoloniality alone is an insufficient explanation for ecological dominance by invasive species.

It is important to note that unicoloniality is also common for many noninvasive species across the ant phylogeny. A key distinction is that many unicolonial noninvasive species form large, long-lasting nests in mature habitats, whereas unicolonial invasive species form small, transient nests in disturbed habitats. Perhaps it is this distinction between the nature of nests that allows invasive species to be transported, to become established, and to increase when rare.

What else might account for the success of invasive ant species? As with other invasive taxa, studies have indicated that escape from natural enemies (e.g., interspecific competitors, disease, and parasitoids) may account for some of the success of invasive species outside of their native ranges. It is most likely that a combination of rapid colony development, coupled with the ability to maintain small, ephemeral networks of nests and with the benefits that large colony size confers (e.g., efficient location and retrieval of food resources), has led to the broad distributions of several introduced invasive species, as well as their impacts on biodiversity and native ecosystems.

IMPACTS

The effect of invasive exotic ant species on populations and communities of native ants and arthropods is not a new problem. In fact, effects of invasive ants were documented as early as the early sixteenth century in the West Indies.

E. O. Wilson surmised that *Solenopsis geminata* destroyed crops and invaded homes on the island of Hispaniola in the early 1500s and that *Pheidole megacephala* ravaged sugarcane fields throughout the Lesser Antilles the late 1700s. These two species are still pests throughout many parts of the world.

Impacts on Ants

A large and growing body of literature indicates the dramatic effects that invasive ant species can have on native ant species. In invaded areas, both richness and abundance of native ants is substantially lower than in the absence of invasive ants. Examples abound on nearly every continent of the diversity and abundance of native ants and invertebrates being lower in the presence of *Linepithema humile* than in its absence. Similarly, the effects of *Solenopsis invicta* on native invertebrates, especially in the southern United States, are well documented. *Anoplolepis gracilipes* greatly reduces the abundance of ants and other invertebrate species on the islands in the South Pacific and in Australia. *Pheidole megacephala* has displaced native ants and other invertebrates in northern Australia and threatens several taxa in Florida and Mexico. *Wasmannia auropunctata* has reduced diversity in the Galapagos, Central Africa, and New Caledonia.

Although most studies have documented how invasive ants reduce richness and abundance, a handful of studies have illustrated more subtle effects. For example, *Solenopsis invicta* may shape biogeographic patterns like the latitudinal gradient in diversity of native ants in the eastern United States. And both *Solenopsis invicta* and *Linepithema humile* disrupt co-occurrence patterns of native species (the tendency of species to occur together more or less than expected by chance).

LONG-TERM IMPACTS Most ecological studies are short—at most, covering a few field seasons. Similarly, most studies of the impacts of invasive ants on native ant communities last only a few field seasons. A couple of notable exceptions exist. A team of researchers at Jasper Ridge Biological Preserve in northern California has tracked the spread and impact of the Argentine ant since 1993. Early work at the site showed that native ant species richness was much lower in the presence of Argentine ants than in its absence. But a recent study has shown that the impact of *L. humile* tends to dissipate with time. The number of native ant species in plots that had *L. humile* in the early stages of the invasion has increased. At Brackenridge Field Station in Texas, one of the first thorough studies of the impact of an invasive ant species showed that native ant

diversity and abundance were dramatically lower in the presence of *S. invicta* than in its absence. However, when the invaded sites were resampled at Brackenridge 12 years later, the ant community had apparently rebounded, and many species had returned. Two counterexamples are worth noting. In southern California, the richness of native ant species has yet to rebound at many sites invaded by *L. humile*, almost ten years after it first invaded intact native ant communities. Similarly, native ant diversity has yet to rebound in areas infested with *Pheidole megacephala* in northern Australia. In fact, native ant diversity was reduced effectively to zero and remains near zero in what were once species-rich sites.

EXPERIMENTS (OR LACK THEREOF) Experiments are the lifeblood of ecology. Without them, separating causation from correlation is challenging. However, most studies of the impact of invasive ants on native ant communities have been based on correlations and have compared native arthropod communities in the presence and absence of the invasive ant species of interest. Of course, there are potential problems with such correlational studies. Namely, the invaded and intact sites may differ in subtle environmental characteristics (e.g., soil moisture, temperature, habitat type, disturbance history) that could actually be driving native ant community structure. Or perhaps invasive ants become established only after native ant diversity has been reduced by some environmental disturbance. But in many cases, evidence that invasive ants affect native ant communities is clear. For example, detailed pre-invasion and post-invasion comparisons, especially with *Linepithema humile*, show that communities can change within a year of *L. humile* becoming established in a community. Well-replicated long-term experimental removals of entire colonies could be an ideal way to assess impacts of invasive ant species. Addition experiments, in which colonies of an invasive ant species are deliberately introduced to a previously uninvaded community, are ethically questionable and probably should not be undertaken.

Impacts on Non-ants

The most obvious impacts of invasive ants are on other ants. But other taxa, ranging from other ground-foraging arthropods to charismatic vertebrates and plants, can also be affected by the spread of invasive ants. These effects result from competition and predation by invasive ants and from indirect factors, such as the potential displacement of other ant species that play key roles in ecosystem function.

IMPACTS ON NON-ANT INVERTEBRATES The effects of *Anoplolepis gracilipes*, *Linepithema humile*, *Pheidole megacephala*, *Solenopsis invicta*, and *Wasmannia auropunctata* on non-ant invertebrates are all well documented in a variety of ecosystem types. The list of affected taxa includes, but is not limited to, spiders, springtails, flies, beetles, yellowjackets, honeybees, ticks, mosquitoes, tree snails, apple snails, butterflies, mites, scorpions, pseudoscorpions, and hemipterans. The impacts of predation by invasive ants on other invertebrates are especially striking in agroecosystems and on oceanic islands. For example, *Pheidole megacephala* apparently led to the extinction of a ground-foraging fly on Oahu. On Maui, the presence of *L. humile* has led to reductions in total arthropod richness of more than 32 percent and to reductions in endemic arthropod richness of over 50 percent.

One particularly striking example comes from several islands in the South Pacific, where *Anoplolepis gracilipes* has displaced crabs by both preying on them and competing with them. On Christmas Island, the presence of *A. gracilipes* has led to a severe decline in the population of the endemic red land crab, *Gecarcoidea natalis*. The loss of crabs has led to dramatic changes in the plant community and has increased the abundance of at least one other nonnative species on the island.

Invasive ant species can also favor other invertebrates. This usually occurs when ants engage in a protective mutualism with hemiptera, whereby the ants protect the aphids from predators and parasitoids, and in return, the aphids provide honeydew, a sugary excretion rich in carbohydrates and amino acids. In the presence of the ants, aphid abundance is usually higher than in their absence (Fig. 2). Few studies have compared the relative



FIGURE 2 *Pheidole megacephala* tending aphids. (Photograph courtesy of Alex Wild.)

impact of invasive ants and native ants on the hemiptera they tend, but the few that have generally found that the invasive ants have much stronger positive effects than the native ants. One consequence of the mutualism between ants and the hemipterans they tend is that the ants remove or prey on the other herbivores on the host plant of the hemiptera. Thus, by engaging in a mutualism with hemiptera, invasive ants can affect many other herbivorous invertebrate taxa. And by reducing the abundance of herbivores and presumably the damage those herbivores cause to the plants, introduced ants can have positive effects on some plant species. This research area deserves more attention.

IMPACTS ON VERTEBRATES Not only do invasive ants affect invertebrates, but they can also have surprisingly big effects on growth or survival of vertebrates. The list of affected species includes about 20 bird species, more than 10 mammal species, and more than 15 reptile and amphibian species. The impacts of *Solenopsis invicta* on vertebrate species are the best studied, but there are documented effects of each of the five worst invasive ant species on the survival, growth, behavior, and in one case morphology, of some vertebrate species.

Predation by invasive ants can affect survival and success of bird nestlings. When exposed to high densities of *Solenopsis invicta*, chicks of bobwhite quail gained weight more slowly than did chicks exposed to lower densities of *S. invicta*. Additionally, long-term bird surveys have linked declines in bobwhite quail populations to infestations of *S. invicta* at several locations in the southeastern United States. *Pheidole megacephala* and *Solenopsis geminata* attack nestlings of seabirds and may have short-term effects on fledging success. Generally speaking, the effects are usually greatest on species that cannot escape attack or predation by the ants (e.g., chicks unable to leave the nest).

There are other means by which invasive ants might affect vertebrate species. For example, invasive ants may reduce the availability of nesting sites or alter the behavior of individuals. Not surprisingly, these effects might act as strong agents of selection on vertebrate populations. For example, the presence of *Solenopsis invicta* has led to adaptive responses in the eastern fence lizard in the southern United States. Fence lizards that have co-occurred with *S. invicta* for a longer time are more likely to exhibit defensive behaviors (body twitching and fleeing) when confronted with *S. invicta*, and they are more likely to have relatively longer hind limbs that are important for removing attacking *S. invicta* workers.

Ant invasions can also have indirect effects on vertebrate populations. In Florida, *Pheidole megacephala* appears to disrupt sea turtle and seabird nestlings. *Wasmannia auropunctata* has reduced the diversity and abundance of birds and reptiles on the Galapagos and has affected lizard populations in New Caledonia. In southern California, *Linepithema humile* has displaced many native ant species, and this might have indirectly led to population declines of coastal horned lizards. One candidate explanation for the decline in horned lizard populations is that *L. humile* displaces the native ants, which make up 90 percent of the diet of coastal horned lizards. Indeed, when individual horned lizards are offered *L. humile* as food, growth rates decline. 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.

IMPACTS ON PLANTS Ant–plant mutualisms are common in nature and range from tightly co-evolved interactions to more diffuse interactions such as seed-dispersal mutualisms. When native ants are displaced by invasive ant species, more often than not, the invasive ants do not adequately fill the roles played by the displaced native species.

Many plant species rely on ants to disperse their seeds, and some of these plants have a clever adaptation to encourage seed dispersal by ants: their seeds have a lipid-rich appendage called an elaiosome. Ant species disperse the seed away from the maternal plant, remove the elaiosome, and then may bury the seed or deposit it in the refuse pile near the nest. Studies on the effects of ant invasions on individual plants or plant communities have yielded mixed results, with some showing that invasive ants effectively replace native ant species without major impact on the plants and others documenting negative effects of ants on plant populations and communities. For example, in many instances, invasive ant species collect and disperse fewer seeds or smaller seed than do native species, disperse the seeds only a short distance, or fail to bury the seeds effectively. Invasive ants may not only be poor seed dispersers: they may in fact be seed predators. Ultimately, these differences in seed dispersal may affect plant community structure, if seeds preferred by invasive ants successfully germinate while seeds not preferred by invasive ants do not. It is important to note that not all studies have found negative effects of ant invasions on seed dispersal mutualisms. However, a recent quantitative

review explicitly compared the effects of invasive ants and native ants and found that the effects of ant invasions on seed dispersal mutualisms are, on average, negative.

In other instances, invasive ants can have net positive effects on plants. In the case of plants that provide extrafloral nectar (EFN) to ants and in return receive protection from herbivores or pathogens, there are several documented cases of invasive ants conferring more positive benefits than do native ants. However, a handful of studies have shown either negative or no effects of invasive ants on the EFN-providing plants.

Generally speaking, the overall effects of invasive ants on seed-dispersal mutualisms is likely to be negative, while the effects of invasive ants on EFN-producing plants is likely to be positive. Too few studies have been conducted over sufficiently long periods to generalize about the magnitudes of the effects of invasive ants on plant communities.

IMPACTS ON HUMANS Invasive ant species also seriously threaten human well-being, and the economic impacts of invasive ant species are likely to be substantial. For instance, *Solenopsis invicta* can inflict painful stings (Fig. 3), which in some cases have led to anaphylaxis and death. One recent study estimated that more than 10 million people are stung each year in the United States by *S. invicta*. In California, for example, it is estimated that the economic impact of *S. invicta* could range from \$3 to \$9 billion over the next ten years if *S. invicta* is left unchecked. The costs in Texas are estimated to be \$300 million per year. Most of the costs come from applying pesticide treatments, restoring and replacing property and equipment, and providing medical and veterinary treatment for stings.

Other invasive ant species also have important impacts on humans. The best-documented impacts



FIGURE 3 *Solenopsis invicta* (red imported fire ant) stinging. (Photograph courtesy of Alex Wild.)

on human well-being are from *L. humile*. Although *L. humile* does not pose serious threats to public health, it has substantial economic impacts, mostly by disrupting biocontrol efforts and facilitating hemipteran pests on crops. The agricultural impacts of *W. auropunctata* are also well documented in many parts of its introduced range. The total costs of control and eradication efforts for invasive ant species likely total tens of millions of dollars, but the outcomes of several successful eradication and control programs indicate that the costs are worth the investment.

There have been failed attempts at controlling invasive ant species. *The Fire Ant Wars* (Blu Buhs, 2004) provides a thorough and compelling review of the U.S. government's failure to control the spread and impact of *Solenopsis invicta*. Although there have been failures, it is worth noting that there have been some successes as well. For example, New Zealand has successfully prevented establishment by several invasive ant species, and the Australian government has had some success controlling *A. gracilipes* on Christmas Island and potentially several other species on mainland Australia. Together, these successes, however moderate, illustrate that control and even eradication is possible. However, it does seem highly unlikely that some firmly established species with broad introduced ranges (e.g., *L. humile* and *S. invicta* in the United States) will ever be totally eradicated.

CONCLUSION AND FUTURE DIRECTIONS

This review has focused especially on a limited number of invasive ant species: *Anoplolepis gracilipes*, *Linepithema humile*, *Pheidole megacephala*, *Solenopsis invicta*, and *Wasmannia auropunctata*. Even within this already limited list, *S. invicta* and *L. humile* are the most thoroughly studied species. The paucity of information on many problematic and potentially problematic species (e.g., *Pachycondyla chinensis*, *Paratrechina longicornis*, *Paratrechina fulva*, *Pheidole obscurithorax*, *Lasius neglectus*, *Monomorium pharoensis*, *Monomorium sydneyense*, *Myrmica rubra*, *Tenomyrmex albipes*, *Tetramorium tsushimae*, *Dolero-myrrma darwiniana*, *Ochetellus glaber*, and several species in the genus *Cardiocondyla*) provides a clear impetus for more research on the basic biology (in both the native and introduced ranges) and potential impact of these species. Additionally, native ant species can have far-reaching effects on ecosystem processes. To date, too few studies have addressed whether and how invasive species might disrupt ecosystem processes provided by ants. More experiments, especially long-term removal experiments, aimed at understanding the effects of invasive species are

an important research aim. Finally, habitat alteration and climate change continue to alter terrestrial ecosystems and affect biodiversity. Understanding how these global change factors interact to mediate the impacts of invasive ants on biodiversity will be a challenging but important area for future research.

SEE ALSO THE FOLLOWING ARTICLES

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APOMIXIS

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Apomixis is the asexual propagation of a plant through seed without meiotic reduction and fertilization. Seedlings that develop via apomixis are genetically identical to the maternal plant and to each other, forming uniform populations that can persist for many years and over large land areas. Most apomixis are also capable of a limited amount