Nevis, Dominica, St. Lucia, St. Vincent and the Grenadines, and Grenada. The Institut de Physique du Globe de Paris (IPGP) monitors volcanic activity in Martinique and Guadeloupe, and the Montserrat Volcano Observatory (MVO) operates a monitoring network in Montserrat. In all of the islands of the Lesser Antilles, these agencies work closely with the civil authorities (typically known locally as national disaster preparedness organizations), which represent the respective local governments.

The mainstay of all volcanic monitoring in the Lesser Antilles is the seismograph network. The Seismic Research Centre of UWI maintains 40 seismic stations in the volcanic islands for which they are responsible; these are located near the 18 live volcanoes spread across these countries. The IPGP maintains eight stations in Guadeloupe and eight in Martinique to monitor La Soufrière and Montagne Pelée, respectively. The seismograph network on Montserrat comprises 11 stations, eight maintained by the MVO and three by the Seismic Research Centre. All these stations form part of the regional seismograph network, which includes a further 16 UWI stations on the surrounding non-volcanic islands (Trinidad, Tobago, Barbados, Antigua, Barbuda, St. Martin); nine stations in northeast Venezuela maintained by the Universidad de Oriente, Cumana, Venezuela; and the Fundacion Venezolana de Investigaciones Sismologicas and several French stations in eastern Guadeloupe and southern Martinique.

In addition to seismic monitoring, programs of volcanic gas surveillance and ground deformation monitoring are also maintained in the volcanic islands of the Lesser Antilles.

SEE ALSO THE FOLLOWING ARTICLES

Antilles, Biology / Earthquakes / Island Arcs / Kick 'em Jenny / Lava and Ash

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ANTS

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The rise of ants to ecological dominance has been called one of the great epics in evolution. The same features associated with their ecological success also make them destructive invaders. Islands provide an exceptional model for studying ant dispersal, extinction, and radiation. Ants often reach oceanic islands via accidental "sweepstake routes," leading to a unique cluster of ant species on different islands. The chance dispersal to islands results in high species turnover between islands and within islands over time. The composition of the ant fauna on any particular island can therefore reflect the age, size, and relative isolation of the island. At the same time, the limited land area and biodiversity of islands also increase their vulnerability to incursions by invasive ant species. Increased habitat fragmentation and the accelerated pace of ant species introductions put endemic island ecosystems at increased risk for invasional meltdown.

ISLAND ANTS

Ants are the glue that holds ecosystems together. These social insects dominate almost every terrestrial habitat throughout the world, in terms of both sheer numbers and ecological interactions. This dominance is particularly remarkable because ants constitute only about 1% of all described insect species. Understanding the processes driving the phenomenal success of ants is an active area of research. Current techniques involve the careful analysis of species distributions as well as the historical and geographical factors affecting dispersal and radiation.

Overall, the study of ant ecology is limited by the fact that up to half of the estimated 20,000 species of ants in the world have yet to be described. However, because islands are much smaller in area and harbor less diverse faunas than do continents, an exhaustive inventory of their ant species is feasible. Analysis of this more limited assemblage can then shed light on processes that affect ant composition and dispersal.

In general, the bigger an island, the more diverse its assemblage of ants. This is certainly true for the world's three largest tropical islands: New Guinea, Borneo, and Madagascar. It is no coincidence that these three land masses also feature more endemic ant genera and species than any other islands on Earth.

Chance Dispersal

Ants on oceanic islands often arrive via a so-called "sweepstakes route," a term that aptly describes the rarity of a successful island landing but also the huge potential payoff. Ant species that do manage to establish themselves on a large island can often then radiate to fill many empty ecological niches.

Island ants typically arrive via one of four common dispersal routes. In many ant species, the reproductive form is a winged queen. Newly inseminated queens taking wing to establish a new colony can be blown across the open ocean to distant shores. Alternatively, an entire ant colony can raft to an island inside a rotten log or tree washed out to sea during a storm. Some islands have received new fauna from the mainland or other islands via land bridges exposed during periods of low sea level. Finally, humans have been transporting ants inadvertently wherever they travel, including on island voyages.

An island's geography can be the determining factor in whether or not dispersing ants can land and establish a foothold. Islands in proximity to other sources of ants are easily reached by prevailing winds or ocean currents and will be colonized more often. The older an island, the more time ants will have had to arrive and establish themselves. By the same token, larger islands offer a bigger target to dispersers.

The extreme isolation and relative youth of the Polynesian islands east of Samoa, including Hawaii, have placed these islands among the few places on Earth that lack native ant species. On these islands, ants have had little opportunity to arrive on their own. In fact, Hawaii's native fauna includes no social insects of any kind. Yet today, 50 ant species are established in Hawaii, having been brought to the islands by humans over the past century. Among them are some of the world's most widespread and damaging invasive species (see below). These recent arrivals have been devastating the highly endemic arthropod fauna, which never evolved defenses against ants and lacks specialized ant predators.

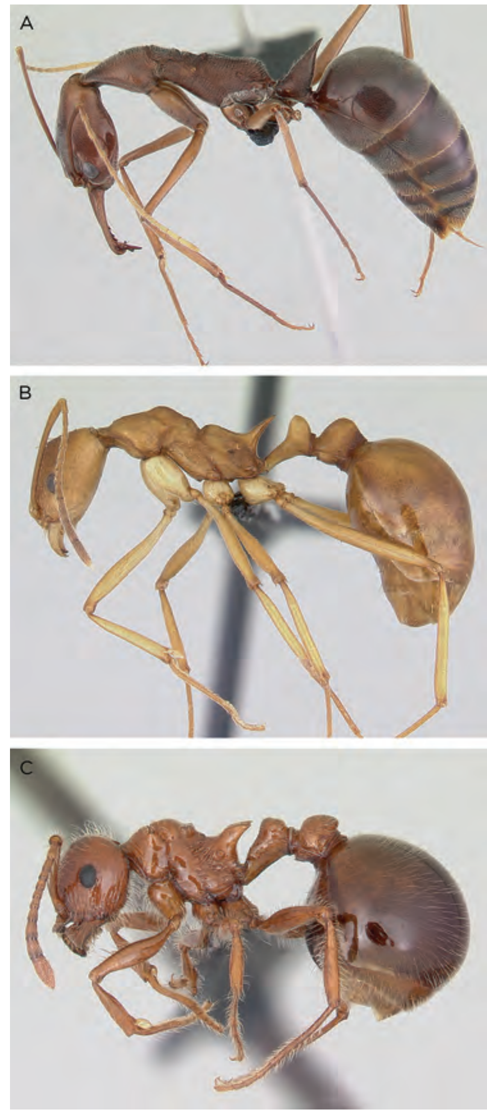

FIGURE 1 Endemic species on islands such as Mauritius and Madagascar are characterized by species with wingless reproductive queens. These colonies reproduce by fission, when the newly inseminated queen walks away from the parent nest with a few workers to start her new colony. (A) *Odontomachus coquereli;* (B) *Aphaenogaster* sp.; (C) *Pristomyrmex bispinosus.*

In contrast, as a very old island long isolated in the southwestern Indian Ocean, Madagascar today harbors an unusually diverse ant fauna. Of its more than 1000 ant species, over 95% are endemic to the island. Madagascar originally formed part of the ancient supercontinent of Gondwana but broke away from Africa approximately 120 million years ago. Its assemblage of native ant species likely evolved only after this breakup. Biologists now believe the extant ant lineages on Madagascar arrived via oceanic dispersal, primarily from Africa, but also from Asia. Although Madagascar is much closer to Africa, ocean and wind currents from the east may explain the connection to Southeast Asia.

On the other side of the world, the Antilles, which arc across the Caribbean in a chain of more than 7000 islands, provide another good example of sweepstakes colonization. Here, islands at increasing distance from the mainland show a corresponding drop in the number of ant genera. Moreover, the larger the size of an island, the greater the number of endemic species it contains; few to no endemics live on Caribbean islands under 1000 km^2. The exception is Trinidad, a large continental island just 11 km from the mainland of Venezuela. The ant fauna there is an extension of species found in South America and includes 17 genera widespread on the continent but absent from the rest of the archipelago.

The existing ant community, vegetation, and habitat of the island also help shape how hospitable the island will be once an ant makes landfall. Despite the African and Asian origins of Madagascar ants, the ant fauna is quite unique when compared to the faunas of neighboring continents. Several of the ant species that dominate ecosystems in Africa and Asia are absent from Madagascar. Among these are army ants (*Aenictus, Dorylus*) of the forest floor and weaver ants (*Oecophylla*) of the forest canopy. Weaver and army ants, especially of the genus *Dorylus* (driver ants), are major predators of other ants. Their presence influences the structure of ant populations as well as the diversity of ant communities. The absence of such keystone species is a common feature of many other islands (e.g., Cuba, Hispaniola, Fiji) where ants have radiated. These island systems thus constitute a natural experiment for evaluating how these dominant ants affect biological communities and how their absence allows the diversification of some unusual groups.

The characteristics of an individual species may also affect how likely it is to become a pioneer. For example, in most continental species, ants reproduce and disperse through a winged queen. After mating, she flies to a new location to establish a new colony. Winged queens are clearly an advantage for dispersing to an island. Interestingly, winged queens may become a drawback once a species has reached an island, because winged queens are more likely to be blown offshore and into the ocean. This may explain why many endemic ant species of the southwestern Indian Ocean islands have evolved wingless queens (Figs. 1, 2).

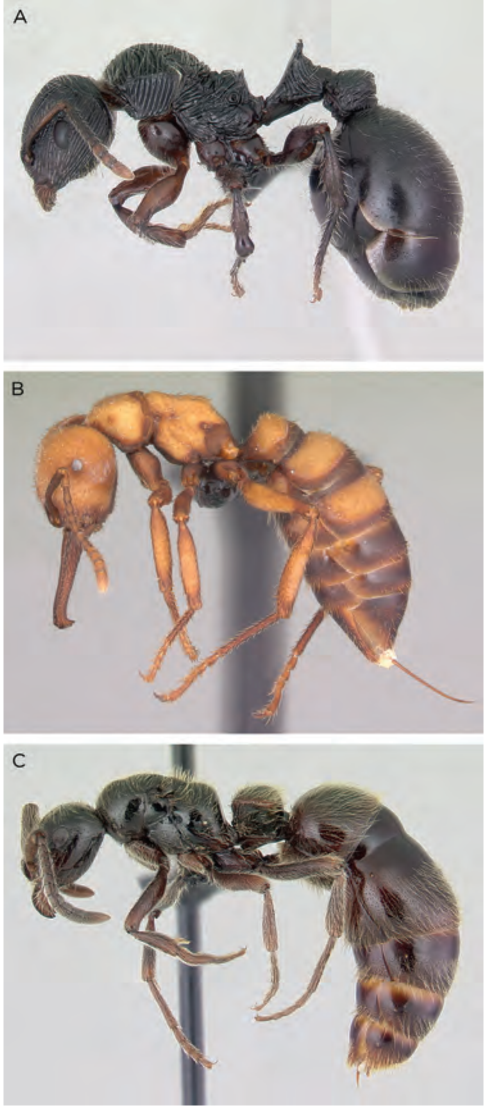

FIGURE 2 Endemic species with wingless reproductive queens. (A) *Terataner* sp.; (B) *Mystrium mysticum*; (C) *Cerapachys* sp.

Radiation

Once an ant species establishes on an island, it may undergo adaptive radiation to fill vacant niches. The number of endemic species tends to be greater on older and larger islands, where ants have had more time to evolve and there has been a greater complexity of local habitats to occupy.

In the Caribbean, for example, endemic ants make up a disproportionate share of the ant faunas of both Cuba and Hispaniola. Endemic radiations of a single genus, *Temnothorax,* now constitute more than 25% of the ant fauna in Cuba alone. The group includes species that have become specialists at nesting in habitats such as soil, limestone crevices, or epiphytic plants. The stunning morphological diversity of these species is comparable to the range usually seen in several genera. The absence of army or driver ants on these islands may have encouraged this evolutionary profusion. Likewise, on the island of Fiji, the diversification of the genus *Leptogenys* might have been possible because of the absence of army ants and the relatively low number of other endemic species from similar genera.

On Madagascar, many groups of ants have undergone an equally spectacular radiation. The five most species-rich ant genera on the island, *Camponotus, Hypoponera, Pheidole, Strumigenys,* and *Tetramorium,* all contain over 100 species. Each group exhibits remarkable morphological and niche diversity. Local diversity is also amazing. For example, on the Masoala Peninsula alone, 98 species from these five genera co-occur. As on Hispaniola, the absence of army and weaver ants likely allowed certain lineages to persist and others to radiate and flourish on the island. An example is the diversification of the tribe Cerapachyinae (*Cerapachys* and *Simopone*), which includes an unprecedented, morphologically diverse assemblage of more than 50 species on Madagascar. In fact, certain *Cerapachys* species show morphological similarity to the army ant genus *Aenictus* found in Africa. Whether the absence of army ants led to the diversification of *Cerapachys* in Madagascar, or simply permitted their persistence, remains unclear.

Another remarkable example of ant radiation in Madagascar is illustrated by the two closely related genera of the ant tribe Dacetini. Dacetine ants rely on the trap-like action of their mandibles to capture and subdue live food. Most of the differences between species reflect various methods of seizing prey. With 89 described species in Madagascar, the dacetines are the island's dominant predatory leaf-litter insect. Local diversity, too, is off the charts. For example, 25 species of dacetines have been recorded in an area roughly 1 km^2 on the Masoala Peninsula.

The ecological context in which ant colonists find themselves may also influence whether or not a lineage has the opportunity to radiate. For example, the relative diversity of *Strumigenys* and *Pyramica* in Africa is very different from their diversity on Madagascar. These specialized trap-jaw predators have oddly shaped mandibles and pear-shaped heads, and are often covered in bizarre hairs and strange outgrowths of whitish sponge-like tissue around their waist segments. *Strumigenys* are quite diverse in Madagascar, with 74 species on the island compared to 50 in Africa. *Pyramica,* in contrast, are much more diverse on the continent, with 81 species in Africa and only 15 in Madagascar. Why *Strumigenys* has undergone this diverse island radiation whereas *Pyramica* has not remains somewhat of a mystery. Maybe the first *Pyramica* arrived after *Strumigenys* had already radiated and filled potential niches.

Taxon Cycle

While studying ants in Melanesia, E. O. Wilson observed that species pass through sequential phases of expansion and contraction in distribution. He coined the term "taxon cycle" to describe the phenomenon. On islands, expanding taxa tend to be recent arrivals from the mainland that occupy lowland habitats along the coastlines of islands. By contrast, contracting taxa have reduced and fragmented ranges and tend to occupy interior and montane habitats. These differences suggest that existing species in the contraction phase of the cycle are pushed upslope and into new habitats by competition from more recent arrivals along the coast.

This pattern certainly holds in Madagascar, where endemic and possibly older ant groups are restricted to mountaintops. An example is the genus *Anochetus,* also known as little trap-jaw ants. Within this group, two species thought to have resided on the island for a long period of time are related to taxa in Asia and found only at interior higher elevation habitats. Two other species, related to taxa in Africa, are widespread across the entire lowlands. Together, these data support the idea that *Anochetus* species arriving on Madagascar first settled in marginal coastal habitats before shifting to anterior lowland forest and finally up to montane forest.

Turnover

The composition of ant species can vary considerably across an island's history. The primary forces that impact island biogeography—size, isolation, and habitats—also exert great influence on species turnover through time.

On Hispaniola, distance to source populations has had a dramatic effect on faunal assembly. Studies of Dominican amber indicate that 20 million years ago, during the Miocene, the island's ant fauna was closely related to the continental fauna of Mexico. Of the 38 genera and subgenera found in amber, only 22 persist today on Hispaniola, whereas 15 native genera have colonized the island since. Interestingly, the amber fauna includes army ants no longer present on the islands. This dramatic species turnover reflects the fact that during the Miocene, the Greater Antilles (including Cuba, Jamaica, Hispaniola, and Puerto Rico) were located nearer to the mainland. Lying further from the mainland today, Hispaniola has lost some of its continental taxa. Highly specialized species or those less able to establish themselves on new ground were the most likely to disappear.

Similar turnovers in ant species have probably swept across many islands as shifts in climate, volcanic eruptions, or other geological factors changed their habitats.

Further Research

Islands are natural laboratories for understanding the processes of faunal distribution and diversification. New methods combining species inventories, taxonomic research, and phylogenetic findings are enabling scientists to investigate these processes through the study of island ants. A comprehensive research effort is now in progress in the southwestern Indian Ocean (SWIO) islands. The coralline, volcanic, and Gondwanaland fragments of this region vary widely in age, size, degree of isolation, and habitat type, making them an ideal place to explore how each of these factors affects species diversity. Some of the questions researchers seek to answer include the geographic origins of the ant fauna and whether the estimated ages of endemic groups correlate with the ages of the islands themselves.

INVASIVE ANTS

Although colonization and species turnover are natural island processes, modern-day incursions of invasive ants are a major threat to natural ecosystems. Small size and limited biodiversity make islands inherently vulnerable to new species introductions. Today, habitat fragmentation caused by development, together with species introductions accelerated by global trade, has further increased this vulnerability.

Combating invasive species is of particular importance on smaller islands. In Mauritius, where only a few patches of original forest still remain, invasive ants may have driven the entire lowland ant fauna to extinction. The big-headed ant, *Pheidole megacephala,* has been implicated in the blanket decimation of Hawaii's lowland arthropods. Entomologists in the early twentieth century described in detail how the native beetle fauna was defenseless again the onslaught of the invading big-headed ant. On the smaller, granitic islands of the Seychelles, Christmas Island, and Zanzibar, invasive ants such as *P. megacephala* have already extirpated native ants and are now threatening nesting bird populations.

Larger islands such as Madagascar, where habitats are severely fragmented, can be just as vulnerable to invasion as their smaller counterparts. And although parks and reserves bolster the chances of survival of native species by protecting habitat, they cannot prevent aggressive exotic ants from driving native species locally extinct.

An island's ant fauna may include dozens of invasive species. However, a few bad actors can cause enough damage to destroy an island system. The usual culprits include the yellow crazy ant *Anoplolepis gracilipes,* the white-footed ant *Technomyrmex albipes,* the little fire ant *Wasmannia auropunctata,* the big-headed ant *Phiedole megacephala,* the tropical fire ant *Solenopsis geminata,* and the Argentine ant *Linepithema humile* (Figs. 3, 4). These ants are especially dangerous when they join forces with another insect like mealybugs, a type of sap-sucking plant parasite that is often invasive on islands. In exchange for protection, the mealybugs provide drops of sugary honeydew to the ants. Fueled by these bonus sources of sugar, invasive ant populations can easily multiply out of control on an island system and trigger an invasional meltdown. This scenario has played out on Christmas Island, where such interactions and the concomitant vast numbers of ants (*Anoplolepis gracilipes*) have led to decimation of the native land crab–dominated ecosystem.

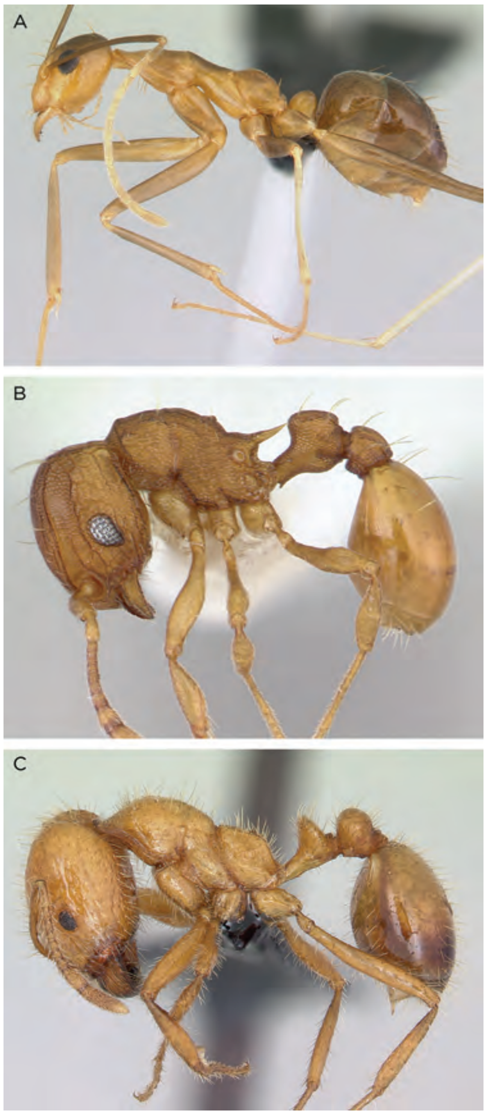

FIGURE 3 The most notorious invasive ants on islands. (A) yellow crazy ant, *Anoplolepis gracilipes;* (B) little fire ant, *Wasmannia auropunctata;* (C) tropical fire ant, *Solenopsis geminata.*

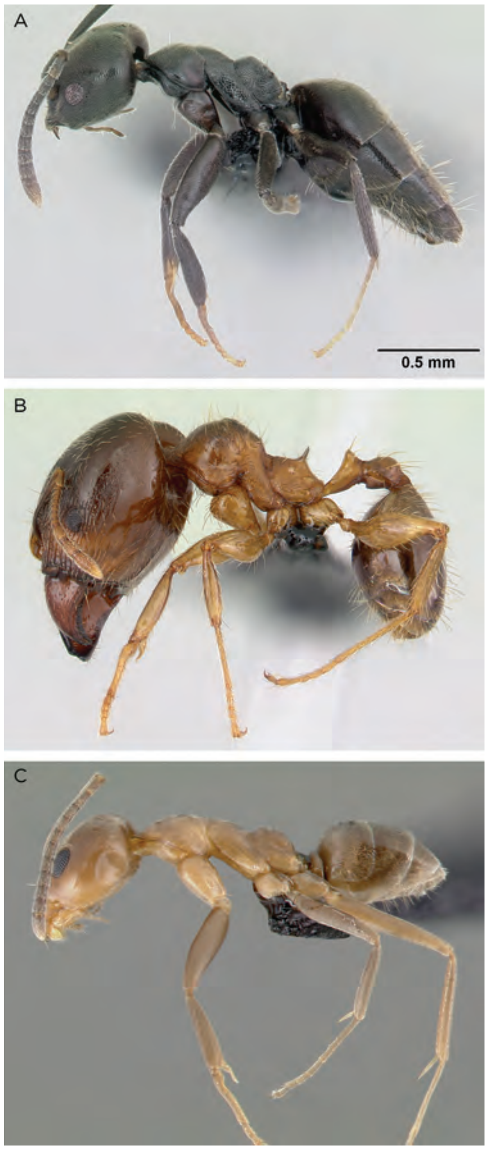

FIGURE 4 The invasive (A) white-footed ant, *Technomyrmex albipes;* (B) big-headed ant, *Phiedole megacephala;* and (C) Argentine ant, *Linepitherna humile.*

Once non-native, invasive ants become established in natural settings, they are difficult, if not impossible, to eradicate. Thus, when preserving an island's native ant species, an ounce of prevention is truly worth a pound of cure.

Impact of Invasives

Worldwide, invading ants have caused impacts that reverberate throughout local ecosystems. In some cases, invasive ants have reduced the abundance and diversity of native ants by more than 90%. Nor are the consequences of ant invasions limited to other ants. The intruders also cause decreases in the diversity of insect herbivores, mammals, lizards, birds, and even plants.

Invasional meltdowns of island ecosystems may be caused in part by the formation of ant supercolonies. The entire population of a newly arrived species may derive from the landing of a single queen or colony. Because all ants of this species are so closely related, they may lose aggression toward others of their own kind, a feature that normally limits colony densities. The resulting supercolonies can attain extremely high densities, can decimate local arthropod communities in the region, and can lead to an oversimplified invertebrate community that fails to provide essential ecosystem services such as nutrient cycling, plant seed dispersal, and a prey base for higher trophic levels.

On Christmas Island, for example, researchers have documented the devastating impact of a supercolony on a local ecosystem. After an accidental introduction, the invasive crazy ant (*Anoplolepis gracilipes*) formed massive supercolonies that tended scale insects. Through direct predation, the supercolonies practically eliminated the red ground crab in the infested area. Without the crab, the principal litter consumer and seed disperser, the habitat changed dramatically. The scale insects killed off many trees and impacted ground-nesting birds.

History

Ants have probably hitched rides with humans since the dawn of history. A recent dig at a Roman bath in Britain uncovered the bodies of 2000-year-old invasive ants. Over the past 500 years, there have been many accounts of ant plagues on different islands. For example, between the sixteenth and eighteenth centuries, several tropical West Indian islands were stricken with a series of ant plagues. Historical documents prove that environmental problems caused by invasive ants ensued just decades after Europeans came to the New World.

At least two different ant species were the culprits of the Caribbean ant plagues. *Solenopsis geminata,* the tropical fire ant, was brought to the islands in the early 1500s; *Pheidole megacephala,* an African ant, came in the late 1700s. The plagues caused widespread crop destruction and may have been accelerated by the arrival of sap-sucking insects. The same scenario has been replayed again and again on other islands.

One interesting feature of ant plagues is that they are relatively short lived. The invasive ants are soon either repressed or driven extinct by later invading ants. For example, *Pheidole megacephala* was the dominant ant species on the Atlantic islands of Bermuda for much of the twentieth century. In 1940, however, the Argentine ant (*Linepithema humile*) arrived in the area and quickly outcompeted the earlier champion. *Pheidole megacephala,* however, persists, and ever-shifting battlefronts now criss-cross most of the islands.

An important note is that islands have a long history of cycling through taxa. For example, historical records for the Indian Ocean island of Réunion indicate that the invasive ant *Anoplolepis gracilipes* was already abundant on the island in 1895. With the capacity to attain extremely high densities, this species can decimate resident vertebrates and invertebrate populations. In the ensuing 100 years, however, *A. gracilipes* has become rare. Research suggests that competition with dominant species such as *Pheidole megacephala* and *Solenopsis geminata* may have reduced its foraging efficiency and, therefore, its abundance. Although *A. gracilipes* is less competitive than other invasives, it thrives on a wide range of islands and must possess superior colonizing ability. The fortunes of this species have followed a similar trajectory in the Seychelles.

The modern twist to this phenomenon is the speed with which species turnover now occurs. As planes and ships have multiplied, and transport times have shrunk, pressures on native species have increased apace.

Further Research

The first step in understanding the level of threat posed by invasive ants is to inventory and map the extent of ant invasions. However, an assessment of invasives has yet to be initiated for many island systems. Once the invasives have been catalogued and mapped, a number of critical questions can be addressed. These include evaluating the risk of spread to other regions and habitats, predicting the effects on native fauna and flora, and assessing the impact of climate change on species interactions. The answers can help provide guidelines for conservation policies and control or eradication initiatives such that native island ants can persist.

SEE ALSO THE FOLLOWING ARTICLES

Dispersal / Insect Radiations / Land Crabs / Madagascar / Species–Area Relationship / Taxon Cycle

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ARCHAEOLOGY

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Archaeology is the systematic study of material remains. The diversity of island environments and biota presents fascinating opportunities for studying the evolution of Oceanic societies that developed from ~40,000 to ~800 years ago.

THE FASCINATION OF ISLANDS

The vast expanse of the Pacific Islands hosted the greatest maritime migration in human history. Venturing across uncharted waters, Pacific colonists over millennia developed remarkable voyaging skills; built massive double-hulled sail-rigged canoes up to 10 m long; and carried vital plants, animals, and indeed the mental templates of their community layouts or "transported landscapes," to every speck of land in this watery world known as Oceania. This journey began ~40,000 years ago in the western Pacific and culminated a millennium ago in the settlement of the isolated outposts of Hawai'i, New Zealand, and Easter Island—the final islands colonized before encountering the continental barrier of South America.

Thousands of islands, scattered over more than one-third of the Earth's surface, display a wide range of size and elevation fostering a diversity of geology, landforms, soils, vegetation, climate, marine biota, and degrees of isolation, providing an endless array of "natural experiments" for human colonists. Archaeologists are challenged to understand, for example, how and why founding human groups settling in the Hawai'ian Islands about AD 900 developed into one of the most highly stratified Oceanic societies, yet with more than 30,000 years of occupation, communities in the southwestern Pacific never attained this level of social complexity. How did humans adapt to