

The ecology of ants (Hymenoptera: Formicidae) on islands

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Abstract

Ants are nearly ubiquitous on islands. Species may reach oceanic islands by three mechanisms: (1) mating flights of reproductives, (2) rafting, and (3) human-assisted dispersal. Past land bridge connections may be important for continental shelf islands. Patterns of species accumulation may be similar even when primary mechanisms of dispersal differ. Colonizing propagules are limited primarily by the presence of suitable habitat and interspecific competition or predation from other ants. Although island area is usually a significant predictor of species richness, the diversity of habitat types is often a better predictor. Distance, or isolation, has often been found to be only a weak predictor of ant species richness, probably because many islands that have been studied are not very distant relative to most species' dispersal abilities. Interspecific competition appears to result in mutually exclusive distributions within islands for some of the more aggressive species, although the effects of habitat affinities have not been well studied. With the exception of very small islands, competition does not appear to result in exclusions of species from entire islands, and robust patterns of nestedness have been observed. Populations go extinct from and immigrate to small islands in ecological time, although such turnover appears to be relatively low compared with other arthropods. Only a few archipelagoes, however, have been the focus of turnover studies. Some species may reach extremely high population abundances on islands but subsequently decline. The exact mechanisms underlying these population fluctuations are not known with certainty, although the presence of honeydew-producing insects has often been associated with the most dramatic cases. Endemicity varies greatly and ranges from 0 to > 96%, peaking at intermediate distances in the Pacific and reaching the highest levels on islands in the Indian Ocean. Anthropogenic disturbances appear to present the greatest driver of change to insular ant communities and result in increasing numbers and abundances of exotic ant species, which may have deleterious effects on the rest of the community.

Key words: Colonization, dispersal, endemicity, invasive ants, island biogeography, mating flights, plague ants, rafting, review, turnover.

Myrmecol. News 23: 1-14 (online 8 March 2016)
ISSN 1994-4136 (print), ISSN 1997-3500 (online)

Received 28 September 2015; revision received 30 November 2015; accepted 2 December 2015
Subject Editor: Nicholas J. Gotelli

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Introduction

Ants are nearly ubiquitous on islands, found in the most remote archipelagoes (e.g., Hawaii, Mid-Atlantic Ridge islands) and on the smallest of islets (e.g., mangrove islands of only a few m³; COLE 1983a). To date, however, no literature review of the ecology of ants on islands has been published. An obvious question is whether the ecology of ants on islands is any different than ant ecology in continental areas. If so, the differences may be most apparent on smaller islands (on which ants face relatively greater challenges of extreme environments, limited habitat types, and more intense competition) and more remote islands (to which dispersal is more difficult). Many studies have focused on smaller and more remote islands and archipelagoes (i.e., those that exhibit a greater degree of "insularity"), and are the subject of this review.

This paper primarily considers the ecological aspects of life on small islands and leaves the evolutionary facets for another review. Endemicity is included, primarily for the inferences concerning dispersal ability and patterns of diversity across archipelagoes. Although studies have been

conducted on ants inhabiting islands in lakes, as well as various types of habitat islands, here the focus is on islands occurring in oceans. Realizing that many collections are incomplete and that many taxa are in need of revision, I attempt to elucidate the broader patterns that seem robust given these sources of uncertainty. Finally, there exists some geographic bias in this review, because some islands / archipelagoes have been studied in greater detail than others, and of these, some have been simply "collected", whereas others have been the subject of biogeographic or ecological analyses. Most insular studies have been conducted in the tropics or low latitudes of the temperate zone, in part because most invasive ants reach their highest densities in these regions, and there is a large invasive ant literature.

In this review, the following questions are addressed: How do ants arrive on islands? What factors are important in their colonization success? How are they distributed, within and among islands and archipelagoes, and how persistent are their populations? What allows some species to

reach high abundances and threaten other members of the community? Finally, what threats do ants on islands face / pose in the future?

Dispersal

Ants may reach oceanic islands (i.e., islands that have never been connected to continental areas) by three mechanisms: (1) mating flights of reproductives, (2) rafting, and (3) human-assisted dispersal. In most, but not all species, aerial mating occurs between winged reproductives, after which the mated queen lands and establishes a new colony (HÖLDOBLER & WILSON 1990). To obtain an idea of the distances involved in such mating flights, it is instructive to consider the literature on one of the most studied of all ant species, the red imported fire ant, *Solenopsis invicta* BUREN, 1972. It has been estimated from an energetics model that the flight capability of *S. invicta* female alates is < 5 km (in the absence of wind) (VOGT & al. 2000).

Empirical observations, however, have revealed that *Solenopsis invicta* female alates cover distances two to three times that of the theoretical prediction, presumably assisted by wind. Observations of mating flights along the shore of the Gulf of Mexico yielded discoveries of alates on the water surface or on boats in the range of 4.8 to 8 km from shore, up to a maximum of 9.6 km (MARKIN & al. 1971). Alates were discovered at even greater distances on two islands on which the resident ant populations had been exterminated with the insecticide mirex. Thirty-six alates were found on an island 11.2 km from shore, and one alate was found on an island 16 km from shore.

Species differ in various characteristics of mating flight behavior (HÖLDOBLER & WILSON 1990), although it is likely that distances covered by mating flights of other ant species are of the same order of magnitude. It is largely unknown how far alates may travel when aided by wind. Distributional evidence from the Florida Keys revealed that a number of species were capable of dispersing over an 8 km water barrier, but very few were able to successfully cross a 65 km water barrier (WILSON 1971).

The numbers of alates involved in mating flights of the more common species are often truly astounding. For example, during a mass mating flight of the black garden ant, *Lasius niger* (LINNAEUS, 1758) near Normandy, France, an estimated 25 million alates per km were found washed up on beaches (JONES 2013). Almost all alates examined were males, indicating these estimates did not take into account the female fraction. Alates may be components of the aerial plankton, and have been caught in aerial nets at relatively great distances from land (e.g., HOLZAPFEL & HARRELL 1968, BOWDEN & JOHNSON 1976), although it is unknown whether such specimens represent viable colonists.

Entire ant colonies may raft to islands within logs or other plant material, as observed anecdotally by WHEELER (1916) and HEATWOLE & LEVINS (1972). Little scientific documentation exists on this mechanism of dispersal. Rafting probably occurs relatively infrequently, or at least is rarely observed. It is likely to be more important for islands near the mouths of large rivers, which often carry rafts of vegetation (KING 1962). Rafting is more likely to occur with species that nest in vegetation than in the soil. Distances covered would depend upon the speed of ocean currents and the time until vegetation became waterlogged.

Human-assisted dispersal represents a major source of island colonists, as ants frequently stowaway in boats, planes, or cargo. Upwards of 150 species are known to be dispersed anthropogenically (MCGLYNN 1999). The Hawaiian Islands, one of the more remote island archipelagoes in the world, are home to over 50 species (KRUSHELNYCKY 2015), with at least 50 additional species having been intercepted in quarantine without becoming established (KRUSHELNYCKY & al. 2005b). All ants in the Hawaiian Islands are thought to have been introduced by humans, and if so, this demonstrates the archipelago is too isolated for aerial dispersal of alates or rafting. Although most anthropogenic introductions to Hawaii are relatively recent, it is likely that a few species may have been introduced by aboriginal peoples prior to the modern era. For example, some species may have spread across Polynesia in the canoes of the ancient Polynesians (WILSON & TAYLOR 1967a), and analogous dispersal events may have been associated with the Arawak and Carib Indians in the Bahamas (MORRISON 1998a).

Some species of ants have been able to disperse naturally to all except perhaps the most remote islands. It has long been thought that some islands, for example those of Eastern Polynesia, were too isolated for natural dispersal (WILSON & TAYLOR 1967b). Recent sediment cores from Easter Island, however, contained the remains of ant species that were dated much earlier than the generally accepted period of human settlement (HORROCKS & al. 2013). Sediment cores from the Austral Islands revealed the existence of several apparent native ant species (N. Porch, unpubl.). The remote Mid-Atlantic Ridge islands (Ascension, St. Helena, and Tristan de Cunha) have 20 known species, "most, if not all" of which were determined to be exotics (WETTERER & al. 2007), and it is possible that some may predate humans.

For continental shelf, or land bridge, islands, a fourth mechanism is possible: the ants were already present when the island was cut off from a continent by rising sea levels. Alternatively, species may have dispersed over land bridges that existed during periods of lower sea level. For example, many of the present-day islands in the Bahamas were, during the Pleistocene, interconnected by much larger, emergent banks that would have made overland dispersal possible (DEYRUP & al. 1988). Even when greater emergent land area did not result in the complete bridging of water gaps, narrower water barriers would have made it easier for species to disperse via wind-assisted mating flights. During the last glaciation, for example, the water gap between the Bahamas and Cuba would have been only ~ 15 km (OLSON & PREGILL 1982).

Thus, to summarize the four main vectors of ant dispersal to islands: Mating flights occur annually and involve the majority of ant species, but are usually limited to relatively short distances. Rafting likely occurs infrequently, involves primarily arboreal species, and may cover short to intermediate distances. Human-assisted dispersal is occurring with increasing frequency, involves primarily tramp or invasive species, and may cover practically unlimited distances. Land bridges appear over geologic timescales, may involve in theory all ant species, cover distances that vary regionally based on geography, and in the case of incomplete bridging may increase dispersal occurring through mating flights or rafting.



Fig. 1: (A) Small marine limestone island in the central Exumas, Bahamas. (B) Larger Bahamian marine limestone island revealing honeycomb nature of substrate. Photographs by the author.

Colonization

Once a colonizing propagule capable of reproduction has dispersed to an island, it faces two immediate challenges: finding suitable habitat, and avoiding lethal competition or predation. A propagule may represent either an inseminated female alate or an entire or partial colony with at least one mated queen. Most colonization attempts by female alates fail. LEVINS & al. (1973), for example, working on a set of 144 small islands near Puerto Rico, estimated that thousands of female alates representing species that were not already present dispersed to the islands each year, but only a small fraction (~ 4%) successfully colonized.

Some islands may be too small to support a population, and the minimum size requirement varies among species (e.g., COLE 1983a). Each species has its own habitat requirements, and generalists will be more likely to survive than specialists. Species that nest arboreally, for example, require woody vegetation, and those that tend aphids require the presence of aphids as well as their host plants (VEPSÄLÄINEN & PISARSKI 1982).

In a study of ants that were intercepted in commerce inspected by the United States Department of Agriculture

between 1927 and 1985 in the continental United States, a high diversity of species (232 species from 394 records) were included. Only 12% of these species have become established. The probability of establishment increased with the number of times a species was transported. Nesting habit was also important, as ground nesting species were more likely to become established than arboreal species. This is presumably due to the lack of suitable nest sites in new environments, as arboreal ants often exhibit preferences for particular types of trees. The arboreal ants that have become established all exhibit flexibility in the choice of nesting sites and persist in a wide variety of tree species (SUAREZ & al. 2005). Although this was a continental, rather than insular, analysis, similar patterns likely characterize island colonization.

A study of ant communities on small mangrove islands in the Florida Keys revealed that certain species never coexisted on the same islands, while other pairs of species were only found if the island was large enough (COLE 1983a). Arena experiments revealed that aggressive interactions were the mechanisms underlying the observed patterns (COLE 1983a). A similar result in terms of predictability of species present on small islands was found on

limestone islands in the Bahamas (Fig. 1A). If only one species was present on an island, it was *Brachymyrmex obscurior* FOREL, 1893 93.7% of the time. If two species were present, the second species was *Dorymyrmex pyramicus* (ROGER, 1863) 74% of the time (MORRISON 2006).

Not all ant species are antagonistic to each other, however. On islands of the Tvärminne Archipelago of the Baltic Sea, it has been estimated that one third of the species are dependent upon another ant species during colonization (VEPSÄLÄINEN & PISARSKI 1982). Mechanisms of dependence range from the need to found a colony in another established species' nest to workerless parasitic species. Whereas dependence on other ant species is prevalent in this archipelago, such social parasitism is not as common in many other insular systems, as parasitic ants represent < 2% of all described species (BUSCHINGER 2009).

Variation in characteristics such as the morphology, behavior and life history of a species may affect colonization abilities. For example, colonies of species that invest more in larval feeding, have large queen to worker size ratios, and have a monomorphic caste structure can increase in abundance more quickly (COLE 1983b). Nest location may also be important; in mangrove ant communities species that placed their nests in the periphery of mangrove trees experienced a reduced frequency of aggressive encounters with other species (COLE 1983b).

Because competition from other, established species may be particularly intense to incipient colonies, colonists that arrive earlier are more likely to be successful. For ecologically similar species, the early arrival of one may even preclude or retard colonization by another; this has been termed the "priority effect" (VEPSÄLÄINEN & PISARSKI 1982). In addition to which species arrives first, the outcome of competitive interactions may also depend upon habitat. For example, the Argentine ant, *Linepithema humile* (MAYR, 1868), is known from only three locations in Polynesia: the big islands of Hawaii and Maui, where it exists primarily in the higher elevations (> 900 m; COLE & al. 1992, WETTERER & al. 1998), and on Easter Island (MORRISON 1997). *Linepithema humile* is adapted to a more temperate climate than that found on most Polynesian islands, and apparently has been outcompeted by other ants in the lower, more tropical elevations of Hawaii and Maui (REIMER 1994, KRUSHELNYCKY & al. 2005a). *Linepithema humile*, however, has apparently outcompeted other ants previously established across the more temperate Easter Island (MORRISON 1997).

Very little experimental work has been conducted regarding ant colonization of islands. LEVINS & HEATWOLE (1973) introduced *Pheidole megacephala* (FABRICIUS, 1793) (the big-headed ant), to Palominos Island near Puerto Rico. The introduction failed, presumably because of competition from the resident ant fauna.

In the classic mangrove island experimental study conducted in the Florida Keys, WILSON & SIMBERLOFF (1969) defaunated islands of all terrestrial arthropods by fumigation with pesticides. Before fumigation, ants demonstrated highly predictable patterns of species composition (i.e., nestedness), with species richness increasing both with increasing island size and decreasing distance from shore (SIMBERLOFF & WILSON 1969, SIMBERLOFF 1976). Ants were among the last terrestrial arthropods to re-colonize, but they displayed "the most orderly pattern of coloniza-

tion". In other words, certain species consistently colonized before others, and species identities were to some degree predictable based on island area and distance. The similarity in species composition between pre-defaunation and final surveys 322 - 542 days later (depending on the island), however, was on average only 53% (Sørensen's index, my calculations based on Tab. 3 in SIMBERLOFF & WILSON 1969). Thus, almost half of the species identities had changed, although average species richnesses were similar: 5.2 (pre-defaunation) compared to 4.6 in the final survey. SIMBERLOFF & WILSON (1969) concluded that it "seems probable" a priority effect occurred, with the first species to arrive excluding later colonists, although they found no direct evidence of aggressive behavior, and postulated that nest site pre-emption may have been the underlying mechanism.

Thus, the vast majority of potential colonists that reach an island likely fail to become established, due either to lack of appropriate habitat or competition (or predation) from other ants. Generalist species, or those that have certain morphological, behavioral, or life history traits that confer an advantage in colonization, will be more successful, all else being equal. Given the availability of appropriate habitat, the priority effect is probably very important in most cases, and species that arrive earlier are more likely to successfully colonize.

Accumulation

Two interesting data sets allow for the comparison of accumulation of ant species in two archipelagoes with varying recent histories: the Krakatoa Islands and the Hawaiian Islands. The Krakatoa Islands include four small volcanic islands in the Sunda Straits between Java and Sumatra, Indonesia. Massive eruptions in 1883 are thought to have resulted in the mortality of practically all life present at the time (THORNTON 1996). It is thought all ant species that have since colonized have dispersed either by mating flights or rafting, although anthropogenic transport cannot be precluded for a few species (YAMANE 2013). The islands are ~ 30 km from Sumatra and ~ 40 km from Java, but only ~ 12 km from Sebesi Island, which could function as a stepping-stone from Sumatra.

Five surveys of Krakatoan ants have been conducted since the eruptions, in: 1908, 1919 - 1922, 1929 - 1933, 1982 - 1985, and 2005 - 2007. Over the 114-year interval, 125 cumulative species have been found (Fig. 2), although some species found in the earlier surveys were not found in the later ones, possibly due to changes in habitat associated with succession (YAMANE 2013). The discovery of a *Leptogenys* species in which the queens cannot fly and colonies multiply by fission (dependent colony foundation) is strong evidence that at least this species arrived by rafting (ABE & al. 2012). A relatively high proportion of the ants present nest in dead wood and twigs (74%), as opposed to the ground surface and soil (14%), which led YAMANE (2013) to postulate that rafting as a dispersal method for the Krakatoan ants may be relatively important, although no direct evidence for the dispersal of ants by rafting to Krakatoa exists.

The Hawaiian Islands, in contrast, are thought to be so remote that ants have not been able to reach them by natural mechanisms of dispersal, and all species present represent anthropogenic introductions. Naturalists first began

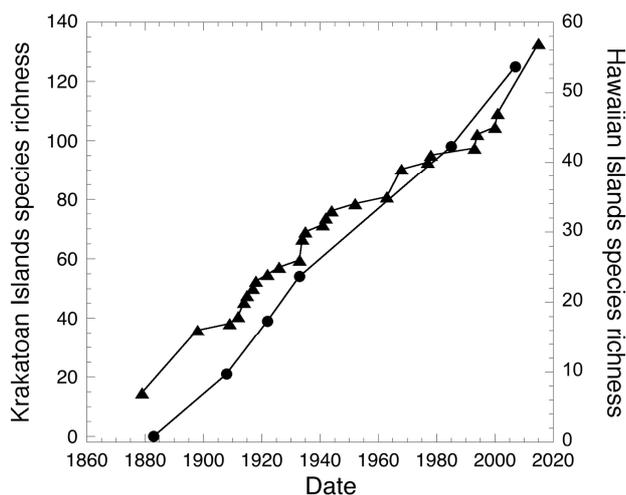


Fig. 2: Accumulation of ant species on Krakatoa (filled circles) and Hawaii (filled triangles). Note different scales on y-axes. Krakatoa data are from YAMANE (2013). Hawaii data are from KRUSHELNYCKY & al. (2005b), with the exception of the final data point, which is from KRUSHELNYCKY (2015).

collecting ants in Hawaii in the 1880s – about the time of the Krakatoa eruptions – and 57 established species are currently known (KRUSHELNYCKY 2015) (Fig. 2). Although some species were present before the earliest collections, KRUSHELNYCKY & al. (2005b) consider the lag period between establishment and the first record to have been fairly constant over time, so that the pattern of species detection approximates the pattern of accumulation. In 2005, it appeared that the rate of species accumulation was beginning to decrease (KRUSHELNYCKY & al. 2005b: fig. 1). Given the number of new species that have been discovered since, however, this does not appear to be the case now (Fig. 2).

The Krakatoa Islands have accumulated species at a faster rate (note differences in y-axes in Fig. 2), although in the Hawaiian Islands at least 50 species in addition to those established have been intercepted in quarantine (KRUSHELNYCKY & al. 2005b). If these also had become established, the rates would be similar. In neither archipelago does the species accumulation curve reveal any sign of saturation.

Thus colonization in the Krakatoan ant fauna has apparently been limited by natural dispersal ability in crossing a relatively wide water barrier and the presence of suitable habitat types. Colonization in the Hawaiian ant fauna has been limited by the ability of species to travel with humans, and the suitability of the climate. Only 12% (15 / 125) of the Krakatoan fauna are classified as tramp species (YAMANE 2013), whereas nearly all of the Hawaiian species qualify as tramps (KRUSHELNYCKY 2015). Yet despite these fundamental differences, species accumulation on these two archipelagoes is remarkably similar in several aspects.

Extreme environments

Although ants are present on almost all islands, there do exist some notable exceptions: islands at high latitudes and islands lacking terrestrial vegetation as the base of insular food webs. For example, there are apparently no ants on the Falkland Islands or the South Georgia islands (WET-

TERER & al. 2007). Only a single species is known to have a persistent population on Iceland – the exotic *Hypoponera punctatissima* (ROGER, 1859) – although it is present only in houses and geothermal areas.

At a minimum, some terrestrial vegetation appears to be a necessary base of insular food webs that allow the survival of ants. In a survey of 242 small islands in four Bahamian archipelagoes, ants were never found on islands lacking vegetation ($n = 54$), but were almost always present on islands with vegetation (MORRISON 2006). Ants have been reported, however, on an island in the Puerto Rican bank that lacked terrestrial vegetation (HEATWOLE & al. 1981). Apparently the base of this insular food web was supplied by relatively great inputs of allochthonous (i.e., originating off the island) material transported by sea birds. Other islands with large enough marine-based allochthonous inputs may also support ants (and other terrestrial arthropods), although little information from such islands is available. A diversity of other types of arthropods has been reported from very small islands with relatively small amounts of allochthonous inputs in the Bahamas (MORRISON 2005).

A number of species of ants are known from mangrove and other regularly inundated habitats, displaying various strategies of surviving in such extreme conditions (NIELSEN 2011). Some species nest in the intertidal zone, blocking off their nest entrances during high tide (YENSEN & al. 1980, MAITLAND & MAITLAND 1994). On small islands in the Bahamas, *Brachymyrmex obscurior* nests in crevices and galleries in the marine limestone substrate. The substrate of some of the most low-lying islands is completely inundated during spring tides, and this species maintains persistent populations by surviving in air-filled chambers or blocked-off tunnels (MORRISON 2006). Ant colonies inhabiting low-lying islands in the Bahamas have survived complete inundations from hurricanes, presumably due to the "Swiss cheese" type structure of the substrate (MORRISON 2010) (Fig. 1B).

Thus ants may exist on very small islands (even those that are periodically submerged) due to behavioral adaptations or the appropriate type of substrate. The presence of terrestrial vegetation may in many cases be a good predictor of whether ants are present on very small islands. Nesting in the vegetation (e.g., COLE 1983a, SIMBERLOFF & WILSON 1969) is another mechanism of surviving periodic submergence of the island substrate.

Distributions

Just as the colonization process is strongly affected by available habitat type and interspecific interactions, the ultimate distribution of ants within and among islands also depends largely on these two factors. Basic island biogeographic theory (MACARTHUR & WILSON 1967) predicts that the number of species on an island is a function of area and isolation. The increase in species richness with area has been called "one of community ecology's few genuine laws" (SCHOENER 1976), and some of the classic studies of insular ants have revealed robust species-area relationships (e.g., WILSON 1961, MACARTHUR & WILSON 1967, WILSON 1988).

A number of studies, however, have revealed that some expression of habitat is an even better predictor of species richness than area per se. In a study of small islands

off the coast of Connecticut, GOLDSTEIN (1975) reported that the amount of plant cover above nest sites explained more of the variation in ant species number than did island area (total or vegetated). Working in an archipelago of islands in the North Sea, BOOMSMA & al. (1987) reported that an equilibrium model, containing parameters on area and distance, was "equally suitable" to a habitat diversity approach. In the equilibrium model, once area was taken into account, the effect of isolation explained only 3% of the remaining variation.

A study of ants on small islands in the Bahamas found that plant species richness was a better predictor of ant species number than island area (total or vegetated) (MORRISON 1998b). In a similar analysis of the correlates of ant species richness conducted on islands near Puerto Rico, the number of habitats was found to be a significant predictor, whereas island area was not (TORRES & SNELLING 1997). Considering the distribution records of ants in the Florida Keys, DEYRUP & al. (1988) remarked that there seemed to be "few, if any, effects of equilibrium island biogeography", and that most species occurred "wherever their preferred habitat is available", although he conducted no formal analyses.

These findings should not be interpreted as evidence that ants are somehow not subject to the species-area relationship in these archipelagoes. With the exception of the Puerto Rican study, area was a significant predictor of ant species richness, just not as strong as the other predictor variables specified above. Moreover, one of the mechanisms underlying the species-area relationship is that larger areas contain additional habitats (CONNOR & MCCOY 1979).

Distance was not a significant or important predictor in any of the studies above. Distances of the most remote islands (e.g., 1.6 km in the Connecticut study, and 2.4 km in the Bahamas study), however, were relatively small compared to the dispersal ability of alates. Moreover, the possibility of intervening islands acting as "stepping stones" would effectively decrease the distances involved even further.

Thus, while area and isolation may be important factors affecting distributions over larger spatial scales, over smaller scales their effects may not be as obvious. The positive association of area with habitat diversity may obfuscate determination of the more important driver of species richness. Isolation may only be important over relatively large distances, and differentially affect species depending upon their propensity to raft or disperse anthropogenically.

Competition

Interspecific competition is so prevalent in ant communities that HÖLDOBLER & WILSON (1990) dubbed it the "hallmark of ant ecology". Although a recent review (CERDÁ & al. 2013) concluded that interspecific competition may not be as important as previously thought, the evidence suggests that it is, in general, the predominant force structuring ant communities. Although the distributions of many species within and among islands may be dependent to varying degrees upon habitat, particularly for specialist species, interspecific competition also plays an important role. Differences in social organization among species lead to competitive hierarchies, resulting in "locally expected" versus "locally improbable" combinations of species (VEP-

SÄLÄINEN & PISARSKI 1982). In other words, some species pairs occur more frequently than expected by chance, and others less frequently (e.g., MORRISON 1996a). The complementary distribution patterns observed within many islands (described below) have largely been attributed to interspecific competition.

Mutually exclusive distributions within islands have been well documented for some of the more invasive and aggressive species. On Bermuda, for example, *Linepithema humile* and *Pheidole megacephala* have mutually exclusive distributions, which have shifted over time, as myrmecologists have closely watched to see if one species could completely exclude the other (HASKINS & HASKINS 1965, CROWELL 1968, LIEBERBURG & al. 1975, HASKINS & HASKINS 1988, WETTERER & WETTERER 2004). Despite shifts in distributions over time, these species have co-existed on Bermuda for more than 60 years.

In the Hawaiian Islands, *Linepithema humile*, *Anoplolepis gracilipes* (SMITH, 1857) (the yellow crazy ant), and *Pheidole megacephala* have mutually exclusive distributions, and laboratory experiments have demonstrated the existence of direct interspecific interactions (FLUKER & BEARDSLEY 1970). In the Society Islands of Polynesia, the three behaviorally dominant and numerically abundant ant species (*Solenopsis geminata* (FABRICIUS, 1804), *Pheidole oceanica* MAYR, 1866 and *Pheidole fervens* FR. SMITH, 1858) exhibited complementary distribution patterns within islands (MORRISON 1996a). Strong competition over territory or food was observed among all three pairs of species, both in the lab and in the field. *Solenopsis geminata* was found almost exclusively at disturbed sites, however, whereas *P. oceanica* was found at significantly more undisturbed sites, indicating the importance of habitat affinities (MORRISON 1996a).

Although some of the more aggressive, generalist species are able to exclude each other from portions of islands, they do not appear to be able to exclude each other from entire islands, with the exception of very small islands (e.g., as in COLE 1983a). The ant faunas inhabiting small islands around Puerto Rico, for example, were found to be significantly nested (i.e., species present at species-poor sites represented subsets of the species present at species-rich sites) (TORRES & SNELLING 1997). The nested pattern was attributed to an increase in the number of habitats with size of island. Remote Polynesian ant faunas are also highly nested (MORRISON 2008). The main reasons certain species are not present on particular Polynesian islands appear to be either a lack of opportunity for introduction or lack of appropriate habitat (MORRISON 2015).

Within islands, ant communities appear to be coherent associations of species that are influenced to a large extent by the identity of the dominant species (typically dominant species are both numerically abundant and behaviorally aggressive). In the Society Islands of Polynesia, each of three recognized dominant species was positively associated with its own subset of subordinate species (MORRISON 1996a). Ordination analyses of occurrence data revealed non-overlapping groups of sites that were based on the identity of the dominant species (MORRISON 2015), and a substantial number of species pairs co-occurred less frequently than predicted by chance. On the islets of Nukunonu Atoll at Tokelau, species also tended to co-occur less frequently than expected by chance (LESTER & al. 2009). Thus the

Tab. 1: Rates of annual relative turnover and immigration / extinction ratios of ants from published studies. Turnover rates are given as mean \pm SD; units are % year⁻¹. Imm/Ext = immigration / extinction ratio; number of immigrations per extinction. ¹ According to LEVINS & al. (1973); not enough information given to calculate actual rate. ² According to data for Cayo Ahogado in LEVINS & al. (1973). ³ According to data for Cayo Ahogado in HEATWOLE & LEVINS (1973). ⁴ Not recalculated because exact date ranges were not given, and much cryptoturnover is likely with an ~18 year interval.

Location	Date range	Number of islands	Turnover (annual)	Imm / Ext	Study
Puerto Rico	1964 - 1970	2	"high" ¹	0.86 ² 0.059 ³	LEVINS & al. (1973), HEATWOLE & LEVINS (1973)
Connecticut	1971 - 1972	6	33.0 \pm 36.5	0.75	GOLDSTEIN (1975)
Puerto Rico	(1964 - 1968) - (1981 - 1983)	21	Not reported ⁴	4.71	TORRES & SNELLING (1997)
Exumas, Bahamas	1990 - 1994	86	2.4 \pm 4.2	1.61	MORRISON (1998b)
Exumas, Bahamas	1994 - 1998	88	1.3 \pm 3.0	1.82	MORRISON (2002a)
Exumas, Bahamas	1998 - 2003	87	1.7 \pm 3.0	0.11	MORRISON (2010)
Exumas, Bahamas	2003 - 2007	85	1.5 \pm 3.9	0.29	MORRISON (2010)
Andros, Bahamas	1990 - 1999	20	1.4 \pm 1.8	1.65	MORRISON (2002a)
Andros, Bahamas	1999 - 2003	21	5.4 \pm 8.0	0.86	MORRISON (2010)
Andros, Bahamas	2003 - 2007	21	4.0 \pm 7.8	0.60	MORRISON (2010)
Abaco, Bahamas	2003 - 2007	34	8.1 \pm 10.2	0.40	MORRISON (2010)

identities of the subordinate species in a community are somewhat predictable based on the identity of the dominant. These patterns may exist because each dominant species competes more strongly with some subordinates than others. Alternatively, shared habitat affinities of the subordinate species may result in the observed species combinations. Unfortunately, the relative importance of habitat affinities is often not well known (e.g., KRUSHELNYCKY & al. 2005b).

If the identity of the dominant species does structure overall ant communities on islands, then experimental removal of the dominant should result in cascading effects throughout the community. This is exactly what was observed in an experiment conducted on small islands near Oahu, Hawaii. PLETOVICH & al. (2011) used chemical baits to experimentally remove the dominant ant species *Pheidole megacephala*. Pronounced fluctuations were observed in the ant community, including increases in the abundances of subordinate species, apparent invasions by three new species, and over time the establishment of a new dominant species – *Anoplolepis gracilipes*.

A recent review (MORRISON 2014) compared ant community structure and function on remote Polynesian islands, where most or all species have been introduced, to coevolved ant communities in continental areas and found them to be similar. The same is generally true for insular ant communities that contain predominantly native species. Interspecific competition appears to be the underlying mechanism that results in complementary distributions of dominant species within islands. Community and meta-community structure are characterized by dominance hierarchies and strong nestedness. Dominant species affect the diversity of other ants, and changing the identity of the dominants has repercussions throughout the ant community.

Turnover

Once ants colonize and become established on an island, how persistent are their populations? According to the equilibrium theory of island biogeography (MACARTHUR & WILSON 1967), in an equilibrium situation, species numbers

should remain relatively constant over time, although species compositions are expected to change. In other words, occasional immigrations and extinctions of species will result in turnover. Turnover may be calculated on a per-island basis (the classic MACARTHUR & WILSON [1967] island biogeographic approach), in which case the turnover rate indicates the percentage of species on an island that immigrate or go extinct. Turnover may also be calculated on a per-species basis (a metapopulation approach), in which case the turnover rate indicates the percentage of islands on which a particular species immigrates to or goes extinct (see MORRISON 1998b).

Early studies suggested that insular ants may be characterized by high rates of turnover, although these studies did not encompass very broad spatiotemporal dimensions (Tab. 1). LEVINS & al. (1973) reported a "high turnover" rate for ants on small islands of the Puerto Rican bank, although only two islands were thoroughly surveyed at multiple intervals. One of the islands was visited at 13 intervals over a six-year period, during which time 14 species of ants were recorded, "none of them permanent and seven were present only once" (HEATWOLE & LEVINS 1973).

GOLDSTEIN (1975) surveyed the ants on a set of six islands off the coast of Connecticut, in each of two years, reporting that, averaging over all islands, 33% of the ant species turned over (on a per-island basis). If turnover is calculated on a per species basis from Goldstein's data, the average annual relative turnover rate is 46%. Turnover rates obtained by Goldstein varied greatly, however, whether calculated on a per-island or a per-species basis (range: 0 - 100% for both).

TORRES & SNELLING (1997) revisited 21 of the small islands that had been surveyed by LEVINS & al. (1973) 18 years later. They reported that immigrations outnumbered extinctions by a factor of 4.7. They did not calculate turnover rates, but with an 18-year interval, it is likely that numerous undetected immigrations and extinctions occurred between surveys. This phenomenon has been

termed cryptoturnover (LYNCH & JOHNSON 1974); as the time interval between surveys increases, true turnover will be underestimated to a greater degree (DIAMOND & MAY 1977). TORRES & SNELLING (1997) stated that their surveys were probably more thorough than the surveys of LEVINS & al. (1973), but believed that the differences were too great to result from a sampling artifact. TORRES & SNELLING (1997) concluded that the ants of small Puerto Rican islands represented a "non-equilibrium case".

A study of turnover encompassing over 140 small islands in three archipelagoes of the Bahamas and spanning up to 17 years for some islands revealed relatively low turnover rates (Tab. 1). Surveys were conducted at 1- to 5-year intervals, with one 9-year interval. Some degree of cryptoturnover (i.e., unobserved immigrations and extinctions) was likely present (MORRISON 1998b), although the magnitude was probably relatively small due to the small number of immigrations and extinctions observed. Averaging over all species, on a per island basis, annual turnover rates were always < 9% per year, and in one archipelago (the Exuma Cays) < 3% per year (MORRISON 2010). Persistence clearly varied among species, however. Averaging over all islands, on a per species basis, annual turnover rates varied between 0 and 17% per year, with the more common species being characterized by lower rates of turnover (MORRISON 2002a). Immigration rates were 60 - 80% greater than extinction rates during the period from 1990 to 1998 or 1999 (depending on the archipelago). Extinction rates, however, exceeded emigration rates, by as much as a factor of nine, in the ensuing eight or nine years (MORRISON 2010).

Despite the observed turnover, the ant faunas of some islands were remarkably persistent. In the Exumas archipelago, after 17 years, 46% of the islands had experienced no turnover. In the Andros archipelago, 29% of the islands maintained the same species composition throughout the 17-year period (MORRISON 2010).

Combining the Puerto Rican and Bahamian results allows for inferences to longer-term regional trends in turnover: The species richnesses of ants on small islands near Puerto Rico increased from the mid-1960s to the early 1980s (immigrations exceeded extinctions by a factor of 4.7). Ant richness on small Bahamian islands increased during the 1990s, but to a lesser degree (immigrations exceeded extinctions by a factor of 1.6 - 1.8). Beginning in the late 1990s, however, ant richnesses on small Bahamian islands declined dramatically (extinctions exceeded immigrations by a factor of 1.7 - 9.2). While the immigration - extinction dynamics of ants on small Puerto Rican islands may be independent of those in the Bahamas, the islands in question are geologically similar and have many species in common. Thus the variation in immigration and extinction rates observed over this period in the separate studies may be representative of the larger region, and due in part to variability in hurricane activity (see MORRISON 2010).

The turnover study with the broadest spatiotemporal dimensions and regular survey intervals (i.e., the Bahamian study) found turnover in ants to be relatively low compared to other arthropods. In a review of turnover rates for different types of organisms, SCHOENER (1983) reported that annual turnover rates for arthropods, calculated on a per-island basis, ranged between 25 and 59%

per year. Ants may have lower turnover rates than other arthropods because most arthropods live only one year or less. Although worker ants may live only a few months, colonies may be very long-lived, depending upon the life span of the queen or number of queens present. Queens of some species have been observed to live for decades, and the most long-lived insects known are ants (HÖLLDOBLER & WILSON 1990).

Overall, most of the available information on turnover in ants is derived from the Bahamas / Caribbean region. The above conclusions may not be representative of other geographical areas. Additionally, the thoroughness of the surveys that have been done varied among studies, as did the time periods involved (and thus potential for missed turnover events).

Over much longer timescales (i.e., geologic time), insular ant faunas may experience relatively high degrees of turnover, even on larger islands. WILSON (1988), for example, examined ants preserved in amber from Hispaniola dating to the late Tertiary period and compared their identities to the present fauna of the island. He concluded that the Hispaniolan fauna has undergone "considerable turnover" since the late Tertiary, while the number of genera have remained similar.

Plague ants

A few ant species have the potential to become so abundant as to displace or reduce the populations of native ant species (or other arthropods). Five of the 100 "world's worst" invasive alien species (LOWE & al. 2000) are ants: *Anoplolepis gracilipes*, *Linepithema humile*, *Pheidole megacephala*, *Solenopsis invicta*, and *Wasmannia auropunctata* (ROGER, 1863) (the little fire ant). All are known to colonize islands.

Other invasive ants may also negatively impact ant or other arthropod populations, and colonize islands. *Solenopsis geminata* (the tropical fire ant), for example, is often considered to be in the same category as the five species above (HOLWAY & al. 2002). Additional ant species have recently demonstrated invasive characteristics and are considered as emerging invasives (e.g., *Nylanderia fulva* (MAYR, 1862), the tawny or Raspberry crazy ant) (WITTMAN 2014).

On some islands, introduced ants have demonstrated explosive population growth, often followed by a rapid decline. In historic accounts such occurrences have been referred to as "ant plagues", and the ants responsible as "plague ants" (WILSON 2005, WETTERER 2006, 2007). In the earlier recorded instances (e.g., Hispaniola in 1518 - 1519, the lesser Antilles in 1760 - 1770, Bermuda in the 17th and 19th century) the responsible species are not known with certainty, although the identities have been hypothesized (WILSON 2005, WETTERER 2006, 2007).

In modern times, similar phenomena have occurred, and although they are not usually referred to as ant "plagues", the underlying mechanisms are likely similar. Table 2 lists some of the best-documented examples. In many other cases invasive ants have reached relatively high abundances on islands at some point after being introduced, although perhaps not reaching "plague" status. Thus the phenomenon represents more of a continuum of increased densities that vary among species and across islands, although likely with shared underlying mechanisms.

Tab. 2: Population outbreaks of ants on islands. Date range refers to periods of unusually high abundances. ¹ Hypothesized, identity not known with certainty. ² Known to attend, or suspected of attending, honeydew-producing insects. ³ Identified as *Nylanderia pubens* (FOREL, 1893) in WETTERER (2007), but more likely to have been *Nylanderia fulva* according to GOTZEK & al. (2012).

Date	Island / Archipelago	Species	Reference
1518 - 1519	Hispaniola	<i>Solenopsis geminata</i> ^{1,2}	WILSON (2005)
1760 - 1770	Lesser Antilles	<i>Pheidole megacephala</i> ^{1,2}	WILSON (2005)
1600s, 1800s	Bermuda	<i>Nylanderia fulva</i> ^{1,3}	WETTERER (2006, 2007)
1850s	Madeira	<i>Pheidole megacephala</i> ²	WETTERER & al. (2006)
1890s	Madeira	<i>Linepithema humile</i> ²	WETTERER & al. (2006)
1970s	Mahé, Seychelles	<i>Anoplolepis gracilipes</i> ²	HAINES & HAINES (1978)
1989 -	Christmas Island	<i>Anoplolepis gracilipes</i> ²	O'DOWD & al. (2003)
1997 - 2002	Bird Island, Seychelles	<i>Anoplolepis gracilipes</i>	GERLACH (2004, 2005)
2000s	Tokelau	<i>Anoplolepis gracilipes</i>	LESTER & TAVITE (2004), GRUBER & al. (2013)
2002 -	St. Croix	<i>Nylanderia fulva</i> MAYR	WETTERER & KEULARTS (2008), WETTERER & al. (2014)

The mechanisms underlying this phenomenon are likely the same traits that allow invasive ant species to reach high abundances generally in many introduced areas. These include an omnivorous diet and unicoloniality (i.e., the lack of intraspecific aggression resulting in expansive colonies without distinct behavioral boundaries between physically separate nests) (HOLWAY & al. 2002). It has been hypothesized that the low genetic diversity of introduced populations facilitates the formation of such supercolonies (TSUTSUI & al. 2003). The use of previously untapped food resources and an escape from natural enemies may also play a role in some cases (PORTER & SAVIGNANO 1990).

In many of the documented cases (Tab. 2), the ant species in question were known or suspected to attend honeydew-producing insects, which could provide a large source of carbohydrates. In fact, the five worst invasive ant species all form extensive associations with honeydew-producing insects in their introduced ranges (HELMS 2013). Such associations may promote large populations of these ants because carbohydrates readily available in honeydew allow for increased colony growth. The ants provide protection for the honeydew-producing insects, and this may result in a type of positive feedback loop, in which larger populations of invasive ants promote larger populations of honeydew-producing insects, which then result in even greater abundances of invasive ants (HELMS 2013).

In some cases, the species in question had been present on the island for some time in much lower densities, raising the question of what triggered the population increase. For example, WETTERER & al. (2006) reported that *Linepithema humile* was present for at least 30 years on Madeira before it underwent a population explosion, and hypothesized that this event may have been triggered by the arrival of a "new species of mutualist scale insect or a new crop variety that made a better host for a mutualist scale insect already present". *Anoplolepis gracilipes* has been known from Tokelau since 1934, although a genetically distinct population apparently invaded more recently (ABBOTT & al. 2007). This new halotype reached much higher overall abundances (LESTER & TAVITE 2004). By 2011, however, this new halotype was more widespread but, surprisingly, less abundant (GRUBER & al. 2013).

Although islands provide some of the best examples of this phenomenon, similar population cycles have been described for invasive species in mainland areas. The red imported fire ant, *Solenopsis invicta*, for example, reached high densities in invaded areas of central Texas in the late 1980s (PORTER & SAVIGNANO 1990), replacing native fire ants by a ratio of 6 to 1 (PORTER & al. 1988). By the late 1990s, however, *S. invicta* densities had declined by an order of magnitude (MORRISON 2002b).

The mechanisms underlying the declines of such populations are not as well understood as those underlying their rise. Hypothesized mechanisms include depletion of the resource base and change in social organization. The disappearance of *Anoplolepis gracilipes* from some areas in the Seychelles, for example, was hypothesized to be due to a diminished source of protein (HAINES & HAINES 1978). GERLACH (2005) hypothesized that the dramatic reduction in population size of *A. gracilipes* on Bird Island (a reduction of over 99% in two years) was caused by intra-colonial social fragmentation (i.e., transition from a single super-colony to at least ten separate colonies).

Although most insular ants described as "pests" are introduced, exotic species may not always dominate natives. On Surprise Island, near New Caledonia, CERDÁ & al. (2012) found only eight ant species, seven of which were introduced and only one of which – *Pheidole oceanica* – could be considered native. *Pheidole oceanica* was the numerically dominant species in one of the four main habitat types and the overall top competitor in the island-wide dominance hierarchy. None of the "world's worst" invasives were present, however. Because of the remoteness of Surprise Island (230 km from the main island of New Caledonia), it is possible that *P. oceanica*, while considered native to the region, may be as recent an introduction as the other species.

Endemicity

Island endemics are usually found near the edge of a taxon's natural dispersal range; a colonizing propagule has to arrive, but many colonists will lead to too much gene flow for speciation to occur. Radiations, or diversifications into many new forms or species, are often observed on large,

high, remote islands near the edge of the dispersal range (PAULAY 1994). Thus, evaluation of endemism patterns in insular ants is instructive in relation to understanding natural dispersal distances and vacant niche space that may lead to ecological release, although prior land bridge connections must also be considered.

Overall, the percentage of endemic ant species varies greatly by islands and archipelagoes, ranging from 0 to > 96% worldwide. Across the Pacific, from west to east, 25% of the known species of Micronesia are potentially endemic (CLOUSE 2007). Rates of endemism are 18% in both Tonga (WETTERER 2002) and Samoa (WETTERER & VARGO 2003). In Fiji, however, ~ 70% of the species are endemic, with radiations of many genera (SARNAT & ECONOMO 2012). No certain endemics are known from remote Polynesia, although a few species are currently only known from French Polynesia and may represent true endemics (MORRISON 2014). In the Galapagos, of 51 known species, nine are "probably native or endemic" (HERRERA & al. 2014).

In the Western Atlantic, only a few species are possibly endemic to the Florida Keys (DEYRUP & al. 1988) or the Bahamas (MORRISON 1998a). In the Caribbean, WILSON (1988) concluded that 46% of the West Indian ant fauna was endemic, with 40% of the species known only from a single island, although acknowledging that West Indian ants had been poorly sampled. Cuba had the highest endemism, with 50% of its species known from nowhere else. A radiation is clearly apparent in *Leptothorax*, with 38 different species on Cuba. Focusing on the Lesser Antilles, JAFFE & LATTKE (1994) came to a different conclusion, however, finding no clear evidence of endemism. They concluded that endemism reported from the Lesser Antilles was "probably due to incomplete taxonomic study of the collections rather than true endemism".

In the Eastern Atlantic, endemism varies greatly across the islands of Macaronesia. Percentages of endemism for each island group are: the Azores (0), Madeira (3%), the Savage Islands (0), the Canary Islands (51%), and Cape Verde (7%) (ESPADALER 2015). Radiations have occurred in *Temnothorax* (12 out of 14 species are endemics) and *Monomorium* (six endemics with apterous queens). None of the Macaronesian islands were ever connected to a continent; the Canary Islands, with the highest percentage of endemism, are the nearest archipelago to a continent. The extremely remote South Atlantic islands of Ascension, St Helena, and Tristan da Cunha likely have no endemics (WETTERER & al. 2007).

In the Indian Ocean, endemism is > 96% on Madagascar (FISHER 2015), and of a similar level for the larger Malagasy region (Mauritius, Reunion Island, Seychelles, Comoros, Aldabra, Farquhar, Chagos, and Rodriguez Islands) (FISHER 1997). Although Madagascar was once connected to Africa and India, many of the genera present on Madagascar today are thought to have evolved more recently, indicating natural dispersal occurred (FISHER 1997).

Thus, endemism peaks at an intermediate distance across the Pacific, which may provide the clearest pattern given the vast area and relatively large numbers of islands / archipelagoes. In the Western Atlantic / Caribbean, the Greater Antilles appear to have the most endemics, and are the largest islands, although they have had land bridge connections. In the Eastern Atlantic, endemism decreases

with island isolation. Curiously, perhaps, endemism seems very high on islands across the Indian Ocean. It is possible that conditions for rafting have been more favorable in this region. The distances involved, however, are generally shorter than for the more remote Atlantic and Pacific Islands. Dispersal from Africa or India to the Indian Ocean islands involves shorter overall distances than that to Fiji in the Pacific, for example, although more stepping stone islands exist in the Pacific.

Threats

The threats faced by native and endemic insular ant species are generally the same as those that threaten biodiversity in general, and include habitat degradation / loss, invasive species, and climate change. In this case, however, the invasive species are often other ants. Furthermore, habitat degradation and climate change may aid the introduction and spread of invasive ants on islands. Most factors that drive extinction do not act in isolation, and synergistic processes may have the greatest effects (BROOK & al. 2008). Climate change, for example, may increase the invasion potential for some, but not all, exotic ants (BERTLESMEIER & al. 2016).

Exotic ants are common on many islands, with the percentage of exotic species ranging upwards to 100% on the most remote islands (e.g., Hawaiian Islands, Mid-Atlantic Ridge islands). MCGLYNN (1999) listed upwards of 150 species that are known to have been transported around the world anthropogenically, but considered only nine of these to be invasive. A few additional species have since exhibited invasive characteristics (WITTMAN 2014). These invasive species may reach high enough population densities to have widespread negative impacts on the recipient biota, and population outbreaks, as described above, are possible. Although native and endemic ant species may be among the most directly impacted (primarily through competition), other species may also be affected, and in some cases the effects can be far reaching. The *Anoplolepis gracilipes* invasion on Christmas Island, for example, resulted in direct and indirect effects measured across three trophic levels (O'DOWD & al. 2003).

The impacts of exotic ants on other taxa may be best observed on more remote islands that have few or no native ant species. The Hawaiian Islands are a classic case study in this respect, and the effects of exotic ants on the native fauna have been recently reviewed (MORRISON 2014). The Galapagos Islands represent another archipelago of interest in this respect, in that many endemic taxa are present, but few native ants. The Galapagos has been invaded by *Wasmannia auropunctata* (see CLARK & al. 1982), *Solenopsis geminata* (see WAUTERS & al. 2014), and most recently, *Pheidole megacephala* (see HERRERA & al. 2013). These invasive ants pose serious threats to endemic Galapagos species (LUBIN 1984, CAUSTON & al. 2006).

Disturbance of insular habitats may change ant species compositions and provide opportunities for exotic ants to invade. A diversity of studies on islands worldwide have provided evidence for effects of anthropogenic disturbance. For example, in a study of Seychelles ants, the composition of the fauna was found to be more constant in undisturbed habitats than in habitats that have been strongly influenced by humans (MÜHLENBERG & al. 1977). In an archipelago of islands off the coast of Java, islands with

settlements or boat docks contained significantly more tramp species than islands without (RIZALI & al. 2010), and the diversity of non-tramps decreased with habitat disturbance.

In a survey of coral cays on the southern end of the Great Barrier Reef, Australia, the distribution of *Pheidole megacephala* among islands was best explained by human activities. Frequent human visitation and, to a lesser extent, the presence of human disturbance, explained significant amounts of variation in the occurrence of *P. megacephala* (see BURWELL & al. 2012). Colonies of *P. megacephala* are usually founded by budding, thus long distance dispersal of *P. megacephala* queens over water is thought to be highly unlikely. Consequently this species is primarily spread by human activities; the greater the visitation by humans, the more potential opportunities to colonize. The severity of infestation by *P. megacephala* was the predictor variable that explained the most variation in species richness, abundance and assemblage composition of other ants (BURWELL & al. 2012).

In the Society Islands of French Polynesia, the invasive *Solenopsis geminata* was found almost exclusively at disturbed sites, whereas *Pheidole oceanica*, which is considered to be native to the region, exhibited a significant preference for undisturbed habitat (MORRISON 1996a). On the island of Okinawa (Ryukyu Islands, Japan), primary forests contained many endemic species but open lands were occupied predominantly by tramps (YAMAUCHI & OGATA 1995). In the Balearic Islands, exotics were primarily found at sites under anthropogenic influence (GÓMEZ & ESPADALER 2006). In the Florida Keys, populations of exotic ants have increased with increasing disturbance of native habitats (DEYRUP & al. 1988).

Thus, while some invasive ants represent threats to colonize almost any islands within a suitable climatic zone, anthropogenic disturbances may increase their abundances or be necessary for other exotic ant species to colonize. Once established, exotic ants may affect a diversity of native species, and overall impacts are likely to be greater on relatively remote islands with fewer native ants. The best protection against exotic ant invasions appears to be prevention of habitat disturbances and restoration of existing habitat.

Opportunities

Many islands have not been thoroughly sampled for ants. Many of the older collection records have been found to be incomplete when compared to more recent (and thorough) surveys (e.g., MORRISON 1996b). This may result partly from ants being collected as part of more generalized insect surveys. Ants are extremely diverse in their habits and life history, and comprehensive collections cannot be obtained through a single sampling method. Also, because many species show affinities to particular habitat types, searching only certain habitat types or regions of islands will produce incomplete species lists, which preclude robust inferences from many types of biogeographic analyses. Incomplete collections also result in much uncertainty regarding the status of putative endemics. Thus, comprehensive collections covering all the major habitat types of an island are still lacking (and needed) in many archipelagoes. Employing a diversity of sampling techniques will likely produce the most complete species lists,

although many species may be captured by each of multiple techniques, if employed over a large enough scale (GOTELLI & al. 2011). Hand sampling may be the most efficient method of collection for generating species lists (MORRISON 1996b, ELLISON & al. 2007, GOTELLI & al. 2011).

Little is known about prehistoric ant faunas. Some information exists from specimens preserved in amber (e.g., WILSON 1988), although such amber deposits are relatively rare. The use of sediment cores to identify fossil or sub-fossil ant remains (e.g., HORROCKS & al. 2013) could be applied more widely. Such investigations could provide insight into when, and how, ants arrived on various islands. This type of information may also provide inferences into historical rates of insular turnover, and whether the disappearances of certain species are correlated with the arrival of other, more aggressive species. Additional turnover studies of ants in ecological time would also be welcome, particularly in temperate archipelagoes, as almost all work to date has been done in tropical and subtropical systems.

Finally, many islands are at risk from invasive ants. Vigilance may prevent or at least slow the spread of invasive species to islands. Species distribution models may be useful tools in predicting which islands are susceptible to invasion by known invasive ant species. A species distribution model employed to assess the potential spread of *Solenopsis invicta*, for example, revealed that many islands had a suitable climate for this invader (MORRISON & al. 2004). Anthropogenic disturbances create opportunities for exotic ants to invade, and should be minimized and disturbed areas monitored for the arrival of invasive species.

Acknowledgments

Thanks to Nicholas Gotelli and Florian Steiner for inviting me to write this article, and to Ken Helms and an anonymous reviewer for their insightful comments. Much of my work on ants cited here was funded by the the National Geographic Society.

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