Primer

How ants shape biodiversity

Joseph Parker[1]
and Daniel J.C. Kronauer[2]

In between Earth's poles, ants exert impacts on other biota that are unmatched by most animal clades. Through their interactions with animals, plants, fungi and microbes, ants have cultivated — or succumbed to — relationships ranging from metabolic mutualisms to exploitation by social parasites. The diversity of these relationships implies that ants are keystone taxa in many habitats, directly or indirectly supporting a menagerie of other species. Yet, beyond these interactions is a less obvious but arguably as significant impact: through their collective ecological pressure, ants have imposed survivorship bias on the species that we observe inhabiting terrestrial environments. If life on land has passed through an ant-shaped selective filter, it is imperative we understand how these insects have sculpted ecological communities and are enmeshed within them. Here, we describe how ants have shaped biodiversity, and the often-devastating consequences of humanity's impact on these social insects.

Ant hegemony

What if we could transport ourselves to a tropical forest at the base of the Cretaceous, 145 million years ago? Surrounded by *Araucaria* trees, pterosaurs zoom overhead; the thud of a distant sauropod shakes the ground. A profoundly unfamiliar landscape, but to an entomologist, the most alien feature may be what is missing: the ants. These insects — so omnipresent in modern landscapes — have not yet fully branched from their wasp-like ancestors. For the other organisms in this ancient ecosystem, the ramifications of their absence are as significant as the presence of the reptilian megafauna. By some estimates, ants comprise a quarter of animal biomass in today's tropical forests, and their profusion permeates the temperate zone where they are similarly integral. Briefly put, ants are ecosystem engineers, shaping community structure in innumerable ways. Ants negatively impact other animal species on which they prey or which they outcompete; create enemy free-space around animal species that they farm; act as hosts to animal social parasites; control bulk energy flows through defoliation, decomposition and bioturbation (influencing plant life and soil properties); impact seed dispersal and pollination (both positively and negatively); and serve as a significant food source for still other animal species.

Hard evidence of ants first appears later in the Cretaceous: rare, stem-group ants in 99 million-year-old Burmese amber. Yet, it is only within the past 40–50 million years that ant abundance and diversity increase dramatically in fossil deposits, implying that — in evolutionary terms — their current hegemony is a new phenomenon (Figure 1A). More than fourteen thousand ant species are known, and their Cenozoic rise represents one of the most significant changes to the biosphere in Earth history. It has split modern ecosystems into two parts: a central, ant-dominated volume through which ants forage (the topsoil, leaf litter,

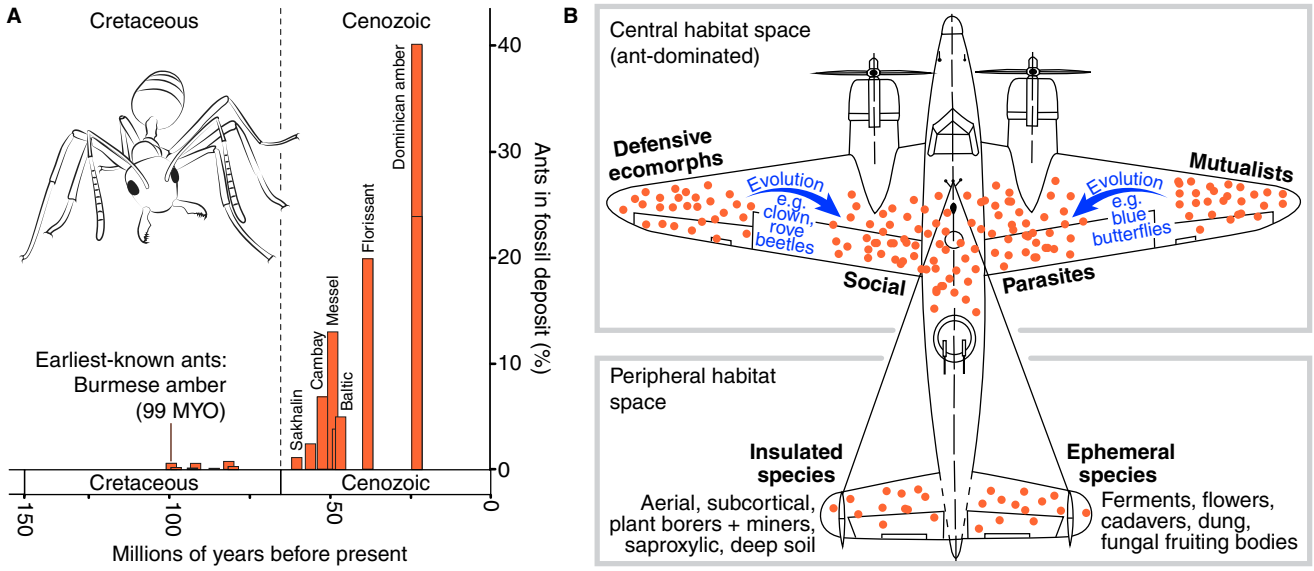

Figure 1. Rise of the ants.
(A) The percentage of insects that are ants in fossil deposits from the Cretaceous to the Recent (adapted from Parker and Grimaldi, 2014). (B) Survivorship bias in modern, ant-dominated terrestrial ecosystems. Analogous to areas of enemy damage inflicted on military aircraft that are still able to fly home, we only observe species that have passed through ant selection and fit into the limited number of available niches. Species that inhabited other niches — the parts of the plane without bullet holes — were selected against, and never made it into the Recent. (Image adapted from Martin Grandjean, McGeddon and Cameron Mol (CC BY-SA 4.0).)

much of the surface area of plants, extending into forest canopies) and peripheral pockets that are more insulated from ants (Figure 1B). The phenotypes and life histories of invertebrates in both sectors have been molded by ants: the former through the evolution of traits that enable coexistence, the latter via traits for ant avoidance. What we no longer see, but infer must have once existed, are myriad ant-incompatible lineages that never made it into the Recent — ghosts of ant selection past.

Competitive asymmetry

Assembling into colonies of individuals that serve the collective confers competitive supremacy over solitary invertebrates. In tropical forests — the most ant-rich environments on Earth — ant colonies are the primary resource sink for seeds, protein, and carbohydrates. This function is irreplaceable: when ants were experimentally removed from Malaysian forest plots, rates of resource removal dropped by >50%, meaning that the remaining invertebrates and vertebrates could not compensate. Defending the colony, policing local resources against competitors, and the evolution of generalist or predatory diets in many ant species have fostered innate aggression of ants towards other species. Solitary invertebrates are impotent by comparison, their populations exposed to chronic predation, as well as interference and exploitation competition. The upshot has been ecosystem-wide selection for defensive or evasive strategies that permit coexistence with ants, or investment in *R*-selected strategies (maximizing reproduction) that buffer against high ant predation. Arthropod mimics of aggressive ants have also proliferated.

On the flip side, the ecological dominance and aggressive nature of ants have opened new ecological opportunities for other organisms. First, significant ecosystem energy became concentrated inside ant colonies in the form of harvested resources and their converted products: ant brood, adult workers, and substantial processed refuse. The result has been the diversification of invertebrate symbionts that exploit these resources, as well as the emergence of guilds of myrmecophagous vertebrates. Second, colonies are energetically costly to run, and ants offer their protection in exchange for energy-rich carbohydrate sources either from herbivorous insects or from plants directly. Additionally, some ants have unlocked limiting nutrients by outsourcing metabolism to fungal symbionts and endosymbiotic bacteria. Below, we examine how the ecological niches ants create have shaped communities over ecological and evolutionary timescales, and what happens when ants are unleashed on naïve ecosystems.

Selection for the well defended

Ant colonies achieve cohesion via cuticular hydrocarbons (CHCs), non-volatile chemicals found on the body surface. These blends of long-chain alkanes and alkenes are colony-specific, enabling nestmates to recognize each other and mercilessly police the nest against intruders. The payoff for successful colony infiltration is huge, however, spawning widespread evolution of 'myrmecophiles' (ant-lovers) — symbiotic organisms, specialized for life as social parasites inside nests. It has been estimated that 10,000–100,000 such species exist, many capable of forging intimate relationships with their hosts. Adaptation to colony life can involve dramatic changes in behavior, chemical ecology, anatomy and life history, with extreme phenotypes seen in species that are integrated into the social fabric of the nest. Such lifestyles have evolved sporadically across the phylogeny: for example, caterpillars of some blue and metalmark butterflies (Lycaenidae and Riodinidae, respectively) are adopted into nests by workers; inside, they are socially accepted, being fed mouth-to-mouth by the ants or preying on brood (Figure 2A). Integration is achieved by deceptive strategies, including chemical mimicry of ant larval CHCs and production of vibrational signals mimicking those of the queen. Similarly, in crickets (Orthoptera), the genus *Myrmecophilus* includes species that engage in feeding and grooming interactions with ants — the latter to steal CHCs from workers for chemical disguise (Figure 2B).

A seemingly endless array of other invertebrate myrmecophiles have also been discovered, including silverfish, flies, wasps, mites, spiders, millipedes and even snails. Yet, it is in the beetles (Coleoptera) where myrmecophily explodes: at least thirty-three of 177 beetle families include myrmecophilous species, and it is informative to ask why this should be. The principal key innovation of beetles — physically protective elytra (wing cases) — may confer a relative advantage, but perhaps 90% of myrmecophile beetle lineages emerge within just two families: Histeridae (clown beetles) and Staphylinidae (rove beetles). Histeridae are predaceous and exceptionally robust, tank-like beetles. Numerous genera scattered across this family are myrmecophilous, including two speciose subfamilies, Chlamydopsinae and Haeteriinae. Haeteriines are notable for containing hundreds of species that have radiated in colonies of Neotropical army ants in the subfamily Dorylinae. These beetles are accepted into nests of these infamously hostile ants and emigrate through the forest in their hosts' nomadic colonies. Some haeteriines walk in lockstep with the ants; others hitch a ride by clinging onto workers, while still others, such as *Nymphister kronaueri*, bite onto the waists of workers and are carried along, resembling a second ant abdomen (gaster) (Figure 2C).

Myrmecophily reaches its fullest elaboration in the Staphylinidae — a clade of 64,000 species that comprise Metazoa's most species-rich family. Most staphylinids are predatory litter-dwellers, but dozens to hundreds of lineages have convergently evolved into myrmecophiles with radical symbiotic adaptations. Staphylinids usually possess short elytra, exposing a flexible abdomen that permits rapid movement through substrates and often bears chemical defense glands. One subfamily, Aleocharinae, contains the bulk of symbiotic lineages and here, species have repurposed the defense glands to produce compounds such as alarm pheromones that distract host ants. Others bear novel

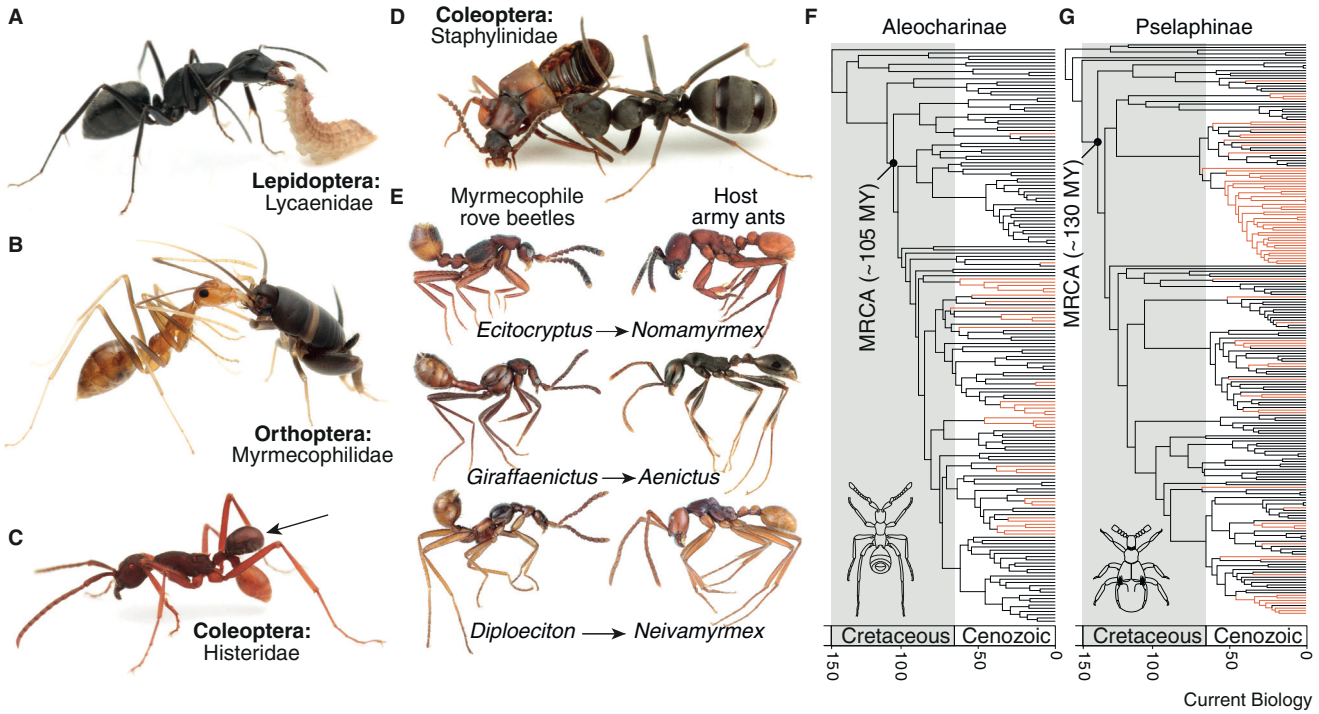

Figure 2. Myrmecophiles.
(A) A lycaenid butterfly caterpillar (*Niphanda fusca*) being fed via trophallaxis with a *Camponotus japonicus* worker ant. (Photo credit: Taku Shimada/Antroom.) (B) A *Myrmecophilus albicinctus* cricket engaging in trophallaxis with an *Anoplolepis gracilipes* worker ant. (Photo credit: Taku Shimada/Antroom.) (C) The haeteriine clown beetle *Nymphister kronaueri* clasping onto the waist of an *Eciton mexicanum* army ant. (Photo credit: Daniel Kronauer.) (D) A *Lomechusa sinuata* rove beetle exuding an abdominal secretion to a *Formica lemani* worker. (Photo credit: Taku Shimada/Antroom.) (E) Three examples of myrmecoid aleocharine rove beetle genera together with their respective host army ants. (Photo credit: M. Maruyama/J. Parker.) (F) Time-calibrated phylogenetic tree of aleocharine rove beetles with myrmecoid lineages in orange. All such lineages arose convergently during the Cenozoic as army ants diversified, and share a free-living common ancestor ~105 million years ago. (Adapted from Maruyama and Parker, 2017.) (G) Time-calibrated phylogenetic tree of pselaphine rove beetles with genera containing myrmecophiles colored orange. The transition from a free-living to a myrmecophilous lifestyle occurred convergently in numerous lineages during the Cenozoic. (J. Parker, unpublished data.)

'appeasement' glands that exude secretions to pacify ant aggression, promoting the beetle's acceptance into the colony (Figure 2D). As with the clown beetles, Aleocharinae includes many army ant-associated lineages, some of which exhibit remarkable ant-like 'myrmecoid' body plans. This morphology may confer mimicry of ant tactile cues, leading to exceptionally close social interactions between these beetles and their hosts. This symbiotic syndrome has evolved independently over a dozen times, with potentially every army ant genus hosting its own parasitic clade of myrmecoid aleocharines (Figure 2E).

Why has myrmecophily evolved with such frequency in these beetle clades? The answer provides a case study of survivorship bias in ant-dominated ecosystems. The anatomical ground plans of histerids and aleocharines are ultra-defensive — the former physically, the latter chemically — and both likely evolved *prior* to the ecological rise of ants. These beetle groups were thus outfitted for coexistence with ants. Both families were also predatory; hence they were poised to specialize on resource-rich niches inside nests as ant colonies began permeating the landscape (Figure 1B). How strongly predisposed these beetles were to evolving myrmecophily is underscored by the discovery of clown beetle–ant relationships close to the dawn of ant eusociality: a fossil haeteriine in Burmese amber was likely a myrmecophile of long-extinct stem-group ants. Similarly, the most recent common ancestor of myrmecoid aleocharines is inferred to have been a chemically defended, free-living beetle that existed ~105 million years ago; yet, multiple of its descendants evolved symbiosis in parallel as army ants diversified in the Cenozoic (Figure 2F). Other aleocharine lineages moved into colonies of other ant groups, while most lineages remained free-living, but capable of withstanding the rising ecological ant pressure due to effective chemical defense. An equivalent scenario occurred in another rove beetle subfamily, Pselaphinae. Here, the ancestral ground plan was physically protective, akin to Histeridae, and arose long before the Cenozoic period of ant dominance when these beetles convergently evolved myrmecophily (Figure 2G). Such patterns underscore how, when ants prevailed, taxa that serendipitously possessed defensive ecomorphologies were able to coexist and diversify. Today, Aleocharinae and Pselaphinae together number ~27,000 described species, attaining incredible diversity and abundance in ant-dense habitats such as tropical leaf litter.

Selection for the beneficial

Species with something to offer ants can capitalize on the ecological pressure that ants exert on other arthropods. In many cases, the offering is sugary liquid, and the return is protection. Such mutualistic associations are common among certain phytophagous insects, especially the sap-sucking Sternorrhyncha (aphids, scale insects, and white flies) and Auchenorrhyncha (cicadas, leafhoppers, and planthoppers), as well as some other hemipterans (Figure 3A). Plant sap is rich in carbohydrates, but lacks substantial quantities of other essential nutrients like nitrogen and amino acids. Sap-sucking insects therefore process large volumes of sap, and excrete a filtered version referred to as honeydew that ants consume. Caterpillars in the butterfly families Lycaenidae, Riodinidae, and Tortricidae also produce honeydew, in these cases from specialized exocrine glands. Relationships in which ants gain food are called trophobioses, and the nutrient providing symbiont is called the trophobiont. Of the 4,000 or so aphid species alone, ~25% are tended by ants, and the same is true for ~75% of the more than 6,000 species of Lycaenidae. Initially, ants are thought to have used aphids primarily as prey, and aphids have evolved defensive adaptations, such as waxy coverings and siphunculi, or cornicles, that secrete a gooey substance that not only impedes attack, but also triggers an escape response in aphids nearby. Beginning in the late Cretaceous, however, this relationship began to shift toward a more cooperative one; lineages that formed mutualistic associations with ants reduced their defensive structures and defensive behavior, and some developed morphological adaptations to retain honeydew droplets for the ants to harvest. In some Lycaenidae at least, the relationship has progressed still further and become exploitative; honeydew of one lycaenid, *Narathura japonica*, lowers dopamine levels in worker ant brains, reducing their movement and forcing them to stand guard around the caterpillar.

While most associations between ants and hemipteran trophobionts remain facultative, some have become highly specific and mutually dependent. Ants in the genus *Acropyga*, for example, live in subterranean nests in which they farm mealybugs that feed on plant roots. The ants are dependent on their symbionts for survival, and young queens carry mealybugs on their mating flight to seed the new colony. This intricate relationship is an ancient one, with Dominican amber inclusions of *Acropyga* queens carrying mealybugs dating to ~20 million years ago. In the Lycaenidae, ~30% of species are obligately associated with ants, and some are highly host specific on just single ant hosts. These specialized mutualisms appear to offer an evolutionary route to social parasitism (Figure 1B). More than 300 lycaenid species, scattered across the phylogeny, have made the remarkable switch from feeding on plants to feasting on ant brood, or soliciting trophallaxis from workers (Figure 2A).

While it is unclear whether beneficial associations with ants generally result in higher net speciation rates among trophobionts, mutualisms can be highly successful ecologically. Ants that tend arboreal trophobionts have conquered forest canopies, while species that farm aphids and mealybugs on plant roots need never leave their subterranean realm. Ant attendance often results in higher trophobiont fecundity and ultimately large colonies of trophobionts. The shielded environment provided by ants has allowed some aphids to become less dependent on particular host plants, and therefore to expand their geographic distribution. The concurrent increase in the ants' ecological footprint and their impact on biodiversity has been studied particularly in agricultural landscapes, where the presence of ants often promotes aphid abundance but suppresses other arthropods, including aphid predators and parasitoids. From an agricultural point of view, ants are therefore a double-edged sword — while they can be useful in managing certain crop pests, their favorable attitude towards sap-sucking insects can be problematic.

Many ants also consume sugary liquids provided by plants directly, often at extrafloral nectaries (Figure 3B). Extrafloral nectaries are common, and occur in species belonging to over 90 plant families. The relationships between ants and plants with extrafloral nectaries are often unspecific, and different ant species forage on the same plant. The presence of ants typically comes at a

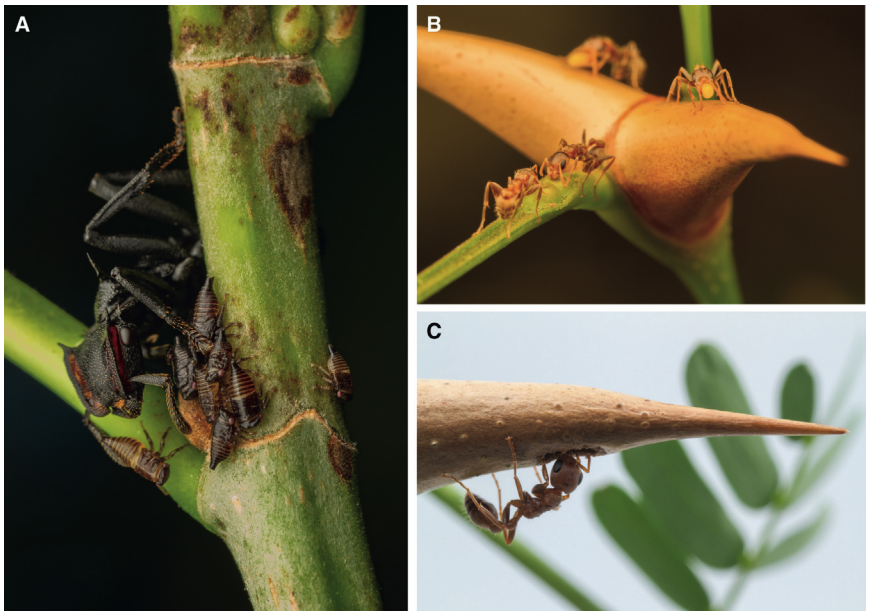

Figure 3. Mutualists.
(A) A *Cephalotes atratus* turtle ant tends membracid nymphs for honeydew. (B) Two *Pseudomyrmex* needle ants drink from extrafloral nectaries on their host plant, a bullhorn acacia in the genus *Vachellia*. The two ants in the background are carrying nutritious Beltian food bodies. (C) A *Pseudomyrmex* worker at the entrance to her nest inside a swollen acacia thorn. (Photo credits: Daniel Kronauer.)

net benefit to the plant, primarily via a reduction in herbivory. More specific mutualistic interactions exist between ants and myrmecophytes, plants that house ants in specialized structures, so-called domatia. Depending on the plant, the nest cavities can be located in hollow thorns, stems, or leaf pouches, for example (Figure 3C). In addition to extrafloral nectaries, many myrmecophytes also produce protein-rich food bodies (Figure 3B), and trophobionts often co-inhabit the domatia. The ants viciously defend their host plant against herbivores, invertebrates and vertebrates alike, and they prune back encroaching vegetation. In some cases, they also provide nutrients to the plant via the refuse accumulating inside the domatia.

Myrmecophytes mostly occur in the tropics, and are distributed across over 100 plant genera. The plants' association with their aggressive little tenants is so successful that ant plants are often ecologically dominant. In the American tropics, for example, *Cecropia* trees housing *Azteca* ants are pioneer species that dominate early succession forests, and *Macaranga* trees with their *Crematogaster* ants occupy a similar niche in tropical Asia. In the Amazon rainforest, large patches of *Duroia hirsuta* trees, known as devil's gardens, persist because the associate *Myrmelachista* ants poison all other plants with formic acid. These examples illustrate that ants exert significant selective pressure not only on invertebrates, but also on plant communities.

In the tropics, analysis of ^{15}N isotopic data from ants at different forest strata revealed that those on the forest floor are primarily carnivorous or omnivorous, whereas canopy ants rely excessively on carbohydrates from trophobionts or extrafloral nectaries. Evolutionarily speaking, the ants' craving for sugar has thus shifted the foraging stratum of many species from the soil and leaf litter up into the vegetation. This is especially true for the ant subfamilies Dolichoderinae, Ectatomminae, Formicinae, Myrmicinae, and Pseudomyrmecinae, which together account for about three quarters of ant biodiversity. This shift implied that, just like soil and leaf litter faunas, vegetation-dwelling organisms would be subject to ant-mediated selection and survivorship bias. One concrete example comes from British bracken ferns (*Pteridium*), which secrete nectar that is attractive to *Myrmica* and *Formica* ants. When moth caterpillars belonging to a non-adapted, naïve control species were experimentally introduced onto bracken, these ants rapidly attacked and killed them. This is in contrast to an entire assemblage of native insects that feed on bracken and can coexist with the ants — each species having evolved its own defensive behavior or avoidance strategy. Ant predation has thus shaped the structure of the bracken-feeding insect community.

Human–ant relationships

Given the centrality of ants in many ecosystems, understanding how human activity impacts ants and their organismal interactions is critical for safeguarding these environments. By translocating ant species from their native ranges into naïve habitats with few natural enemies or competitors, humans have unwittingly performed 'rise of the ants' experiments that have changed the face of ecosystems. At least 200 alien ants have become established in this way, but only a handful can be considered truly invasive, capable of penetrating native communities. These species are often superior competitors by virtue of their ability to form supercolonies with multiple queens and negligible inter-nest aggression. Supercolonies can massively elevate ant abundance, raising habitat-wide levels of predation and causing widespread defaunation of other taxa — both invertebrate and vertebrate (Figure 4A,B). Invasive supercolonies on oceanic islands, where biological communities have often evolved without native ants, provide case studies of how ant pressure can cause wholesale changes in ecosystem structure. On Christmas Island, invasive yellow crazy ants (*Anoplolepis gracilipes*) decimated local populations of native land crabs over a period of just two years. The ants overwhelm these charismatic crustaceans, which succumb to the ants' formic acid spray (Figure 4A). Loss of the crabs, which are keystone omnivores, permitted seedlings to grow, creating a dense understory and a decrease in litter decomposition. Secondary invasions by adventive giant African land snails occurred, where previously this species had been excluded by predation from crabs. Up in the canopy, the ants intensively farmed scale insects — themselves introduced species. Populations of these trophobionts exploded, promoting the growth of honeydew-dependent fungi. Canopy dieback and tree death ensued, disrupting frugivory and hence seed dispersal by birds.

It is tempting to think of such island communities as having approximated the ancient ecosystems that existed in the time before ants. On the Hawaiian archipelago, trophobiont hemipterans and extrafloral nectaries are scarce; radiations of endemic spiders and carabid beetles take the place of ants as the main predatory taxa. Few native invertebrates have evolved chemical defenses or other protective strategies. Many insects have evolved to be flightless. Little wonder that the introduction of almost 60 ant species over the past 200 years has decimated this vulnerable community.

Invasions in parts of the world with native ants can be no less devastating, however. In the US, numerous studies document the catastrophic impacts of two of the most infamous invasives: the Argentine ant (*Linepithema humile*) and the red imported fire ant (*Solenopsis invicta*). In their exotic ranges, these species suppress native ant populations by up to 90%. In California, *L. humile* excludes the majority of native ant species, which are scattered across the ant phylogeny and encompass highly diverse life histories (Figure 4C). The upshot is a scarce, taxonomically and ecologically impoverished native ant fauna (Figure 4D). Rich organismal communities that depended on these vanishing native ants suffer, with some species undergoing local coextinctions. One native Californian ant that has been strongly impacted by *L. humile* is the velvety tree ant (*Liometopum occidentale*). Huge colonies of this ant disappear from oak forests, along with the remarkable myrmecophile community their nests support (Figure 4E). Colonies of harvester ants

(*Pogonomyrmex* spp.) are also lost, with cascading effects on species such as myrmecophagous horned lizards (*Phrynosoma* spp.) that rely on these ants for the bulk of their diet. Direct impacts are felt well beyond the native ants: in addition to suppressing populations of many invertebrates, eggs and helpless offspring of ground-nesting birds and reptiles have proven vulnerable targets. In the southern US, *S. invicta* preys on eggs and chicks of Northern bobwhites (Figure 4B) and black-capped vireos; the ants also cause nest disruption of gopher tortoises and sea turtles and are linked to population declines of these and other vertebrates. As is the case for perhaps all invasive ants, successful invasions of *L. humile* and *S. invicta* are sustained by honeydew. The ants opportunistically forge mutualisms with novel hemipteran partners, which in turn reap the benefits of increased ant attendance, their populations expanding to the detriment of their food plants.

Human activity endangers native ants beyond introducing invasive ants, with detrimental consequences for ecosystems. Ants' high resource consumption, often combined with large foraging ranges, specialized diets and narrow thermal tolerances, render many species sensitive to habitat disturbance and climate change, with ripple effects on their organismal interactions. In African savannah, *Acacia drepanolobium* trees develop domatia that house colonies of *Crematogaster mimosae* ants. These ants defend the tree from herbivores such as elephants and giraffes, as well as wood-boring cerambycid beetles. The ants are further rewarded by nectar from the trees' extrafloral nectaries. Remarkably, a decade-long exclusion of herbivores led to reduced investment in both domatia and extrafloral nectaries by the trees. In turn, *C. mimosae* increased its attendance of damaging trophobiont scale insects while its own dominance subsided, making way for a different ant, *C. sjostedti*, which failed to police against cerambycid attack. Tree mortality rose. Hence, pressure from herbivory is critical to the persistence of the ant-*Acacia* mutualism, which is itself essential for defending the trees

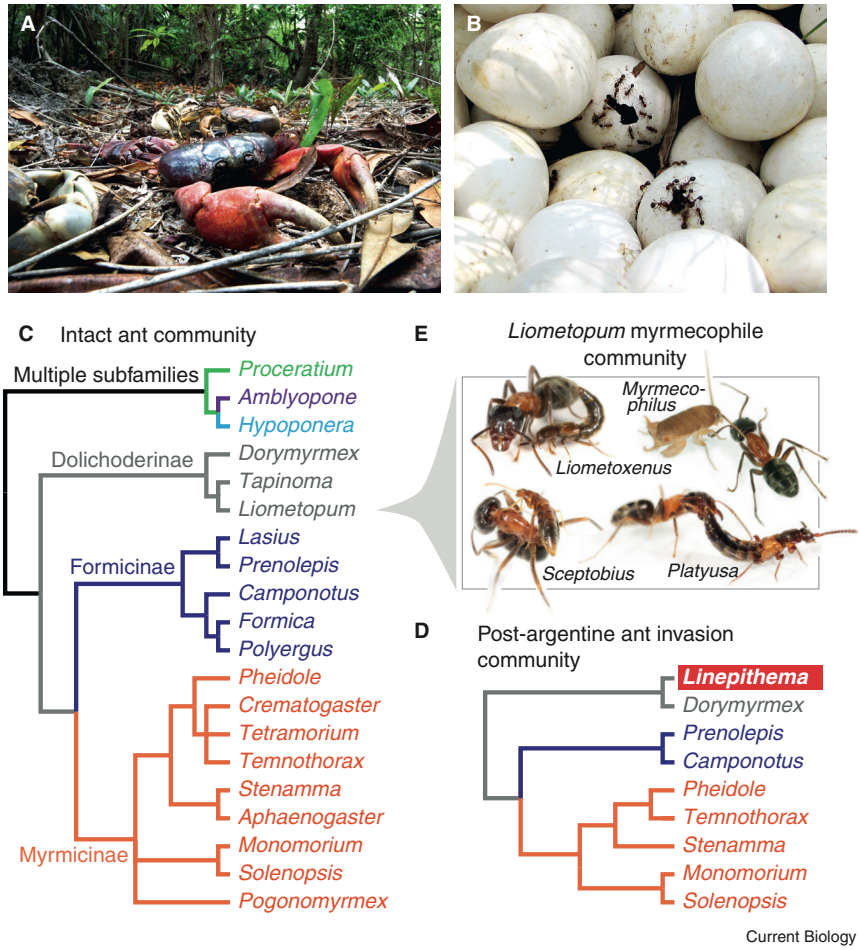

Figure 4. Invasive ants.
(A) Carcasses of the Christmas Island red crab (*Gecarcoidea natalis*) and blue crab (*Discoplax hirtipes*), their deaths caused by invasive yellow crazy ants. (Photo credit: Minden Pictures.) (B) *Solenopsis invicta* fire ants feeding on eggs of the Northern bobwhite (*Colinus virginianus*). (Photo credit: Michael Seymour/LSU.) (C) Phylogenetic tree of genera comprising the ecologically diverse, native ant fauna typically found in California. (Adapted from Lessard *et al.*, 2009.) Each ant species is connected to a community of other native organisms, including species that are dependent on the ants, such as the *Liometopum* myrmecophiles in (E). (D) Following invasion of the argentine ant, *Linepithema humile*, many ant lineages are pruned, leaving an impoverished ant fauna dominated by *L. humile*. Organismal communities associated with native ants undergo secondary losses. (E) Colonies of the velvety tree ant, *Liometopum occidentale*, number hundreds of thousands to millions of workers, and support a diverse community of myrmecophiles including the aleocharine rove beetles *Sceptobius*, *Platyusa* and *Liometoxenus*, and the ant cricket, *Myrmecophilus*. (Photo credit: David Miller.)

from herbivores and preventing the savannah ecosystem from converting to grassland.

These and other responses to disturbance underscore the community-wide connectedness of ants. In Neotropical rainforest, marked reductions in ant diversity occur in forest fragments relative to neighboring continuous forest, with one of the most significant losses being that of the army ant *Eciton burchellii*. Nomadic colonies of this ant number up to ~one million workers and have been estimated to require a home range of ~30 hectares over which to forage. Across its geographical range, *E. burchellii* supports an entourage of at least 300 other animal species including mites, beetles, springtails, millipedes, flies, wasps, butterflies, bristletails and birds, which make a living in and around its colonies. All the symbiotic species are expected to disappear if the ant experiences local extinction. Vanishing flocks of

ant-following birds is one noticeable consequence of *E. burchellii* vacating forest fragments. Some thirty species have evolved to track *E. burchellii* as it carries out swarm raids through the forest. The birds form populous, mixed-species flocks that are specialized to hunt arthropods flushed from the leaf litter. An analogous avian fauna has evolved in association with *Dorylus* army ants in Africa; in the Kenyan rainforest, fragmented landscapes similarly fail to sustain populations of ant-following birds.

Abundances of myrmecophyte plants also decrease markedly in forest fragments, making these mutualisms prone to stochastic, local extinctions. Compounding all of these impacts, regeneration of the forest is no guarantee of community restoration: secondary regrowth lacks the rich diversity of ants found in primary forest, implying that ants and their associated species may be amongst the most vulnerable organisms to habitat shrinkage and fragmentation. The few existing population genetic studies of myrmecophiles add further weight to this inference: populations of the lycaenid *Phengaris alcon* and myrmecophilous hoverflies of the genus *Microdon* are spatially disjunct, highly inbred, with extremely small estimated effective population sizes. Myrmecophiles with potentially poorer dispersal abilities, such as many beetles, may be still more precariously positioned. How will these species, along with the myriad others whose livelihoods are directly or indirectly affected by ants, fair as our planet continues to warm? The composition of ant communities is predicted to shift at a global scale, the gears already in motion, as thermally tolerant species and those from warmer habitats spread at the expense of more vulnerable species. If we are to nurture our own mutualistic relationship with these miniscule sculptors of the biosphere, there is an urgency to better understand the details of their relationships with other life forms.

FURTHER READING

Barden, P. (2016). Fossil ants (Hymenoptera: Formicidae): ancient diversity and the rise of modern lineages. Myrmecol. News *24*, 1–30.

Davidson, D.W., Cook, S.C., Snelling, R.R., and Chua, T.H. (2003). Explaining the abundance of ants in lowland tropical rainforest canopies. Science *300*, 969–972.

Depa, Ł., Kaszyca-Taszakowska, N., Taszakowski, A., and Kanturski, M. (2020). Ant-induced evolutionary patterns in aphids. Biol. Rev. *95*, 1574–1589.

Elizalde, L., Arbetman, M., Arnan, X., Eggleton, P., Leal, I.R., Lescano, M.N., Saez, A., Werenkraut, V., and Pirk, G.I. (2020). The ecosystem services provided by social insects: traits, management tools and knowledge gaps. Biol. Rev. *95*, 1418–1441.

Griffiths, H.M., Ashton, L.A., Walker, A.E., Hasan, F., Evans, T.A., Eggleton, P., and Parr, C.L. (2018). Ants are the major agents of resource removal from tropical rainforests. J. Anim. Ecol. *87*, 293–300.

Hölldobler, B., and Wilson, E.O. (1990). The Ants (Harvard University Press).

Ivens, A.B.F., von Beeren, C., Blüthgen, N., and Kronauer, D.J.C. (2016). Studying the complex communities of ants and their symbionts using ecological network analysis. Annu. Rev. Entomol. *61*, 353–371.

Kronauer, D.J. (2020). Army Ants (Harvard University Press).

Lach, L., Parr, C., and Abbott, K. (2010). Ant Ecology (Oxford University Press).

Leal, I.R., Filgueiras, B.K.C., Gomes, J.P., Iannuzzi, L., and Andersen, A.N. (2012). Effects of habitat fragmentation on ant richness and functional composition in Brazilian Atlantic forest. Biodivers. Conserv. *21*, 1687–1701.

Lessard, J.-P., Fordyce, J.A., Gotelli, N.J., and Sanders, N.J. (2009). Invasive ants alter the phylogenetic structure of ant communities. Ecology *90*, 2664–2669.

Maruyama, M., and Parker, J. (2017). Deep-time convergence in rove beetle symbionts of army ants. Curr. Biol. *27*, 920–926.

Menzel, F., and Feldmeyer, B. (2021). How does climate change affect social insects? Curr. Opin. Insect Sci. *46*, 10–15.

O'Dowd, D.J., Green, P.T., and Lake, P.S. (2003). Invasional 'meltdown' on an oceanic island. Ecol. Lett. *6*, 812–817.

Palmer, T.M., Stanton, M.L., Young, T.P., Goheen, J.R., Pringle, R.M., and Karban, R. (2008). Breakdown of an ant–plant mutualism follows the loss of large herbivores from an African savanna. Science *319*, 192–195.

Parker, J., and Grimaldi, D.A. (2014). Specialized myrmecophily at the ecological dawn of modern ants. Curr. Biol. *24*, 2428–2434.

Parker, J. (2016). Myrmecophily in beetles (Coleoptera): evolutionary patterns and biological mechanisms. Myrmecol. News *22*, 65–108.

Pierce, N.E., Braby, M.F., Heath, A., Lohman, D.J., Mathew, J., Rand, D.B., and Travassos, M.A. (2002). The ecology and evolution of ant association in the Lycaenidae (Lepidoptera). Annu. Rev. Entomol. *47*, 733–771.

Sprenger, P.P., and Menzel, F. (2020). Cuticular hydrocarbons in ants (Hymenoptera: Formicidae) and other insects: how and why they differ among individuals, colonies, and species. Myrmecol. News *30*, 1–26.

Stadler, B., and Dixon, A.F.G. (2008). Mutualism: Ants and Their Insect Partners (Cambridge University Press).

[1]Division of Biology and Biological Engineering, California Institute of Technology, 1200 East California Boulevard, Pasadena, CA 91125, USA. [2]Laboratory of Social Evolution and Behavior, The Rockefeller University, 1230 York Avenue, New York, NY 10065, USA.
E-mail: joep@caltech.edu (J.P.); dkronauer@rockefeller.edu (D.J.C.K.)

Primer

Invertebrate biodiversity and conservation

Nico Eisenhauer[1,2] and Jes Hines[1,2]

Biodiversity is changing at alarming rates as a result of human activities; yet biodiversity is the basis for ecosystem services upon which humans depend. Most of what we know about past, current, and projected biodiversity trends, as well as the ecosystem consequences of biodiversity change, is based on charismatic species, mostly plants and vertebrates. But 31 out of 32 animal phyla are invertebrates, representing roughly 75% of all described species on Earth. Evolution has not only produced an astonishing taxonomic diversity of invertebrates, but also an unparalleled morphological and functional diversity that has allowed invertebrates to populate marine, terrestrial, and freshwater realms. Invertebrates are responsible for many ecosystem services and disservices, which makes their appreciation and conservation a top priority of future research and policy.

In this Primer, we describe the diversity of invertebrate life on Earth and briefly summarize the evolutionary history of invertebrates. We highlight several ways that invertebrates influence the functioning of ecosystems and, consequently, human nutrition and health. Through their manifold effects on ecosystems, humans are changing invertebrate communities and, by extension, the balance between services and disservices provided by invertebrates. Given recent reports on dramatic changes in invertebrate diversity, as well as current major data gaps in the temporal and spatial distribution of invertebrates, we highlight the need for future research to identify and address drivers of invertebrate diversity. Such research focused on invertebrate biodiversity will contribute to the informed conservation actions and legislation that are required to maintain and improve ecosystem functioning.