Impacts of invasive ants on native ant communities (Hymenoptera: Formicidae)

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Abstract

The most commonly documented consequence of alien ant invasions is the displacement and local extinction of native ant species. However, several processes may lead to low native ant diversity in the presence of non-native species. Invasive ants may, indeed, competitively exclude native ants. Conversely, invasive ants may not be able to spread into diverse, competitively dominant native ant communities. Finally, complementary distribution of invasive and native ants may be non-interactive and instead driven by divergent responses to heterogeneous environmental factors. Here, I review studies of non-native ants that have associated negative impacts on native ant communities, discuss how native ant communities are reorganized in invaded habitats, summarize reports of vulnerable and resistant ant species, and examine evidence for mechanisms of reduced native ant diversity. Invasive ants are often, but not always, associated with lower native ant abundance, reduced species diversity, and randomly structured, homogenized native ant communities. Native ants are unlikely to co-occur with invasive ants 1) in habitats with environmental conditions suitable to and / or modified for the invader, 2) during the height of an invasion when an invading species is at its peak density, 3) when native ants are ecologically similar to the invading species and lack potent chemical defenses. Little evidence supports the biotic resistance hypothesis for native ants. Instead, suitable environmental conditions are primary determinants of the establishment and success of invasive ants. While invasive ants generally thrive in disturbed areas, many studies document the spread of invasive ants into undisturbed habitats and support the notion that invasive ants can drive declines in native ant diversity. More experimental studies are needed to explicitly test the importance of interactive and non-interactive processes in determining the spread of invasive ants and their impacts on native ant diversity.

Key words: Biotic resistance, competitive exclusion, disturbance, diversity, invasive ants, native ant communities, review.

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Introduction

Alien ants are among the most deleterious predatory invertebrates threatening native biodiversity, negatively impacting ant species, other invertebrates and vertebrates, ecosystem function, agriculture, economy, and human health (LOWE & al. 2000, HOLWAY & al. 2002, LACH & HOOPER-BÙI 2009, RABITSCH 2011). Accordingly, invasive ants have been the subject of several reviews, including the causes (HOLWAY & al. 2002, KRUSHELNYCKY & al. 2009) and consequences (HOLWAY & al. 2002, KENIS & al. 2009, LACH & HOOPER-BÙI 2009) of ant invasions, the management of invasive ants (HOFFMANN & al. 2009, RABITSCH 2011), and species- (*Solenopsis invicta* BUREN, 1972: TSCHINKEL 2006; *Linepithema humile* (MAYR, 1868): SANDERS & SUAREZ 2011) and geographic-specific (Australia: COMMONWEALTH OF AUSTRALIA 2006, LACH & THOMAS 2008; Hawaii: KRUSHELNYCKY & al. 2005) treatments.

The most commonly reported change to native ant communities is the reduction in abundance and species density in areas of high densities of invasive ants. Competition has long been held as a central structuring force of ant communities (HÖLLDOBLER & WILSON 1990, CERDÁ & al. 2013) and it can be difficult to conclude that invasive and native ants are non-interactive, especially where invasive ants grossly outnumber native ants, repel native ants from resources, and spread into undisturbed areas with subsequent declines in native ant numbers. However, relatively few studies have been able to experimentally demonstrate or distinguish interactive from non-interactive processes, or directly test the mechanisms by which invasive ants may impact native ants. Furthermore, as many invasive ants are associated with disturbed habitats, both disturbance and invasive ants may interact to impact native ant communities.

Understanding how invasive ants interact with native ant communities informs fundamental questions in community ecology, invasion biology, and conservation management. Studies of invasive ants broaden our understanding of the role of competition in structuring ant communities, the importance of biotic resistance in controlling the spread of invasive ants, and the relative benefit of killing invasive ants to aid in the recovery of native ants.

This review will focus on the impacts of the five ants recognized among the IUCN's "World's Worst" invaders, and introduce four other non-native ant species that have documented negative associations with native ant communities. Review of native ant impacts will be discussed with

respect to the role of disturbance and habitat type. Specifically, the review will 1) introduce established and emerging invasive ant species, 2) briefly summarize characteristics of invasive ant species linked to their ecological success, 3) discuss patterns of native ant communities in invaded and uninvaded habitats, 4) identify ant species and ecological traits that are most vulnerable and resistant to invasion, and 5) discuss the mechanisms which may drive patterns of native ant communities in invaded habitats.

The players

While over 150 non-native ant species are established outside of their range (MCGLYNN 1999), most of these species have not been documented to have measureable impacts upon native ant communities. This review will summarize the impacts of the five ant species included among the 100 world's worst invasive alien species (LOWE & al. 2000): *Anoplolepis gracilipes* (SMITH, 1857) (yellow crazy ant, long-legged ant), *Linepithema humile* (Argentine ant), *Pheidole megacephala* (FABRICIUS, 1793) (big-headed ant, coastal brown ant), *Solenopsis invicta* (red imported fire ant), and *Wasmannia auropunctata* (ROGER, 1863) (little fire ant, electric ant). Four additional non-native ant species, included among the 19 ants listed in Global Invasive Species Database (www.issg.org), with associated negative impacts on native ant communities are reviewed: *Lasius neglectus* VAN LOON, BOOMSMA & ANDRÁSFALVY, 1990, *Myrmica rubra* (LINNAEUS, 1758), *Nylanderia fulva* (MAYR, 1862), and *Pachycondyla* (= *Brachyponera*) *chinensis* (EMERY, 1895).

Characteristics of invasive ants

Reviewed elsewhere (HOLWAY & al. 2002, KRUSHELNYCKY & al. 2009) the following will briefly introduce characteristics of invasive ants linked to their ecological success and ability to impact native ant communities.

The majority of invasive ants lack intraspecific aggression and exhibit a reduction or absence of behavioral boundaries among nests within a population (unicoloniality). Their colonies contain several queens (polygyny) within multiple nests (polydomy), mating occurs close to or within the natal nest, and newly mated queens disperse on foot with nestmate workers (dependent colony formation). The establishment of new colonies through budding restricts dispersal distance but results in a contiguous network of mutually tolerant nests. Exceptions to this pattern are seen in *Solenopsis invicta*, which possess both monogyne and polygyne forms. The monogyne form of *S. invicta* is multicolonial, and new colonies are founded independently through mating flights, whereas the polygyne form primarily disperses via dependent colony formation (TSCHINKEL 2006).

Ants with polygynous, polydomous colony structure distributed continuously across a habitat function as a "supercolony", capable of achieving incredible densities. For example, *Anoplolepis gracilipes* has the highest recorded density of ants (ABBOTT 2005), *Solenopsis invicta* can achieve a 30-fold greater abundance than natives (PORTER & SAVIGNANO 1990), and *Pheidole megacephala* can obtain up to 62 times greater abundance than natives (HOFFMANN & PARR 2008). Superior competitive ability in invasive ants is linked to numerical advantage (reviewed in HOLWAY & al. 2002, KRUSHELNYCKY & al. 2009), and

extreme abundance confers obvious advantage in the location, recruitment, and defense of resources. Invasive ants, able to both quickly find and defend resources, break the dominance-discovery trade-off (FELLERS 1987), a potential mechanism underlying coexistence in ant communities (DAVIDSON 1998).

While competition for food is the most conspicuous and well-studied form of invasive-native species interactions, invasive and native ants may also compete for nest sites (BUCZKOWSKI & BENNETT 2008). Agonistic interactions by invasive ants can prohibit colonization of native ants (HUMAN & GORDON 1996) and may prompt emigration. Raiding behavior is also common among invasive ants (DE KOCK 1990, HOOK & PORTER 1990, ZEE & HOLWAY 2006, ROWLES & O'DOWD 2007, CARPINTERO & REYES-LÓPEZ 2008, DEJEAN & al. 2008, VONSHAK & al. 2012), and has been observed in *Linepithema humile*, *Pheidole megacephala*, *Solenopsis invicta*, and *Wasmannia auropunctata*. Raids by invasive ants can result in the reduction of native ant foraging activity (HOOK & PORTER 1990, ZEE & HOLWAY 2006), the capture of native ant brood (ZEE & HOLWAY 2006, CARPINTERO & REYES-LÓPEZ 2008) and increased native ant worker mortality (HOOK & PORTER 1990, ZEE & HOLWAY 2006). Raiding has been proposed as a mechanism for the size-dependent impacts of *Nylanderia fulva*, in which smaller ants may be afforded protection due to their inaccessibly small tunnels (LEBRUN & al. 2013).

Invasive ant impacts on native ant communities

Reduction in number of co-occurring species. One of the most commonly cited impacts of invasive ants is their ability to reduce native ant diversity. Although direct impacts of invasive ants on native ant diversity are difficult to assess directly, the pattern of fewer co-occurring ant species occupying invaded areas has been documented extensively across invasive ants and in habitats around the world.

World's worst invasive ants

Anoplolepis gracilipes. Native to sub-Saharan Africa or tropical Asia, *A. gracilipes* has spread primarily to tropical moist lowlands in the Old World, including tropical Asia and Australia and several Indo-Pacific islands, but also parts of subtropical Asia and western Mexico (WETTERER 2005). The majority of impact studies on co-occurring ants are reported from tropical islands (Christmas Island: ABBOTT 2006; Tokelau: LESTER & TAVITE 2004, ABBOTT & al. 2007, SARTY & al. 2007; Sulawesi, Indonesia: BOS & al. 2008; the Samoan Archipelago: SAVAGE & al. 2009; Borneo: DRESCHER & al. 2011; Mahe Island, Seychelles: HAINES & al. 1994) comprised of few to no native ant species and often in human disturbed habitats (digital Appendix S1 at the journal's web page). However, *A. gracilipes* has invaded a variety of undisturbed habitats in tropical mainland Australia, in which fewer native ant species (~ 20 - 42%) were found in invaded areas (HOFFMANN & SAUL 2010).

Linepithema humile. Native to central South America, *L. humile* has spread to areas with similar Mediterranean-like climates, including western and southeastern United States, the Mediterranean, southern Africa, Australia, New Zealand, and Japan (WETTERER & al. 2009). The majority of ant impact studies have occurred in riparian woodland

and coastal scrub habitats in California, U.S. (WARD 1987, HUMAN & GORDON 1996, HOLWAY 1998a, KENNEDY 1998, SUAREZ & al. 1998, WETTERER & al. 2001, HOLWAY 2005, DIGIROLAMO & FOX 2006, TILLBERG & al. 2007) and document relatively large reductions in species densities (60 - 99%) within native ant communities in undisturbed habitats (Appendix S1). Impacts on native ants in moderately disturbed habitats are reported from Chile (STACEY 2011), Portugal (CAMMELL & al. 1996, WETTERER & al. 2006), and Spain (CARPINTERO & al. 2005), and impacts on ant communities in urban areas are documented from Western Australia (MAJER & FLUGGE 1984, HETERICK & al. 2000), South Australia (WALTERS 2006), and Japan (TOUYAMA & al. 2003, SUNAMURA & al. 2007).

Pheidole megacephala. Native to sub-Saharan Africa, *P. megacephala* has spread to tropical lowland regions in Australia, southeast Asia, Central and South America, tropical Pacific Island groups, tropical and subtropical Atlantic Islands, as well as temperate areas in Australia, New Zealand, and South Africa (WETTERER 2012). The majority of ant impact studies are recorded from Australia, where the biggest reduction in native ant density (~84 - 96%) is documented in tropical rainforest patches in the Northern Territory. Impacts on native and introduced ants are noted in rehabilitated mine sites (MAJER 1985) and undisturbed open forest (VANDERWOUDE & al. 2000) in Queensland, Australia and in urban areas in Western Australia (HETERICK & al. 2000, MAY & HETERICK 2000, CALLAN & MAJER 2009). Impacts on native and introduced ants in moderately disturbed habitats are also reported on Madeira (WETTERER & al. 2006) and the Capricorn and Bunker Group islands (BURWELL & al. 2012).

Solenopsis invicta. Native to tropical and subtropical South America, *S. invicta* has spread across the southern United States and northeastern Mexico, several West Indian islands, as well as Taiwan, China, and Australia (WETTERER 2013a). The majority of ant impact studies have occurred in southeastern U.S. In Texas, large reductions in native ant species density (60 - 85%) are documented within relatively undisturbed habitats (PORTER & SAVIGNANO 1990, MORRIS & STEIGMAN 1993, KASPARI 2000) (Appendix S1). Experimental manipulations of disturbance and *S. invicta* demonstrated negative impacts of both on native ant communities in intact pine flatwoods of Florida (KING & TSCHINKEL 2008). Fewer native ant species (~ 20%) cooccurred with *S. invicta* in wet, undisturbed habitats in Texas coastal plains (LEBRUN & al. 2012). Negative impacts on native ants by *S. invicta* has also been found in remnant urban forest in Brisbane, Australia (NATTRASS & VANDERWOUDE 2001).

Solenopsis invicta may also depress the numbers of native ants on a biogeographic scale. While a latitudinal gradient in species richness (greater richness at lower latitudes) is well documented for ants (GOTELLI & ARNETT 2000), the pattern does not hold in eastern North America. In a study that sampled communities from Florida to upstate New York, ant species density increased with lower latitudes, as expected, until Virginia, where species density began to decrease. The location of this peak statistically corresponded with the northern range of the *S. invicta* invasion, suggesting *S. invicta*'s displacement of native ant species may have altered biogegraphical patterns of species density (GOTELLI & ARNETT 2000). Note, however, that non-interactive factors (e.g., mid-domain effect) may also contribute to biogeographic diversity patterns (COLWELL & LEES 2000, TSCHINKEL 2006).

Wasmannia auropunctata. Native to tropical Central and South America, *W. auropunctata* has established throughout the West Indian and Pacific island groups and West Africa, and recently spread to the Central Africa Republic, Papua New Guinea, Australia, Guam, Italy, and Israel (WETTERER 2013b). No ants have been found to co-occur with *W. auropunctata* in surveys in the Galapagos (CLARK 1982, LUBIN 1984) and on New Caledonia rainforest trees (LE BRETON & al. 2005). Large reductions in species density (83 - 96%) are recorded from New Caledonia forest edges (LE BRETON & al. 2003) and variably disturbed and infested habitats in Gabon National Forest (WALKER 2006) (Appendix S1). High *W. auropunctata* abundance is associated with lower native ant diversity in tropical dry forest fragments (ARMBRECHT & ULLOA-CHACÓN 2003) and in suburban areas in Israel (VONSHAK & al. 2010).

Emerging invasive ants

Lasius neglectus. Most likely native to Asia Minor (SEIFERT 2000, CREMER & al. 2008), *L. neglectus* lacks intraspecific aggression (STEINER & al. 2004), is polygynous (BOOMSMA & al. 1990), exhibits dependent colony formation through budding (VAN LOON & al. 1990), and forms supercolonies. No ants have been found to coexist in the center of *L. neglectus* supercolonies in Hungary (VAN LOON & al. 1990, TARTALLY 2000), Germany (SCHULTZ & BUSCH 2009) and Belgium (DEKONINCK & al. 2002), and fewer native ant species have been found within *L. neglectus* infested areas in Hungary (NAGY & al. 2009) and Spain (ESPADALER & BERNAL 2011). Though it possesses many characteristics of prominent invasive ants and is expanding its range (ESPADALER & al. 2007), *L. neglectus* has been reported from primarily highly urbanized areas and has not been documented to impact natural areas.

Myrmica rubra. Native to the Palearctic north temperate region (GRODEN & al. 2005), *M. rubra* has spread across southeastern Canada and northeastern United States (WETTERER & RADCHENKO 2011). *Myrmica rubra* is associated with a decline in native ant diversity in Maine, U.S. (GARNAS 2004, MORALES & al. 2008), and is able to invade natural habitats in Acadia National Park, Maine (GRODEN & al. 2005). Impacts in some areas can be severe, with complete displacement of native ants (GARNAS 2004). Unlike other invasive ants, *M. rubra* social structure in invaded areas is multicolonial, not unicolonial (GARNAS & al. 2007).

Nylanderia fulva. Most likely native to South America (GOTZEK & al. 2012), *N. fulva* has invaded primary forest and agricultural areas in Colombia where it can achieve ecological dominance (ZENNER-POLANIA 1990) and co-occurs with fewer (~ 95%) native ant species (ZENNER-POLANIA 1994). An outbreak of the tawny (Rasberry) crazy ant, recently identified as *N. fulva* (GOTZEK & al. 2012), was first recorded around Houston, Texas and has since spread to 24 counties in Texas (CENTER FOR URBAN AND STRUCTURAL ENTOMOLOGY 2013), Mississippi (MACGOWN & LAYTON 2010), Louisiana (HOOPER-BÙI & al. 2010) and Florida (GOTZEK & al. 2012). It is capable of attaining extremely high densities, wherein fewer ant species co-occur, including *Solenopsis invicta* (LEBRUN & al. 2013).

Pachycondyla chinensis. Native to north temperate to subtropical Asia (NELDER & al. 2006), *P. chinensis* was introduced to the United States from Japan (YASHIRO & al. 2012) and is recorded throughout the eastern coast of the U.S. (GUÉNARD & DUNN 2010). Reduction in native ant species is sometimes (GUÉNARD & DUNN 2010) but not always (RODRIGUEZ-CABAL & al. 2012) observed. *Pachycondyla chinensis* can displace *Linepithema humile* at the northern edge of its range (SPICER RICE & SILVERMAN 2013). Recent collections in Wisconsin and Washington through the School of Ants (http://schoolofants.org/) may indicate a possible massive range expansion across the United States.

Reorganization of invaded communities

While it is common for fewer native ant species to persist with invasive ants, the reorganization of native ant community structure may also occur. Studies of both *Solenopsis invicta* and *Linepithema humile* have found co-occurrence patterns of native ants in invaded communities to be less structured than those in low density or uninvaded areas (GOTELLI & ARNETT 2000, SANDERS & al. 2003, LEBRUN & al. 2012). In communities sampled pre- and post-invasion, the shift from segregated co-occurrence patterns to random or slightly aggregated co-occurrence patterns occurred within one year, suggesting invasion by *Linepithema humile* can cause rapid and dramatic reorganization of ant communities (SANDERS & al. 2003). Invasive ants may reduce population densities of co-occurring ants, and therefore the intensity of competition among them, or they may have differential impacts on native species, altering interactions among persisting species.

The reorganization of invaded communities may also result in changes in community phylogenetic structure. Meta-analysis of invaded and intact communities indicated intact communities are phylogenetically evenly dispersed (members are more distantly related than expected by chance), whereas invaded communities are phylogenetically clustered (members are more closely related than expected by chance) (LESSARD & al. 2009). Assuming competition is more intense among more closely related species, these findings suggest that the phylogenetically evenly dispersed intact communities are primarily structured by competition, whereas strong environmental filtering by invasive ants results in phylogenetically clustered invaded communities in which only closely related taxa with certain traits can persist.

Variable impacts

Of course, not every invasion study tells the same story. Impacts may vary with the social form of the invasive ant, with the diversity of the invaded ant community, when keystone processes are altered, and with time since invasion.

Social form

While monogyne forms may have greater dispersal potential, polygyne forms can reach higher colony densities and cause greater native ant impacts. Nests of the polygyne form of *Solenopsis invicta* occur at densities 3 - 10 times higher than the monogyne form (PORTER & SAVIGNANO 1990, MACOM & PORTER 1996), recruit higher numbers to baits (MACKAY & al. 1994) and coexist with a smaller number of native ants (PORTER & al. 1991, HELMS

& VINSON 2001). Several studies report minimal impacts of the monogyne form in the southeastern U.S. Monogyne *S. invicta* does not appear to competitively suppress native ants in a Florida plantation (KING & TSCHINKEL 2006) or frequently flooded pine flatwoods (KING & TSCHINKEL 2013). Native species richness does not vary with monogyne *S. invicta* density in Georgia pine savannas (STUBLE & al. 2009) or in several habitat types in Texas coastal plains (LEBRUN & al. 2012), and large numbers of native ant species coexist with monogyne *S. invicta* in Texas (HELMS & VINSON 2001). These findings are dramatically different to a nearby (140 km) study in which polygyne *S. invicta* populations decimated native ant communities (PORTER & SAVIGNANO 1990; see also MORRIS & STEIGMAN 1993, KASPARI 2000). Significant reductions in native ant species density have been observed in monogyne *S. invicta* invasions (KING & TSCHINKEL 2008, LEBRUN & al. 2012), but are generally less pronounced than impacts found with the polygyne form (~ 8 - 20% vs. ~ 60 - 85%; Appendix S1).

Low diversity of native ant communities

Impacts of invasive ants may not be detectable in locations with depauperate ant communities. High densities of *Anoplolepis gracilipes* on Bird Island in the Seychelles archipelago had no measureable impact on resident ant communities, where only four species were sampled in uninvaded plots (HILL & al. 2003). *Linepithema humile* had no detectable impact on either arboreal or epigeic ant communities in North Carolina, U.S., likely because there were so few arboreal species to displace (ROWLES & SILVERMAN 2010). In those communities where invasive ants may have little impact (e.g., *A. gracilipes* on Bird Island, monogyne *Solenopsis invicta* in southeastern U.S.), invasive ant abundance is positively correlated to the abundance (GERLACH 2004, KING & TSCHINKEL 2006) and species density (MORRISON & PORTER 2003) of native ants.

Altering keystone processes

Ant species may benefit from the presence of an invasive ant when its activity indirectly creates habitat for other species. On Christmas Island, Indian Ocean, *Anoplolepis gracilipes* extirpates the numerically abundant terrestrial red crab (*Gecarcoidea natalis*), a keystone species that regulates seedling recruitment and leaf litter decomposition on the forest floor (GREEN & al. 1997, GREEN & al. 1999). In supercolony areas, litter accumulates creating habitat for litter dwelling ant species. Non-invasive ant abundance is three times higher and species density twice as high in invaded habitats, and smaller-bodied ants in particular are more common in sites where *A. gracilipes* has invaded (O'DOWD & GREEN 2010).

Temporal variability

The impacts of invasive ants can vary considerably through time. Tracking invasion dynamics has demonstrated both prolonged impacts as well as dramatic recoveries by native ant communities.

Impacts of an invasion may be sustained over several years. Over an eight-year period of a *Linepithema humile* invasion in Rice Canyon, California, native ant numbers dropped from 23 species to two, with no recovery of ant communities behind the invasion front (TILLBERG & al.

2007). Sites re-sampled nine years after a *Pheidole megacephala* invasion in the seminatural rainforest of northern Australia indicated that infested sites had worsened, with lower native ant abundance (171 individuals down to one) and species density (at least seven species down to one), as only a single individual native ant was collected in re-sampled plots (HOFFMANN & PARR 2008). Sampling across sites with different invasion histories of *Wasmannia auropunctata* in Lopé National Park, Gabon, found an average of 39 species in uninvaded habitats, 17 species in recent (5-year) invasions, and only three species in well established (> 10-year) invasions (WALKER 2006).

Alternatively, native ant diversity may begin to rebound with time. Early within a *Linepithema humile* invasion at Jasper Ridge Biological Preserve in California, there was very little overlap in invasive ant and native ant distributions (HUMAN & GORDON 1996). As the invasion progressed over a seven year period, the number of plots in which only *L. humile* was found increased (SANDERS & al. 2001). With continued sampling over 13 years, however, the native ant community appeared to rebound slightly, with an increase in the number of plots that contained both Argentine ants and native ants (HELLER & al. 2008).

Native ant diversity may also fully recover and return to levels observed before the invasion. In one of the most notorious impact studies, one to four years into a *Solenopsis invicta* invasion in Texas, *S. invicta* decimated the native ant community: species density dropped 70% and total numbers of native individuals decreased by 90% (PORTER & SAVIGNANO 1990). MORRISON (2002) sampled plots 12 years later (13 - 16 years post-invasion) and observed recovery of the native ant community: *S. invicta* abundance had decreased by an order of magnitude, and native ant community diversity had returned to pre-invasion levels. The collapse of invasive ant supercolonies and rebound by native ants has also been reported for *Linepithema humile* in New Zealand. Ten to 20 years after invasion, *L. humile* had disappeared in 60 of 150 sites across the country, with many more sites reporting a large reduction in *L. humile* distribution and worker density. Community composition in collapsed sites was similar to uninvaded sites, with species density values intermediate to those found in never-invaded and still-invaded sites (COOLING & al. 2012). On Tokelau, sites re-sampled seven years later found a reduction in *Anoplolepis gracilipes* density, and differences in resident ant community composition and species density between invaded and uninvaded habitats were no longer detected (ABBOTT & al. 2007, GRUBER & al. 2013).

Taken together, these studies suggest that a reduction in native ant diversity is more likely to be observed when the polygene form invades, the resident ant community is not depauperate, the invasive ant does not indirectly create habitat for other ant species, or when the invasive ant is able to sustain high density levels.

Species resistant or susceptible to displacement by invasive ants

In general, susceptibility to displacement by invasive ants is related to the degree of ecological similarity with the invader. Invasive ants are abundant, competitively dominant epigeic ants (but see *Pachycondyla chinensis*), and it is the other common, conspicuous (e.g., large bodied), com-petitively dominant epigeic ants - those ants most likely to interact with the invasive ant - that are repeatedly reported to be negatively impacted in invaded habitats (e.g., *Camponotus* spp., *Iridomyrmex* spp., *Odontomachus* spp., *Pheidole* spp., *Solenopsis geminata*; Appendix S2).

Conversely, those ants less likely to encounter the invasive ants are less impacted. Hypogeic and cryptic ants, those that are small, inconspicuous and forage underground and in leaf litter, are commonly found to persist in invaded habitats (e.g., *Brachymyrmex* spp., *Hypoponera* spp., *Temnothorax* spp.; Appendix S3). Native ants with different thermal tolerances than invasive ants may also avoid displacement. This is most commonly noted for the cold tolerant *Prenolepis imparis*, but is also observed for the heat tolerant *Aphaenogaster senillis*, *Cataglyphis* spp., *Dorymyrmex insanus*, *Forelius mccooki*, and *Melophorus* spp. (Appendix S3). Thermophilic *Ocymyrmex cilliei* and *Tetramorium quadrispinosum* also close their nest entrances during cooler times when *Linepithema humile* is most active (WITT & GILIOMEE 1999), further reducing likelihood of contact with *L. humile*.

That invasive ants have a greater impact on those ants with similar ecological traits is further supported by patterns of a *Pachycondyla chinensis* invasion, the first documented invasion by a ponerine and a hypogeic forager. With this invasion, the abundance of hypogeic species was strongly negatively correlated with *P. chinensis*, while the epigeic species were those that were unaffected (GUÉNARD & DUNN 2010, RODRIGUEZ-CABAL & al. 2012).

Additionally, while *Prenolepis imparis* is most commonly noted to persist with *Linepithema humile* through its cold tolerance, it may also resist displacement through potent chemical defense, as *P. imparis* secretions are highly lethal to *L. humile* workers (SORRELLS & al. 2011). Strong repellent chemical defense (BARONI URBANI & KANNOWSKI 1974, HOWARD & OLIVER 1979, ANDERSEN & al. 1991) has also been noted for *Monomorium* spp., a genus commonly noted to persist with invasive ants over the world (Appendix S3).

Solenopsis (*Diplorhoptrum*) species, subterranean predators and food-stealers, are the group most often observed to persist, and even flourish, in invaded areas (Appendix S3). Indeed, this group has been proposed to influence populations of *Solenopsis invicta* more than any other group of ants (BUREN 1983). (See also Biotic resistance.)

Disturbance specialists (e.g., *Dorymyrmex* spp.) are found to do well in invaded areas (Appendix S3). *Dorymyrmex* spp. are strong colonizers of experimentally baited (SUMMERLIN & al. 1977, CALIXTO & al. 2007) and plowed (KING & TSCHINKEL 2008) plots with *Solenopsis invicta*.

Finally, when resident ant communities are populated by both native and non-native ant species, non-native species and tramp species may better resist displacement by the invasive species. *Solenopsis invicta* may not impact resident ant communities in Florida pastures because the majority (89% relative abundance) of resident ants were introduced species (KING & TSCHINKEL 2006). *Anoplolepis gracilipes* in Indonesian cacao agroforests reduced the density of natural forest ant species while ants specific to disturbed habitats were unaffected (BOS & al. 2008). In the Samoan Archipelago, SAVAGE & al. (2009) found a negative relationship between *A. gracilipes* abundance and species density of native ants, but not for non-native ants.
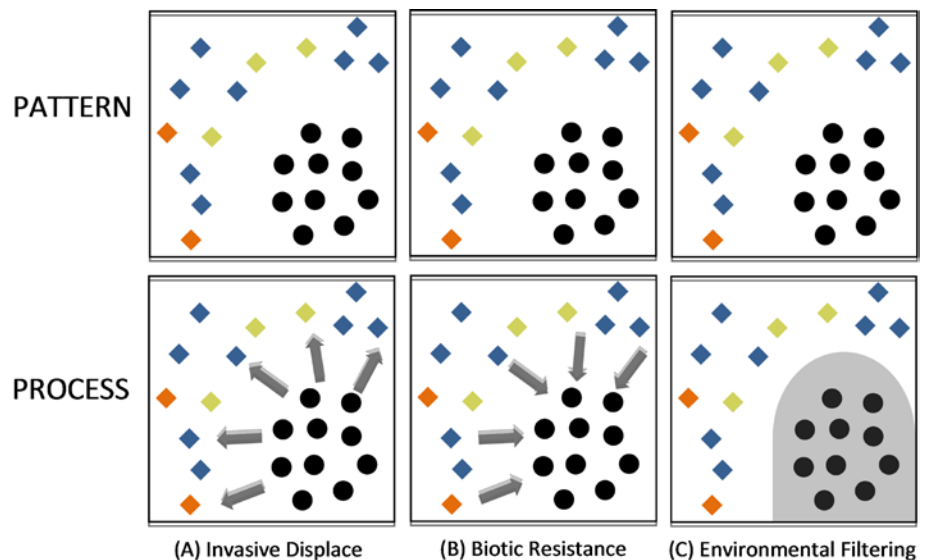
Fig. 1: The commonly observed pattern of invasive ants (black dots) occurring with few native ants (diamonds) may be a product of different, non-mutually exclusive processes. Invasive ants may displace native ants (A: invasive displace), native ants may prevent the spread of invasive ants (B: biotic resistance), or invasive and native ants may respond differently to environmental conditions (gray) (C: environmental filtering).

Lastly, in a Texas coastal disturbed prairie, global tramp species persisted in *Nylanderia fulva* invaded habitats while regionally distributed species were negatively affected (LE-BRUN & al. 2013).

Overall, the reduction and differential displacement of native ant species can result in the homogenization of native ant communities over relatively large spatial scales (HOLWAY & SUAREZ 2006, ROURA-PASCUAL & al. 2010) in which only few, closely-related taxa can persist (LES-SARD & al. 2009).

Potential drivers of native ant diversity in invaded habitats

Different processes may underlie patterns of low native ant diversity in invaded habitats (Fig. 1) – processes that may work separately or concurrently throughout different stages of an invasion (establishment, spread, and contraction). The dominant paradigm is that invasive ants are competitively superior to native ants, and therefore displace native ants during an invasion. In this scenario, fewer native ant species exist in invaded habitats because they are outcompeted (for nests, for food, or via direct mortality) by competitively superior invasive ants (Fig. 1A). Alternatively, the biotic resistance hypothesis posits that diverse, competitively dominant native ant communities may prevent the establishment of invasive ants. In this scenario, invasive ants can only persist in areas with species poor, competitively inferior native ants, producing a pattern in which invasive ant distribution correlates with areas of low native ant diversity (Fig. 1B). Finally, native and invasive ants may be non-interactive, and patterns of native ant diversity may not be due to direct interactions with invasive ants, but rather to different environmental conditions. In this scenario, native and invasive ants do not co-occur because invasive ants possess traits that allow only them to persist under specific physical conditions (Fig. 1C).

Competitively superior invasive ants

As previously discussed, observations supporting the competitive superiority of invasive ants includes the ability of invasive ants to reach extraordinary densities, monopolize resources, and conduct raids, the reduction in native ant abundance and species density in invaded habitats, the disproportionate impact on ecologically similar native ant species, and the recovery of native ant communities with the collapse of invasive ant supercolonies.

Baiting experiments

Broadcast poison baiting experiments have also been used to infer competitive interactions between invasive and native ants. If invasive ants are competitively superior, then reducing their numbers should release native ants, which will then increase in abundance. Alternatively, if native ants are limiting the spread of invasive ants, then the reduction of native ants should result in higher numbers of invasive ants. Although broadcast baits should be monopolized by competitively dominant abundant species (i.e., primarily by the invasive species), this method can also have non-target effects on other ant species (SUMMERLIN & al. 1977) and changes in abundance post-treatment may be due to a combination of direct mortality, colonization, and / or competitive release. Results of broadcast baiting with *Solenopsis invicta* are mixed: Native ants may decline and *S. invicta* reach higher abundance than pre-treatment levels (MARKIN & al. 1974, SUMMERLIN & al. 1977, STI-MAC & ALVES 1994), *S. invicta* and native ants may recover at similar rates (STUBLE & al. 2011), or native ants may increase in treated plots with reduced *S. invicta* abundance (CALIXTO & al. 2007). In the rainforest of northern Australia, broadcast baiting eradicated an early invasion by *Pheidole megacephala*, which resulted in the subsequent recovery of the native ant community (HOFFMANN 2010).

Experiments with targeted reduction of *Solenopsis invicta* in undisturbed and disturbed habitats have produced opposing results. Plots with targeted distribution of poison baits to *S. invicta* mounds in relatively undisturbed sandy grasslands in Texas, U.S., resulted in fewer *S. invicta* colonies, and maintained higher endemic ant diversity than unbaited plots over time (COOK 2003). On the other hand, targeted removal of monogyne *S. invicta* colonies in pas-

tures in Florida, U.S., found no evidence of competitive release of the native ant community with a 70% reduction in *S. invicta* over a two year period (KING & TSCHINKEL 2006). (See also Role of disturbance: drivers, passengers, and back-seat drivers.)

Biotic resistance

Australia's *Iridomyrmex* spp., due to their widespread distribution, high abundance, activity levels, and behavioral aggression (ANDERSEN 1995), have been proposed to limit the spread of invasive ants (ANDERSEN 1997, HOFFMANN & al. 1999, WALTERS & MACKAY 2005). However, *Iridomyrmex* spp. are found in lower numbers in areas invaded by *Anoplolepis gracilipes*, *Linepithema humile*, and *Pheidole megacephala* (Appendix S2). Behavioral observations at baits have found mixed support for resistance by *Iridomyrmex*: *Linepithema humile* may only displace *Iridomyrmex* spp. when at 5 - 10 times greater worker density (WALTERS & MACKAY 2005), under warm, but not hot conditions (THOMAS & HOLWAY 2005), or with ease, and with subsequent raids on *Iridomyrmex* nests (ROWLES & O'DOWD 2007).

Anoplolepis gracilipes is able to invade diverse, highly competitively native ant communities in a variety of undisturbed tropical woodland and rainforest habitats in Australia. Native ant communities with competitively dominant ant species, including *Iridomyrmex* spp., could not prevent invasion by *A. gracilipes*, and invaded native ant communities with many competitively dominant species suffered similar reductions in abundance and species densities than communities with few competitively dominant species (HOFFMANN & SAUL 2010).

Native ant resistance to *Linepithema humile* invasion has been proposed for *Lasius grandis* in Madeira (WETTERER & al. 2006), *Crematogaster scutellaris* and *Pheidole pallidula* in native oak and pine habitats in Portugal (CAMMELL & al. 1996), *Tapinoma nigerrimum* in pasture habitats in Portugal (WAY & al. 1997), and *Tapinoma simrothi* and *T. nigerrimum* in Corsica (BLIGHT & al. 2009, BLIGHT & al. 2010). Supporting evidence has generally been complementary distribution patterns of native and invasive ants. A short-term removal experiment of *P. pallidula* at a contact zone with *L. humile* resulted in *L. humile* moving into its territory four days later (WAY & al. 1997), suggesting the presence of *P. pallidula* resisted spread of *L. humile*. A longer term study reached a different conclusion: tracking a *L. humile* invasion over a year, *P. pallidula* and *C. scutellaris* were those species that experienced the most severe declines in occupancy in newly invaded habitats (ROURA-PASCUAL & al. 2010).

Current studies provide limited evidence of biotic resistance of *Linepithema humile* by native ant communities, and habitat suitability appears to be the primary determinant of its success. In a field experiment that modified abiotic conditions (increased soil moisture through drip irrigation) and biotic resistance (targeted removal of native ant community), *L. humile* could not invade dry plots, even when native ants were removed. Although fewer *L. humile* were found in plots when native ants were present, native ants could not prevent invasion in irrigated plots (MENKE & al. 2007). These findings are consistent with observational studies in which native ant diversity did not prevent or slow the spread of *L. humile* in California

(HOLWAY 1998b, SANDERS & al. 2003) or Spain (ROURA-PASCUAL & al. 2010). While native ants may potentially slow the rate of invasion by *L. humile* at the edge of its range, there is little evidence that biotic resistance occurs where suitable climate and habitat modifications exist for *L. humile* on either the local (HOLWAY 1998b, FITZGERALD & GORDON 2012), regional (ROURA-PASCUAL & al. 2010), or global (ROURA-PASCUAL & al. 2011) scale.

Ants in the *Solenopsis* (*Diplorhoptrum*) group, subterranean predators that steal food and attack founding queens, have been suggested as the group with the greatest influence on *Solenopsis invicta* populations (BUREN 1983). *Solenopsis* (*Diplorhoptrum*) *molesta* was able to destroy small colonies of *S. invicta* in laboratory tests (RAO & VINSON 2004), and *S. invicta* was unable to colonize areas with high *S. molesta* densities (VINSON & RAO 2004) and was absent from plots with high *S.* (*Diplorhoptrum*) *carolinensis* FOREL, 1901 densities (STUBLE & al. 2009).

Overall, as very few studies directly manipulate the native ant community (but see MENKE & al. 2007), it is impossible to conclude to what degree native ants may influence the spread, reproduction, abundance, and longevity of invasive ants.

Role of disturbance: drivers, passengers, and back-seat drivers

Even when invasive ants are the numerically and behaviorally dominant species within a habitat, they may not be exerting strong competitive control over native ant species. Complementary species distributions may be non-interactive and, instead, be the product of differential response to physical conditions or processes. This scenario is best documented in disturbed habitats, in which the invasive species is a disturbance specialist, colonizing and establishing in habitat otherwise unsuitable for many native ant species.

The interplay of disturbance and invasion can be especially difficult to tease apart, as disturbance itself can reduce native ant diversity (LUBERTAZZI & TSCHINKEL 2003, KING & PORTER 2005) as well as facilitate spread of invasive ants (ZETTLER & al. 2004, KING & TSCHINKEL 2008). Accordingly, identifying the processes of native species decline in disturbed habitats can be tricky business, as are definitive labels of invasive ants as drivers (decline in native diversity driven by biotic action of the competitively superior invasive species) or passengers (decline in native diversity driven by direct effects of disturbance; invasive species success not due to competitive exclusion of natives but rather to being better suited to the modified environment). Invasive species may also function as back-seat drivers, wherein disturbance and competition by invasive species interact to impact native communities more than either factor alone (BAUER 2012).

KING & TSCHINKEL (2008) experimentally tested the role of disturbance and *Solenopsis invicta* by both manipulating disturbance (= mowing and plowing) and adding ant colonies in Florida pine flatwoods. Both disturbance and the addition of *S. invicta* reduced the number of species and abundance of co-occurring ants. However, as *S. invicta* is not observed to colonize intact pine flatwood habitat, physical disturbance is likely needed for its establishment and success. Here, disturbance appears to be the primary determinant of ecological change: without it native ants would not be affected by either the disturbance it-

self, or, subsequently, by competition from colonizing *S. invicta*. *Solenopsis invicta* may function as a passenger of ecological change in a variety of disturbed habitats, as no detectable impacts of *S. invicta* on native ants were found in Florida pastures (MORRISON & PORTER 2003, KING & TSCHINKEL 2006), frequently burned longleaf pine stands in Georgia (STUBLE & al. 2009) and frequently flooded pine flatwoods in Florida (KING & TSCHINKEL 2013).

Alternatively, *Solenopsis invicita* populations in Texas can successfully colonize undisturbed habitat and cause significant impacts to native ants communities (PORTER & SAVIGNANO 1990, MORRIS & STEIGMAN 1993, KASPARI 2000, LEBRUN & al. 2012). The role of disturbance was evaluated by LEBRUN & al. (2012) by sampling ant communities in soil of disturbed and undisturbed areas in coastal plains in Texas. Negative impacts of a high density *S. invicta* invasion were observed in wet-undisturbed habitat, whereas no detectable impacts were found in disturbed habitats. Overall, these studies suggest *S. invicta* may function as a passenger of ecological change in disturbed and species poor habitats, and as driver of low native ant diversity in undisturbed habitats.

Observations of invasion patterns and native ant diversity in New Caledonia rainforest and shrubland suggest *Anoplolepis gracilipes* and *Wasmannia auropunctata* may function as back-seat drivers, exacerbating impacts on native ants in fire-altered habitat. BERMAN & al. (2013) sampled ants in intact and fire-disturbed habitats of New Caledonia where *A. gracilipes* and *W. auropunctata* have also invaded. The invasion of *A. gracilipes* after a single-fire event, and of *W. auropunctata* in fire-mediated successional gradient, correlated with a greater reduction in the density of co-occurring native ant species. While disturbance is not always needed for either *A. gracilipes* or *W. auropunctata* to invade successfully (Appendix S1), fire-disturbed habitat may exacerbate their impacts upon native ants in New Caledonia.

Future directions

While we have gained a clearer picture of the ways in which invasive ants may impact native ant communities, there are still many unanswered questions.

At what density threshold do invasive ants start to impact native ant communities? Not all invasions have negative impacts on native ants, and within an invasion, impacts may not be evident in low-density areas (VONSHAK & al. 2010, LEBRUN & al. 2013) or when densities diminish through time (MORRISON 2002, COOLING & al. 2012, GRUBER & al. 2013). There is a continued call for the use of standardized sampling methodology (e.g., card counts) for quick estimates and comparisons of invasive ant abundance and identification of density-dependent thresholds of invasive ant impacts (ABBOTT 2005, GRUBER & al. 2013).

How are invasive ants able to achieve such exceptional biomass? Habitat modification, mutualisms with honeydew producing insects, release from natural enemies (parasitoids, disease, competitors) and social structure may contribute, separately or in combination, to invader densities. We still do not know how invasive ants are able to reach orders of magnitude higher biomass than that of entire, intact native ant communities.

How long and over what area can invasive ants sustain densities at which they are deleterious to native ants?

While invasive ants can achieve extremely high densities, transition zones can be very abrupt, with high invasive ant densities diminishing to zero over 50 meters (VANDERWOUDE & al. 2000, ABBOTT 2006), and impacts on native ant diversity may no longer be detectable 50 - 100 meters from high densities areas (VANDERWOUDE & al. 2000, CALLAN & MAJER 2009, DRESCHER & al. 2011). Although there is much variability in temporal effects of invasive ants, the vast majority of impact studies are conducted over a single sampling season (Appendix S1). Best estimates from current studies on *Linepithema humile* and *Solenopsis invicta* indicate over 13 years native ant diversity can naturally rebound and may sometimes fully recover (MORRISON 2002, HELLER & al. 2008, COOLING & al. 2012). Additionally, what role does low genetic diversity, spread of natural enemies or pathogens, climatic variability, and depletion of resources play in the natural collapse of invasive ant supercolonies? We need more long-term studies to understand the temporal and spatial dynamics of invasive ants and their impacts on native ant communities.

What lasting effects do invasive ants have on native ant communities? There is emerging evidence that competition from invasive species does not cause local extinctions of native species (BAUER 2012 and references therein), and there is little indication of permanent displacement of native ant species by invasive species, with the possible exception of *Solenopsis geminata* and *S. xyloni* by *S. invicta* in certain areas of southeastern U.S. (TSCHINKEL 1988, MORRISON 2002, KING & TSCHINKEL 2013).

Many studies report the spread of invasive ants into undisturbed habitats with associated negative impacts on native ant communities (Appendix S1), but uncertainty remains as to the importance of habitat modification to the ability of different invasive ant species to drive declines in native ant diversity. Impact studies need clear statements of habitat descriptions and disturbance history, and we need to continue investigations of the interaction of disturbance and invasive ants on native ant communities.

Finally, as different processes may underlie the commonly reported association of invasive ants with low native ant diversity, we need more manipulative studies that explicitly test the importance of interactive and non-interactive processes in determining the spread of invasive ants and their impacts on native ant diversity.

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