

An Overview of the Species and Ecological Diversity of Ants

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Advanced article

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Since their appearance during the Cretaceous, ants have diversified to become today the most diverse group of social insects and one of the most influential groups of organisms on the planet. More than 12 500 species of ants are presently described, distributed within 21 subfamilies, with a large majority of the species belonging to only four subfamilies. Ants are present in almost all terrestrial ecosystems, their peak of diversity is found within the tropical regions, and ant richness tends to decline both with increasing latitude and altitude. In most ecosystems the ecological importance of ants, involved in numerous interactions with organisms ranging from bacteria, plants, fungi, arthropods to vertebrates, plays a critical role in the survival or control of many species. Finally, despite the tremendous efforts to understand ant biology over the past decades, the ecology of most species is still poorly understood and many new species are expected to be discovered.

Introduction

Within the diverse class of Insecta, ants (Formicidae) along with termites and certain wasp and bee species belong to a specific group, the social insects. Although most insect species have a solitary or sometimes gregarious life, social or eusocial insects live in a society of individuals organised around one or a few reproductive individuals that contribute to the growth of the colony. These individuals are surrounded by nonreproductive individuals whose main tasks principally include brood care, food collection, nest construction (when present) and the defence of the colony. **See also:** [Eusociality and Cooperation](#)

Ants are one of the most successful group of organisms on the planet (Hölldobler and Wilson, 1990). To date,

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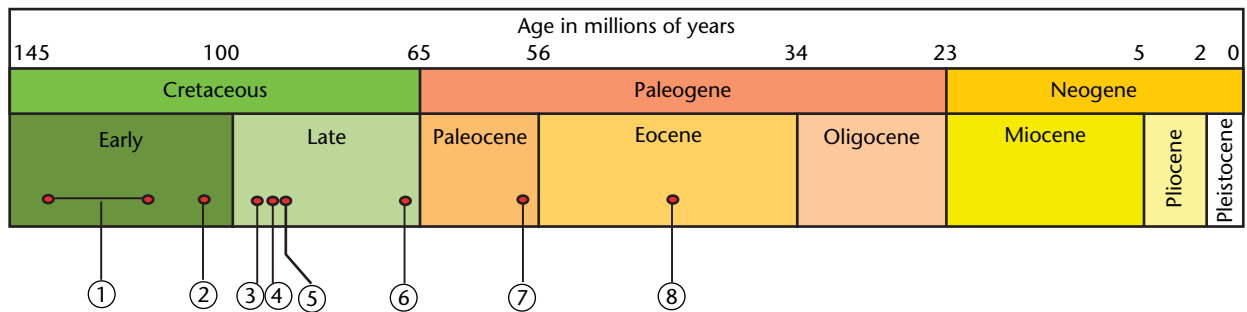
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approximately 12 500 species of ants, all eusocial, have been described and hundreds of new species are described each year. Ant biologists estimate that the Formicidae family could include no less than 20 000 species (Hölldobler and Wilson, 1990). In comparison, there are ‘only’ approximately 3000 termite species (Engel *et al.*, 2009), 2000 species of social bees (8% of the total bees) and 1100 social wasp species (James Carpenter, personal communication) known. **See also:** [Ecology and Social Organisation of Bees](#)

In the first part of this article the diversity of ants from geologic times to the present is reviewed, focusing on four taxonomically dominant groups and their spatial distribution. In the second part, the ecological diversity and importance of ants in ecosystems are discussed. The review presented here is not meant to be exhaustive but tries to present several relevant or recent discoveries in ant biology.

Origin and Diversification of Ants Through Time

Recent molecular phylogenetic studies estimate the origin of ants to the Cretaceous period, approximately 138–115 million years ago (Ma) (Brady *et al.*, 2006; Moreau *et al.*, 2006). Although the oldest fossils of ants recovered from the French and Burmese ambers were estimated to be approximately 100–112 million years (My) old (Figure 1; LaPolla *et al.*, 2013), the recent discovery of new fossil specimens suggest that by that time, the Formicidae family was already diverse and widespread. These findings support an older origin of ants consistent with the findings of molecular studies. However, if ants were present from the Cretaceous period they were probably not as common and successful as they are nowadays. The fossil records known from deposits before the Middle Eocene suggest that during this period ants were relatively rare within the insect communities (Grimaldi and Agosti, 2000; Dlussky and Rasnitsyn, 2002). The increase in the relative abundance of ants in insect communities observed during the Eocene coincides with the appearance of modern genera that now occupy most terrestrial ecosystems.



- ① Estimated age of ant origin
- ② Oldest known and fossil (Myanmar and French amber)
- ③ Oldest known Dolichoderinae fossil (93–95 mya)
- ④ Oldest known Formicinae fossil (92 mya)
- ⑤ Unconfirmed Myrmicinae and Ponerinae fossil (Botswana 91 mya)
- ⑥ Estimated origin of Dolichoderinae (67 mya)
- ⑦ Oldest known Myrmicinae and Ponerinae confirmed fossils (Sakhalin 56–59 mya)
- ⑧ Appearance of rich and abundant ant communities

Figure 1 Timeline of the origin of ants and its four main subfamilies.

Taxonomic Diversity

All ants belong to a monophyletic family, the Formicidae, which belongs to the order Hymenoptera that also encompasses bees, bumblebees, social wasps and several thousands of nonsocial wasps, many of them presenting a parasitoid lifestyle. The 12 500 described extant ant species are distributed within 307 genera and 21 subfamilies. However, most of the ants in these subfamilies are geographically limited to tropical or subtropical regions and are represented by only a few extant species. For instance, only one species is known from each of the subfamilies Aneuretinae, Martialinae or Paraponerinae (although a few extinct species might be known from the fossil record) and several subfamilies are represented by less than a hundred species (Table 1). Four main subfamilies, namely the Myrmicinae, Formicinae, Ponerinae and Dolichoderinae comprise the bulk of ant diversity, and include over 87% of all described ant species.

The Myrmicinae subfamily is by far the most diverse subfamily with over 6000 described species within 144 genera; almost half of all ant species belongs to this subfamily. Fossil specimens from Sakhalin (Far East Russia) estimates the Myrmicinae subfamily to be 56–59 My (Figure 1), although some 91 My unresolved fossils might belong to this subfamily (LaPolla *et al.*, 2013). Among the extant species, charismatic members of this subfamily include the New World fungus-growing ants of the Attine group, the seed harvesters *Pogonomyrmex* (of the New World) and *Messor* (of the Old World) genera, several invasive and now widespread species such as the fire ants (*Solenopsis invicta* and *Solenopsis geminata*), the little fire

ant (*Wasmannia auropunctata*), or the Pharaoh ant (*Monomorium pharaonis*) as well as the members of the hyperdiverse ant genus *Pheidole* (over 1100 species described). Although some species or genera have specialised diet (e.g. attines or *Strumigenys* preying on small leaf litter and arthropods), most exhibit a generalist diet. **See also:** [Invasion of Introduced Species](#)

The second most diverse subfamily, the Formicinae, comprises approximately 3000 species of ants. The oldest fossils known were retrieved from New Jersey (USA) with an estimated age of 92 My (Grimaldi and Agosti, 2000). Charismatic species include the diverse genus *Camponotus* (more than 1000 species described), the Holarctic distributed wood ants of the genus *Formica*, or the Old World tropical weaver ant of the genus *Oecophylla*. Several species of the genera *Anoplolepis*, *Brachymyrmex*, *Nylanderia* and *Paratrechina* are known to be important invasive species in numerous tropical or temperate ecosystems. Formicines species tend to be generalist predators or scavengers with many species having mutualistic associations with honeydew-producing Hemipteran insects.

The Ponerinae subfamily includes a little more than 1100 species and its members are considered to have a rather 'primitive' social organisation (Peeters, 1997). The vast majority of the ponerines species are found in the tropical or subtropical regions. Fossil evidence from Sakhalin (56–59 Ma) and France (50–55 Ma) indicate the Ponerinae to be approximately 50–59 My, with some unresolved specimen from 91 My that could represent the oldest member of this subfamily (LaPolla *et al.*, 2013). Charismatic members include species of the genera *Odontomachus* and *Anochetus*, also known as trap-jaw ants, as well as species of the genus

Table 1 The number of species and genera (in parenthesis), and global extant distribution for each of the 21 ant subfamily

Subfamily	Species richness	Distribution
Aenictinae	152 (1)	Old World tropics
Aenictogitoninae	7 (1)	African tropics
Agrocomymecinae	2 (1)	New World tropics
Amblyoponinae	116 (13)	Global (absent in central parts of the Nearctic and Palearctic regions at high latitudes)
Aneuretinae	1 (1)	Sri Lanka
Cerapachyinae	258 (7)	Global (absent in northern Palearctic and Nearctic regions)
Dolichoderinae	697 (28)	Global
Dorylinae	62 (1)	Old World tropics (absent in Malagasy and Australian regions)
Ecitoninae	153 (5)	New World (absent at latitudes $! > 45^\circ$)
Ectatomminae	269 (4)	New World and Australasian regions (in the Nearctic region, absent at latitudes $> 35^\circ$)
Formicinae	2915 (50)	Worldwide
Heteroponerinae	24 (3)	Neotropical and Australian regions + Western Asia
Leptanillinae	56 (7)	Old World
Leptanilloidinae	15 (3)	Neotropical region
Martialinae	1 (1)	Neotropical region
Myrmeciinae	93 (2)	Australia + New Zealand
Myrmicinae	6162 (144)	Global
Paraponerinae	1 (1)	Neotropical region
Ponerinae	1102 (28)	Global
Proceratiinae	130 (3)	Global
Pseudomyrmecinae	227 (3)	Global (absent at latitudes $> 40^\circ$)

Pachycondyla known for their painful sting. In general, Ponerinae species are predators, more or less specialised on specific prey. For instance, ants of the neotropical genus *Thaumatomyrmex* are specialist predators on the Polyxenida millipedes (Figure 2a; Brandão, 1991).

Finally, the Dolichoderinae subfamily represents the fourth most diverse subfamily of ants with approximately 700 species described. Although molecular phylogenetic estimates the origin of this subfamily at approximately 60–67 Ma (Ward *et al.*, 2010), fossil evidence from Africa suggests an older origin of at least 95 Ma (Perrichot, personal communication). Many Dolichoderinae species have an arboreal lifestyle (*Dolichoderus*, *Tapinoma* or *Technomyrmex*), sometimes forming strong mutualistic associations with plants such as the members of the New World ant genus *Azteca* associated with trees of the genus *Cordia*. Other charismatic members of this subfamily include the widely human-dispersed invasive Argentine ant, *Linepithema humile*, or the Australian ‘meat ant’ of the genus *Iridomyrmex* that often represent the ecologically dominant species. In several amber deposits of the Eocene, Dolichoderinae was the most abundant and commonly encountered subfamily of the ant community, with the extinct genus *Ctenobethylus* being especially abundant (Perkovsky, 2009; Dlussky and Rasnitsyn, 2009). This contrasts with the patterns observed in modern ant communities where this subfamily is not especially abundant, with the notable exception of certain communities encountered in Australian ecosystems. **See also:** [Mutualistic Symbioses](#)

Biogeography and Diversity Patterns of Ants

From the driest deserts to the limits of the cold tree line of the Russian and Canadian taiga ants have colonised most ecosystems on the planet. However, their species richness and abundance are not uniform across these ecosystems, and there are strong disparities depending on the climate, elevation and the past history of the regions considered. Ants, like many other groups of plants or animals, have a strong latitudinal gradient in their diversity, with the highest diversity occurring within the tropical regions close to the equator and declining with increasing latitude. At the generic level, and most likely at the species level too, the highest diversity is encountered in the Australasian and Neotropical regions (Figure 3), where several countries or provinces are known to harbour more than 80 genera, with the highest recorded in Borneo (98 genera), Queensland (96) and Colombia (92) (Table 2). Within the tropical regions of Africa, ant species richness appears to be comparatively lower than in regions of similar latitude in the Neotropics or Australasia (Figure 3; Guénard *et al.*, 2012). However, it is important to note that, as for other groups of insects, our knowledge on ant diversity is still incomplete and poorly synthesised. Future work on biogeography, especially those at the species level, may corroborate or invalidate these regional differences.

Similar to latitude, ant species richness declines with altitude. Although most studies have observed a continuous decline in species richness, with the maximum species



Figure 2 (a) *Thaumatomyrmex* species with specialised pitch-forked mandibles allowing them to manipulate their hairy preys, the polyxenid millipedes, while ‘shaving’ them. (b) Worker of the fungus-growing ant genus *Apterostigma* carrying a piece of mycelium within the nest. (c) Workers of a Neotropical species of *Pheidole* bringing back a prey item (here a Coleoptera) to their nest. Photographs by Benoit Guénard.

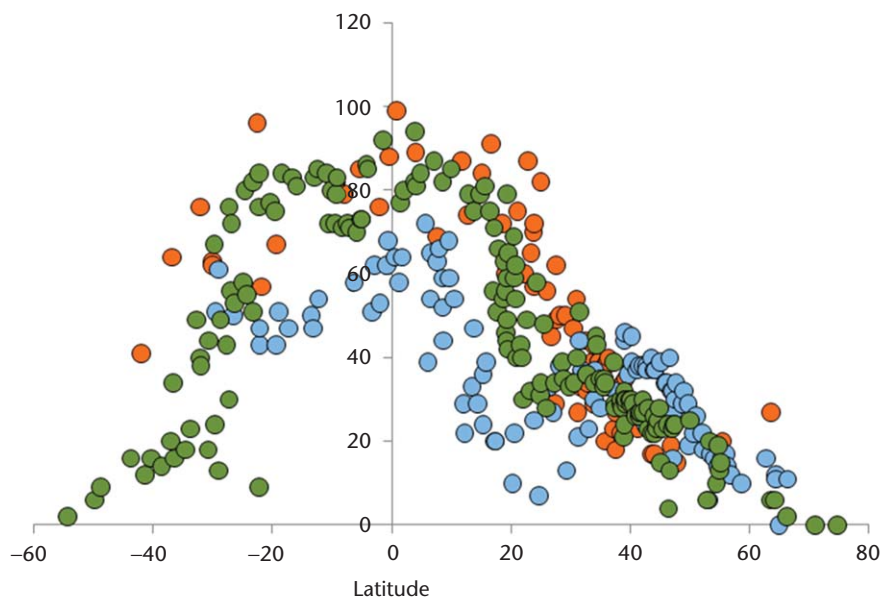


Figure 3 Expected generic diversity as a function of latitude for political regions (modified after data in Guénard *et al.* (2012)) for the New World (green circles) and the Old World, with a separation between the West Palearctic and the Ethiopian regions (blue circles) and the East Palearctic and Australasian regions (orange circles).

richness found in lowland habitats, others have detected maximum richness at midelevation habitats (Sanders, 2002). In both cases, species richness found for higher elevations (above 1500 m) tends to decrease sharply with

increasing altitude. Within tropical latitudes, several studies have estimated the upper limit of ant distribution to be approximately 2500 m (Wilson, 1958; Bruhl *et al.*, 1998; van der Hammen and Ward, 2005; Malsch *et al.*, 2008).

Table 2 Hyperdiverse regions at the generic level where 80 genera and more are known to occur. When known from recent checklists, minimum number of known species is presented in parenthesis

Region's name	Generic richness and species richness (in parenthesis when available)
Borneo (Island)	98 (> 1000)
Queensland (Australia)	96 (> 1300)
Colombia	92 (> 700)
Vietnam	91
Malaysia (Peninsula)	89
India	88 (> 700)
Philippines	87 (> 470)
Ecuador	87
Venezuela	86
New Guinea (Island)	85 (> 800)
Thailand	84 (> 250)
Costa Rica	84 (> 860)
Yunnan (China)	83 (> 410)
Para (Brazil)	83
Sumatra (Island)	82
Bahia (Brazil)	82
Amazonas (Brazil)	81
Sao Paulo (Brazil)	81
Guatemala	80 (> 420)
Paraguay	80 (> 540)

However, it is important to note that several ant species have been collected at altitudes greater than 2500 m and even up to 4800 m. Such observations compiled by Weber (1943) indicate that ants are present at very high altitudes (above 3000 m) and numerous recent studies confirmed that this is a generalised phenomenon found across all continents. Species collected at these altitudes belong to a narrower set of genera with many of them known to colonise ecosystems found at higher latitudes. For instance, for the Old World and more particularly in the Australasian region, species of the genera *Myrmica*, *Lasius*, *Formica*, *Camponotus*, *Aphaenogaster*, *Cataglyphis*, *Temnothorax*, *Perissomyrmex* or *Pheidole* have been regularly encountered at altitudes above 2500 m. Similarly, at the community level, species found at an higher elevation tend to represent a phylogenetically constrained subset of ants that can tolerate more extreme environmental conditions (Machac *et al.*, 2011). The importance of the factors that limit or enhance ant diversity within a given altitude or latitude are still unclear and controversial and, as a consequence, a full review of them is beyond the scope of this article. However, let us note that among the most common factors regularly associated with ant diversity feature net primary productivity, temperature, precipitation, plant diversity, area, etc.

A comparison of ant diversity between multiple large areas (e.g. continents) remains challenging because species richness within specific regions is still unresolved. Ants, like

many other groups of insects, display extremely diverse morphologies and are not trivial to identify accurately. Furthermore, an incomplete taxonomic knowledge of ants in many parts of the world combined with unequal sampling efforts has resulted in important disparities in the present knowledge. One approach has been to monitor ant richness at the generic level rather than the species level in order to circumvent some of these problems (Guénard *et al.*, 2012). Those results have shown that despite the fact that several regions are largely undersampled, Africa in comparison with similar latitudinal regions of Asia or of the New World, exhibited a general trend of lower generic richness (Figure 3). In contrast, South East Asia and especially Borneo is hosting both the highest generic ant richness and endemism (Guénard *et al.*, 2012). Finally, similar to other groups of organisms, ants tend to present a hemispheric asymmetry at the community level, with communities found in the southern hemisphere generally being more diverse than their latitudinal equivalent of the northern hemisphere (Dunn *et al.*, 2009).

Within tropical communities, ants have colonised all habitat types ranging from the soil to the canopy of trees. Species composition of arboreal communities is very distinctive from that of ground or soil dwelling ones (Longino and Nadkarni, 1990). This important turnover in community composition favours the emergence of rich and diverse assemblages that certainly contributes to the high richness observed in tropical regions. In contrast, ant species nesting within the arboreal strata are rare if not absent in temperate regions ecosystems, especially for latitudes greater than 40°.

Ecological Diversity of Ants

If Formicidae are impressive by their ubiquity and abundance, their success lies in the diversity of ecological niches and associations that they have developed with other organisms and their influence on other groups of plants and animals. The following section details the importance of ants either as predators, prey or ecosystem engineers.

Ants as herbivores

Without a doubt, the most notorious group of herbivorous ants is found within the attine ant species, which include approximately 230 species within 15 genera. Also known as fungus-growing ants or leaf cutting ants, species of the genera *Atta* and *Acromyrmex* collect fresh leaf or grass material from the surrounding vegetation (Figure 4a) to cultivate a mutualistic fungi (order Agaricales) within the chambers of their nests (Mehdiabadi and Schultz, 2010). The fungus serves as food for the larvae and workers complement their own diet with sap or plant secretion. The lower attines of the genera *Apterostigma*, *Cyphomyrmex*, *Myrmicocrypta* or *Mycetophylax* (note that more genera constitute the Attini tribe) also grow a fungus but use insect frasses or dead insect bodies as substrate for their fungus

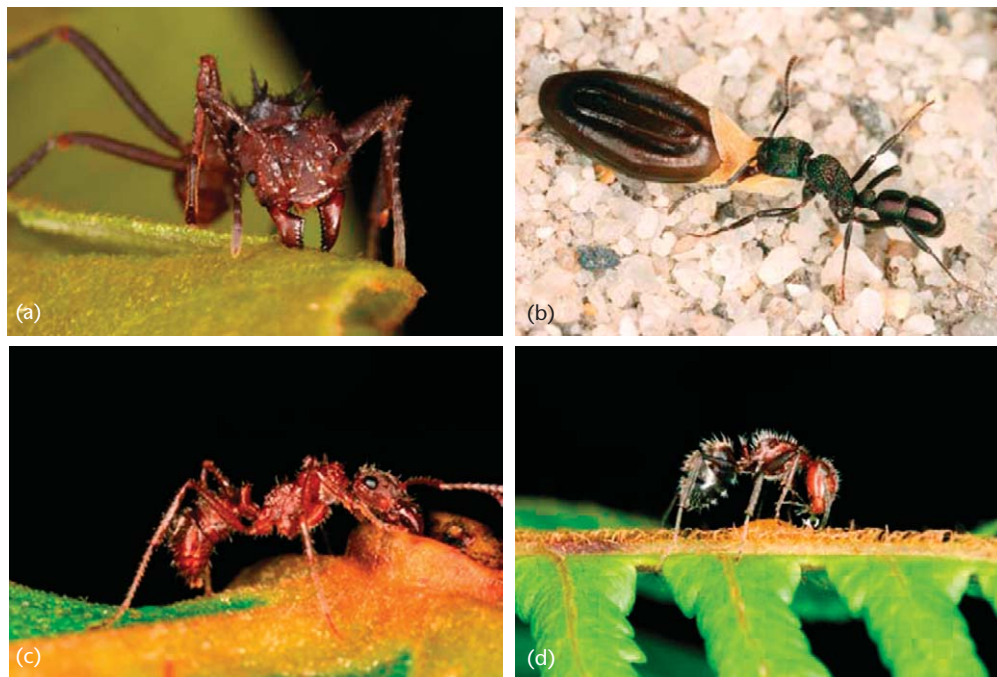


Figure 4 (a) Leaf-cutting ant of the genus *Acromyrmex* cutting a leaf. (b) Ant of the genus *Rhytidoponera* dispersing an Acacia seed in the arid region of Western Australia. Note the presence of the yellow lipid-rich part, the elaiosome that is seized by the ant mandibles. (c) *Ectatomma tuberculatum* feeding on extrafloral nectaries, Rica. (d) *Camponotus* species feeding on the honeydew produced by an Hemipteran (Coccidae) in Costa. Photographs by Benoit Guénard.

partner, which is thought to represent the ancestral condition of agriculture (**Figure 2b**; Mehdiabadi and Schultz, 2010) and as such should not be considered as herbivores, but as scavengers.

A second example of herbivory include the use of pollen, that is, pollinivory, which was first discovered within the Neotropical ant genus *Cephalotes* (Baroni Urbani and de Andrade, 1997). More recent studies have shown that pollen was also part of the diet of a few West Palaearctic species of the genera *Formica*, *Lasius* and *Myrmica* (Czechowski *et al.*, 2008, 2011). Those recent results might suggest that many more species of ants use pollen as part of their diet.

Finally, one of the most widespread examples of plant material use is found among seed-harvesting and seed-dispersing ants. In the first case, ants collect seeds mostly from annual plants in the environment surrounding their nest, and bring them back to the nest where seeds are milled before ingestion. Every year, several millions of seeds per hectare are collected by those species (Johnson, 2001). Seed harvesting is especially common within the Myrmicinae genera specifically *Messor*, *Pogonomyrmex* as well as in some species of *Pheidole* found in arid habitats. In the case of seed-dispersal or myrmecochory, plants produce seeds bearing a lipid-rich part, the elaiosome, which attracts ants but does not play a role in germination. As the elaiosome is usually carried back to the ant nest before it is eaten, this protects the seeds against predation, fire, or desiccation and

promotes seed germination (**Figure 4b**). This mutualistic interaction between ants and plants has been documented for approximately 11 000 species of plants and is geographically widespread and especially common in the arid regions of Australia or South Africa (Lengyel *et al.*, 2009).

Finally, numerous ant species collect plant secretions directly from extrafloral (**Figure 4c**; Koptur, 1992) or floral nectaries (Haber *et al.*, 1981) or indirectly from Hemipteran honeydew where the plant sap is more or less processed and enriched by the insect (**Figure 4d**). In the early 1970s, the ecologist Dan Janzen described another astonishing association between the Neotropical ants of the genus *Pseudomyrmex* and Acacia plants. In some of the most extreme cases, the plant provides shelters in the form of swollen thorns that are colonised and used as nests by the ants and produce different types of food in the form of a sugar-rich secretion produced by extrafloral nectaries. Even more surprising, some plants produce protein-rich food bodies that are essential for the development of the ant brood. In return, the ants actively and aggressively defend the plant against any intrusions from herbivorous insects or mammals (including curious ant biologists), and cut any other plants that may compete with or use the host plant as a support. If many ant species feed directly on plant secretion, all do not necessarily provide benefits to the plant through the removal of herbivorous insects, creating a continuum of mutualism–exploitative ecological interactions. **See also:** [Ant–Plant Mutualisms](#)

Ants as predators

Ants play an important regulatory role on many arthropod populations by their predatory behaviour. For instance, it was estimated that in the European oak forest, a colony of *Formica* species can collect 6.1 million prey pieces during a year (Horstmann, 1974). Similarly, in a Mexican coffee plantation, the Neotropical ant species *Ectatomma ruidum* can collect about 150 000 insects per day and per hectare (Lachaud *et al.*, 1990). Given their efficiency, it is unsurprising that ants are among the first known examples of insects that were used for biological control. As early as 304 AD and since then, ants such as the weaver ant, *Oecophylla smaragdina* (Huang and Yang, 1987), have been used to protect human plantations, especially against defoliator insects (Way and Koo, 1992). The efficiency of ants as plant protectors comes from two main aspects of their biology: (1) their predatory behaviour and ability to capture a wide array of prey and (2) their ability to establish, protect and forage within a given territory. Territoriality is, however, absent in the most impressive predatory ants: the army ants. The term army ants usually applies to a species of the New World Ecitoninae subfamily and to a species of the Old World Aenictinae and Dorylinae subfamilies; although it should be noted that the presence of an army ant syndrome can be found in several species of other subfamilies (Kronauer, 2008). Army ant species are characterised by obligate collective foraging and group predation, the absence of permanent nests, which leads to nomadism, and the presence of a highly specialised queen (Kronauer, 2008). Although some army ant species are specialised predators of other social insect societies, others are voracious generalist predators capturing all invertebrates and sometimes vertebrate preys that fail to escape. In both cases, army ants overwhelm their preys by their abundance (reaching several thousands of individuals). During the hunting phase of some species of the *Dorylus* or *Eciton* genera, the forest floor may appear like a moving carpet, with ants spreading over several square metres and capturing all the preys they encounter.

In contrast to the swarming behaviour of army ants, other ant species have developed trapping mechanisms to capture their preys. For instance, individuals of the Neotropical species *Azteca andreae* cluster side by side along the edge of the lower side of leaves ready to ambush any insect landing on its upper side. Furthermore, to capture large prey, sometimes more than 13 000 times heavier than an individual ant, the ants use the pubescence on the leaf to hold and attach their prey analogous to a natural Velcro® (Dejean *et al.*, 2010). The traps built by the arboreal ants *Allomerus decemarticulatus* are even more sophisticated. On the branches of the plant in which they live, this species builds galleries made of vegetal and fungal matter. These galleries possess multiple holes that are sufficiently wide for the ants to pass their head through and to seize preys walking on the surface. The combined action of multiple pairs of ant mandibles sizing the legs and pulling the prey against the surface, allow the ants to consume the prey

directly (Dejean *et al.*, 2005). The presence of morphological (presence of more or less specialised mandibles), chemical (the production of chemical compounds used as venom or acids to inject or spray on their prey) and behavioural features (sophisticated recruitment mechanisms in some species that allow the ants to overwhelm their preys; Figure 2c) confer to the ants great predatory success over their preys.

If ants are incredible predators, it is noteworthy to mention that ant colonies are also extremely important to a variety of arthropods that live within or near their nest. These arthropods are either commensals feeding on ant garbage or parasites, stealing food directly from ants, or feeding on the brood of ants. By their abundance, ants also constitute an important food resources for many invertebrates (Pekar, 2004) and vertebrates such as amphibians (Bonansea and Vaira, 2007), reptiles (Carretero and Lo Cascio, 2010), birds (Raley and Aubry, 2006) or even small and large mammals (Hartman *et al.*, 2000; Grobe *et al.*, 2003).

Modification of the nesting environment and its impacts on communities

All species of ants occupy a nest structure, either temporarily or permanently. Those can be preexisting cavities, or even made of their own bodies (e.g. army ants) that do not involve much, if any excavation or direct modification of the surrounding environments. However, most species of ants build more or less complex nest structures that modify the substrate properties and have an impact on other organisms. As such, ants can be considered as ecosystem engineers (Frouz and Jilková, 2008). Species establishing nests in the ground affect directly the soil moisture, pH or temperature. To maximise brood development, ants construct nests that reduce temperature and moisture variations within the nest and maintain certain optimal conditions in comparison with the surrounding soil (Petal, 1978). Although variations between species can be observed, the nest moisture levels tend to be generally lower than those in the surrounding soils (Dean and Yeaton, 1993; Lafleur *et al.*, 2002; Holec and Frouz, 2006; Haitao *et al.*, 2010). Through their excavating activities to expand the nest galleries and chambers, ants favour soil aeration and turnover (Lal, 1988; Frouz and Jilková, 2008). The total amount of soil brought from the deeper parts of the nest to the ground surface has been estimated to represent from 2.8 kg to 13 000 kg per year per hectare (Frouz and Jilková, 2008). In Brazil, the amount of excavated soil collected from the surface of a single nest of the fungus-growing ant, *Atta sexdens* was estimated at 40 000 kg (22.7 m³) (Weber, 1966). Furthermore, as a result of their foraging activities, ants enrich and modify soil chemical properties with a constant flow of organic materials (e.g. insect body parts, plant material, etc.). This is especially important for potassium and phosphorous compounds as well as some cations (Ca²⁺, Mg²⁺, K⁺ and Na⁺), which were found to be present at higher

concentrations in soil associated with ant nests compared with adjacent soils (Czerwiński *et al.*, 1971; Dean and Yeaton, 1993; Frouz *et al.*, 2003). Similarly, the pH value observed within ant nests tend to shift towards more neutral values (closer to a value of 7) than in the surrounding soils (Czerwiński *et al.*, 1971; Lafleur *et al.*, 2002; Frouz *et al.*, 2003; Frouz and Jilková, 2008).

The modifications induced by ants on their nesting environments also impact the fauna and flora living within or in the vicinity of the nest. Microbial activity and biomass, in particular, seem to be enhanced by the specific conditions found within ant nests (higher temperature and humidity, high nutrients availability) (Lafleur *et al.*, 2002; Frouz and Jilková, 2008; also see Holec and Frouz, 2006). Similar results have also been found for fungi, whereas the abundance of Actinomycetales bacteria tends to be reduced (Czerwiński *et al.*, 1971; Frouz and Jilková, 2008). Effects of ants on plant communities are balanced as ants can directly contribute to the selection of specific plant species or enhance plant diversity. In the tropical forest of South America, the ant *Myrmelachista schummani* associated with the myrmecophytic plant *Duroia hirsuta* kills all the plants growing close to its host by poisoning them with venom injection (Frederickson *et al.*, 2005). This behaviour results in a monoculture of the myrmecophytic plant *D. hirsuta* in the middle of a diverse plant community typical of tropical Amazonian forest, forming areas described by local inhabitants as 'devil's gardens'. Many other ant species, such as the harvester ants of the genera *Pogonomyrmex* and *Messor* or the fungus-growing ants of the genus *Atta*, keep the vicinity of their nest entrance totally devoid of any plant. Finally, through myrmecochory, ants influence the dispersal and survival rates of specific plant species over others and, as a consequence, alter the plant community composition. **See also:** Ant–Plant Mutualisms

Conclusion

In this review, a general overview of the taxonomic and ecological diversity of ants within ecosystems is depicted. More than 20 years ago, Hölldobler and Wilson (1990) offered a massive synthesis of the ecology of ants. Since then, their work has been built upon by thousands of new publications encompassing new species descriptions and fascinating discoveries of ecological interactions between ants and other organisms in their environment. Despite this, the ecology, distribution, or ecological importance of many, if not most, species of ants are still largely a mystery and numerous species remain undescribed. In this context, a multitude of future discoveries should come to enrich the field of myrmecology.

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