

8 Agricultural and Proto-Agricultural Symbioses in Ants

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Across most terrestrial habitats, ants engage in complicated relationships with other organisms. Ants are the only entirely eusocial family of insects: all 13,628 described species of Formicidae live in organized societies divided into reproductive and worker castes (Hölldobler and Wilson 1990; Bolton 2019). They have profound impacts on their habitats not only through their sheer numbers, but also due to the roles they play in food webs and nutrient cycling, as well as in the diverse symbioses they form with other organisms. The majority of these relationships—with other animals and with plants, fungi, and microorganisms—are poorly understood. Some of those that are better researched are shown to share striking similarities with human interspecies interactions, including agriculture (Schultz et al. 2005). This, in turn, suggests that agriculture is not a unique human behavior but that it has instead evolved convergently in very distantly related organisms (chapters 1 and 2, this volume).

A discussion of the interactions of ants with other organisms could be structured according to any number of organizational frameworks. For example, we could categorize such interactions based on whether they represent parasitism, commensalism, or mutualism. Here we have chosen to broadly survey multiple, mostly nutritional symbioses of ants, organized by symbiont taxon, and to call attention to the cases most similar to agricultural symbioses in humans. For readers interested in more detailed accounts of particular nutritional symbioses in which ants engage, we recommend the many available focused reviews (Way 1963; Weber 1972a; Pierce et al. 2002; Rico-Gray and Oliveira 2007; Stadler and Dixon 2008; Mehdiabadi and Schultz 2010; Orivel and Leroy 2011; Voglmayr et al. 2011; Mayer et al. 2014; Ivens 2015; Chomicki, Janda, and Renner 2017).

To describe the diversity of agricultural or agriculture-like behavior in ants we will use the definitions outlined in the introduction to this book: *Cultivation* is a set of practices that one species (the farmer) may perform to promote the growth of another species (the cultivated symbiont)—for example, preparing the substrate for growing crops, fertilizing, tilling, planting, pest control, protecting, and sheltering; these may be carried out on small scales and in the absence of domestication. *Domestication* is a genetic change in one species (the domesticate) in response to the influence of another species (the farmer) that benefits the farmer but that would reduce the fitness of the domesticate in its original niche. *Agriculture* is cultivation on a landscape-altering scale, characterized by economic

(i.e., obligate) reliance. Although our definition of agriculture does not require domestication, in human agriculture domestication preceded agriculture in most cases (Fuller et al. 2014; chapter 10, this volume), and, in nonhuman agriculture, most cases involve a one-way or a two-way obligate mutualism between the farming species and a domesticated symbiont. Various ecological interactions, such as central-place foraging, niche construction, and incidental cultivation, have been suggested as consistent precursors to agriculture (Smith 2011a, 2011b; Allaby et al. 2015; chapter 14, this volume). Here we will use the umbrella term *proto-agriculture* to refer to such preagricultural ecologies and behaviors.

Ants and Other Animals

Many distantly related groups of ant species have independently evolved relationships with insects that feed on plant sap (figure 8.1A–C), mostly homopterans such as aphids and scale insects (Way 1963; Hölldobler and Wilson 1990). These sap-sucking insects provide ants with an excreted liquid called *honeydew*, which is rich in sugars and amino acids. Ants, in turn, provide sap-sucking insects with protection from predators and parasites, sanitation by removing honeydew from the insects' bodies, and, in some systems, transport and/or shelter. The majority of ant species that tend sap-feeding insects belong to the ant subfamilies Formicinae, Dolichoderinae, and Myrmicinae. The insects that engage in such symbioses with ants occur in the homopteran families Aphidae, Cercopidae, Cicadellidae, Coccidae, Fulgoridae, Membracidae, Pseudococcidae, and Psyllidae, but also in other insect groups such as the lepidopteran families Lycaenidae and Riodinidae (Schultz and McGlynn 2000; Fiedler 2001). About 1,000 of the 4,000 known aphid species, family Aphididae (figure 8.1A), are tended by ants (Bristow 1991; Ivens 2015), and at least 483 species (out of approximately 6,000 total) in the lepidopteran family Lycaenidae (figure 8.1B) are associated with ants (Pierce et al. 2002).

Ant-homopteran mutualisms range from facultative—that is, occurring optionally in response to circumstances—to obligate, in which one or both partners cannot survive outside of the symbiosis. The majority of homopteran-tending ant species are facultative mutualists, with an omnivorous diet that also includes, in addition to honeydew, animal prey, plant nectar, and plant seeds. The proportion of honeydew in ant diets varies greatly between species, from minor in otherwise mainly predatory species such as *Daceton armigerum*, to over 80% in, for example, the red wood ants of the *Formica rufa* species group (Hölldobler and Wilson 1990; Offenberg 2001; Cannon and Fell 2002; Paris and Espadaler 2009; Dejean et al. 2012; Seifert 2018). It also varies within species and within colonies, depending on seasonal or other changes in the availability of other food sources. Further, in addition to deriving nutrition from honeydew, when prey is scarce, the ants consume some of their sap-feeding insect symbionts as an additional protein source (Pontin 1958; Ivens 2015). When tended by ants, some species of ant-associated aphids express different behavioral and physiological traits, such as increased feeding rates and changes in the composition of the honeydew, relative to their phenotypes when unattended by ants (Banks and Nixon 1958; Yao and Akimoto 2001; Stadler and Dixon 2005; Ivens 2015). The dependence in ant-homopteran associations is asymmetric; ant-tended insects are more likely to be obligate symbionts than are their ant hosts, which are more likely to be facultative symbionts (Stadler and Dixon 2008). The distributions of obligate ant-tended

mutualists are restricted not by the presence of their host plants but by the presence of the tending ant species (Hopkins and Thacker 1999). One of the largest species of aphids, *Stomaphis quercus*, lives only on oak trees within the foraging territory of the highly territorial European ant species *Lasius fuliginosus*, its obligate ant host (Goidanich 1957; Hopkins et al. 1999; Depa, Mroz, and Szawaryn 2012). The protection provided by actively tending ants accords well with the definition of cultivation discussed earlier. The morphological, behavioral, and physiological traits present in some ant-tended insects accord with the definition of domestication, as does the facultative/obligate ant/homopteran asymmetry of many of the mutualisms. As per our definition, fully developed agriculture requires a critical level of reliance on the part of the farmer. Because in most of the ant/homopteran systems the homopterans are not the only source of the ants' nutrition, they probably qualify as cultivation rather than as fully developed agriculture.

There are some notable exceptions. At least 12 ant species in the *Dolichoderus cuspidatus* species group, a clade of closely related species widely distributed in tropical Southeast Asia, engage in obligate symbioses with at least 35 different mealybug species from the tribe Allomyrmococcini (Homoptera: Pseudococcidae) (Dill and Maschwitz 1994). All of the ant species in this group depend on the honeydew produced by mealybugs and display a collection of behavioral traits that have earned them the name "migrating herdsmen" (Maschwitz and Hänel 1985). Mealybugs feed on the sap of very young plant parts, so once they have exhausted local resources the ants carry them to a new part of the plant or to a new tree, and they also keep them in their nests during the night. To be able to quickly migrate to new locations and to avoid wasting energy on nest construction, *D. cuspidatus*-group ants create temporary nests (so-called bivouacs) formed by their bodies, keeping the ant brood and the mealybug domesticates in the center. Some other ant species such as army ants form similar bivouacs, but ants of the *D. cuspidatus* species group are the only ant species that have evolved a mobile-nesting behavior as an adaptation to the requirements of their nutritional mutualists. In addition to highly efficient colony relocation, *D. cuspidatus*-group ants have evolved other behaviors and morphological features that facilitate mealybug transport, and, unlike most other ants, they reproduce by budding, in which a young daughter queen and a subset of the workers in her mother's colony depart to begin a new colony, instead of through mating flights (Dill and Maschwitz 1994). In the *D. cuspidatus* group, budding necessarily includes carrying along part of the colony's mealybug herd. Experimental evidence strongly indicates that the mealybugs in this system have evolved behavioral and morphological traits adapted for ant tending and that they are unable to survive without their ant hosts, per our definition of domestication. The adaptations of the host ants further indicate that they obligately rely on the relationship with their mealybugs, per our definition of agriculture.

Additional examples of obligate nutritional mutualism exist in other ant-homopteran symbioses. Ants from the genus *Acropyga* and some species of the ant genus *Lasius* (e.g., *Lasius flavus*) live in highly specialized and mutually obligate nutritional symbioses with root mealybugs and root aphids, respectively (Flanders 1957; Way 1963; Pontin 1978; LaPolla, Cover, and Mueller 2002; Schneider and LaPolla 2011; Seifert 2018). An *Acropyga* daughter queen departs on her mating flight carrying a mealybug symbiont in her mandibles (figure 8.1C) to serve as the "seed" individual for a clonally produced herd that will provide the root-honeydew-derived nutrition for the queen's new ant colony (Silvestri

1924; Wheeler 1935). As in the case of *Dolichoderus cuspidatus* and their mealybugs, these symmetrically obligate ant-homopteran associations involve traits associated with cultivation, domestication, and agriculture.

Ant-Lepidoptera associations, which include mostly lepidopteran larvae or pupae in the families Lycaenidae and Riodinidae, share similarities with ant-homopteran associations. They vary from facultative to obligate for the Lepidoptera but are facultative for the ants, and they depend on nutritious liquids produced by specialized organs of the lepidopteran larvae. In exchange for this nutrition, ants protect the larvae from predators and parasitoids (Hölldobler and Wilson 1990; Fiedler 2001, 2012; Pierce et al. 2002). Ant-tended lycaenid and riodinid larvae have thick cuticles and specialized acoustical structures that produce sounds, which enable them to exploit the ant social communication system and to attract the ants (DeVries 1991; Fiedler 2012; Tartally et al. 2019). A small percentage of ant-Lepidoptera associations have shifted from mutualism to parasitism in a direction opposite to that found in ant-homopteran associations. In these instances parasitic lepidopteran larvae are carried back to the nest, where they feed on ant brood or are fed by worker ants through trophallaxis (Fiedler, Hölldobler, and Seufert 1996; Pierce et al. 2002; Fiedler 2012; Tartally et al. 2019). The nutritious secretions provided by the lepidopteran larvae never comprise the main food resource of the ants, which also depend on plant nectar and homopteran honeydew (Fiedler 2001). Thus, although lepidopteran larvae are clearly genetically modified for life with ants and are thus domesticated, ant-lepidopteran associations better fit the definition of cultivation than of true agriculture.

Thousands of other animals, so-called myrmecophiles, are adapted to the predictable ecological niches created by ant colonies, inhabiting their nests in a spectrum of facultative to obligate symbioses (Hölldobler and Wilson 1990; Navarrete-Heredia 2001; Parmentier, Dekoninck, and Wenseleers 2014). In the majority of cases, rather than benefiting their ant hosts, myrmecophiles are parasites or commensals, so that, although many have evolved complex adaptations for life with ants, these mutualisms in general are best described as proto-agricultural.

Ants and Plants

Ants participate in a diverse array of symbiotic relationships with plants, ranging from diffuse to highly specific (Rico-Gray and Oliveira 2007; New 2017). Foremost among ant-plant associations is the dispersal of seeds by ants (myrmecochory), which occurs in some 11,000 species of plants (Lengyel et al. 2010). In the second-most diverse category of ant-plant associations, plants provide shelter and food and ants provide protection against herbivores and competing plants. Nearly 700 species in 50 different families of vascular plants have evolved “domatia,” preformed cavities within plant stems, thorns, leaf petioles, and leaf pouches in which ants build their nests (Nelsen, Ree, and Moreau 2018). Classic ant-plant systems include, in the Neotropics, *Pseudomyrmex* ants and *Acacia* plants (figure 8.1D) (Janzen 1966, 1967) and *Azteca* ants and *Cecropia* plants (Janzen 1969) and in the Paleotropics, *Crematogaster* ants and *Acacia* plants in Africa (Stanton and Palmer 2011) and *Crematogaster* ants and *Macaranga* plants in Asia (Heil et al. 1998, 2001; Feldhaar et al. 2003). In all these examples, the plant provides the nesting site in the form of hollow structures and produces food in the form of either or both extrafloral nectaries and specialized,

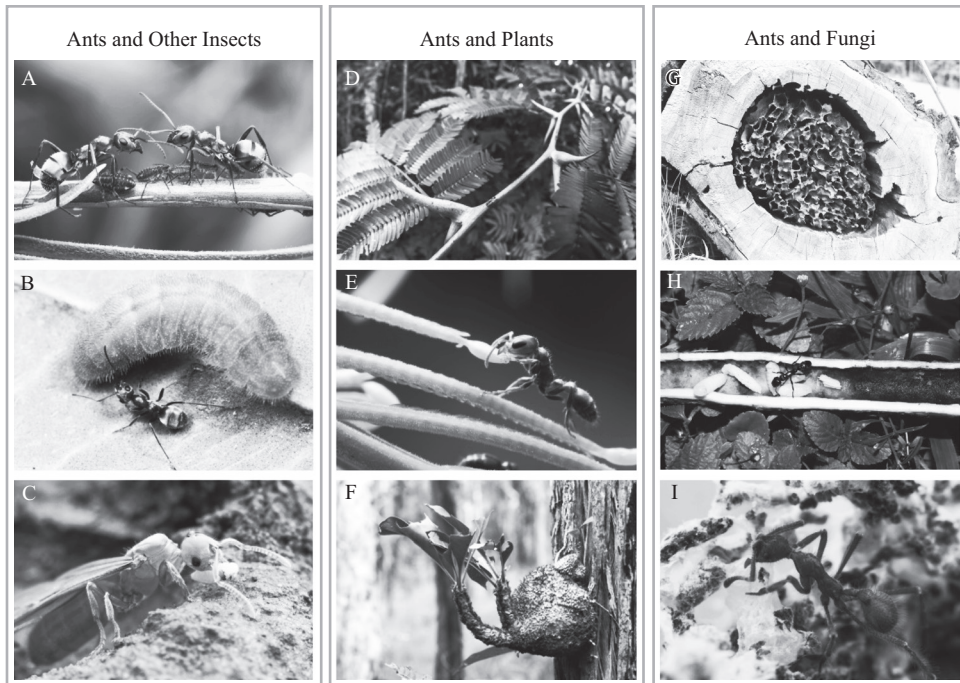


Figure 8.1

Ants and other insects: (A) two workers of the ant species *Formica aerata* tending aphids on a willow branch, California, USA; (B) the ant *Formica francoeuri* tending a larva of the Great Copper Butterfly (*Lycaena xanthoides*), California, USA; (C) the queen of the ant species *Acropyga goeldii* carrying a mealybug in her mandibles, Minas Geiras, Brazil. Ants and plants: (D) worker of the ant species *Pseudomyrmex peperi* on an *Acacia* plant with swollen, hollow thorns that serve as ant nesting sites, Cayóo District, Belize; (E) a worker of the ant species *Pseudomyrmex peperi* harvesting a lipid-rich Beltian body from the leaf tips of an *Acacia* plant, Armenia, Belize; (F) a *Myrmecodia* ant plant that is commonly inhabited by *Philidris* ants, Queensland, Australia. Ants and fungi: (G) a carton nest of the ant species *Lasius fuliginosus* inside of a tree trunk, eastern Austria; (H) nest of the ant species *Tetraponera aethiops* in a twig of *Barteria fistulosa*, with a patch of black fungus of the order Chaetothyriales, Southwest Region, Cameroon; (I) the fungus-farming ant *Apterostigma collare* on its fungus garden, Costa Rica. Photos reproduced with permission from: Alex Wild (A–F, I), Birgit C. Schlick-Steiner & Florian M. Steiner (G), Rumsais Blatrix (H).

protein- and/or lipid-rich food bodies: Beltian bodies in *Acacia* (figure 8.1E), Mullerian bodies in *Cecropia*, and Beccarian bodies in *Macaranga* (Bischof et al. 2013; New 2017). The plant-inhabiting ants are fiercely aggressive and protect their host plants from arthropod and large vertebrate herbivores, including elephants in the African savannas (Goheen and Palmer 2010). They also monitor the area surrounding their host plant and kill competing plants (Janzen 1969; Schupp 1986) and fungal pathogens (Letourneau 1998). Some evidence suggests that *Azteca* ants also provide *Cecropia* with a source of nitrogen (Sagers, Ginger, and Evans 2000). The domatia-inhabiting ants therefore exhibit behaviors associated with cultivation, as they protect, weed, and to some extent manure their plants. However, in the majority of cases they do not play a role in the propagation or dispersal of domatia-bearing host plants, and in many cases they do not obligately depend on the plant for nutrition because they also actively prey on insects. The majority of these ant-plant symbioses may be characterized as shelter and defense mutualisms, although nutrition plays a significant role in a subset of such associations.

Another category of ant-plant relationships is that of arboreally nesting ants and epiphytic plants, known as ant gardens (AGs) (Ule 1901; Janzen 1974; Orivel and Leroy 2011). We will refer to both the plants and the ants in these association as AG plants and AG ants, consistent with the existing literature (Orivel and Leroy 2011). In both Neotropical and Paleotropical forests, diverse epiphyte species grow in arboreal ant nests constructed from soil or carton (a fibrous, paper-like material constructed by ants from plant material, soil, wood, and other sources). Approximately 137 species of epiphytes associate to some degree with ants, but here we will briefly discuss only the smaller number of plants involved in obligate associations with AG ants (i.e., those that are never found free-living outside of the symbiosis) because those associations share the most traits with human agriculture (Orivel and Leroy 2011). A more detailed discussion of plant-farming by ants is provided by Chomicki (chapter 9, this volume). The greatest number of species known to be obligate AG ants occur in the genera *Philidris*, *Camponotus*, and *Crematogaster*, but many also occur in *Pheidole*, *Diacamma*, *Azteca*, *Odontomachus*, and *Pachycondyla* (Orivel and Leroy 2011; Chomicki, Janda, and Renner 2017). True ant garden epiphytes (figure 8.1F), with seeds that are consistently collected by ants and planted in their carton nests, belong to at least 14 plant families, but are most concentrated in the families Rubiaceae, Apocynaceae, Asclepiadaceae, and Gesneriaceae (Orivel and Leroy 2011; Chomicki, Janda, and Renner 2017). AG ants recognize the seeds of their obligate plant symbionts by chemical cues (Youngsteadt et al. 2008, 2010; Chomicki and Renner 2016b), collect them, incorporate them into their nests shortly after nest foundation, and continue to collect and plant new seeds throughout the life of the colony, constantly maintaining and expanding the garden. The plants provide shelter: in Neotropical ant gardens, the roots serve as a scaffold for the carton or soil nest, whereas in Australasia and Southeast Asia the ants nest inside the plant in enclosed nesting spaces, or domatia, formed from the hypocotyl (Chomicki et al. 2019; chapter 9, this volume). AG plants provide protection from abiotic factors such as rain and wind and food in the form of fruits, nectaries, and elaiosome-bearing seeds. In most cases these do not constitute the major portion of the ant diet, because the ants also forage for other food (Orivel and Leroy 2011). In addition to dispersing them, ants actively protect their AG plants from herbivores and provide them with nutrients. Canopy-inhabiting plants are particularly nutrient-deprived relative to ground-living plants, especially in the seedling phase. The ant nest, containing soil, vertebrate feces, ant feces, and various other organic materials, provides a continuous source of nutrients for the plants (so-called myrmecotrophy).

Obligate AG symbioses possess many of the traits of cultivation, but for most cases data are insufficient for drawing conclusions about whether domestication has occurred. One of the best-studied examples, however, convincingly demonstrates the domestication of a clade of plants by an ant species (Chomicki and Renner 2016a, 2016b; Chomicki et al. 2019, 2020; chapter 9, this volume). In this system, from Fiji, colonies of a single species of ant, *Philidris nagasau*, cultivate a clade of six closely related plant species in the genus *Squamellaria*, sometimes incorporating up to three species at a time into their ant gardens. Research has established the obligate dispersal and active planting of seeds by ants, fertilization of plants by ant fecal droplets, protection from herbivores, crop yield optimization by growing plants in full sun, and dependency of ants on the plants' fruits for food (Chomicki et al. 2020). Both symbionts (ants and plants) have evolved phenotypic

traits unique to the symbiosis (e.g., loss of carton-nest building in the ants, specialized root structures that enable rapid development of the first domatia in the plants). This has led researchers to consider this a case of co-evolution. By the definition used in this book, such genetic change constitutes domestication. In Fiji, AGs can become very large, containing over 50 individual *Squamellaria* plants, a productivity comparable to that of early human agriculture (Chomicki et al. 2016b, 2020).

A different type of ant “garden” results from the association of the Amazon ant species *Myrmelachista schumanni* and several ground-living myrmecophytic plants, most notably *Duroia hirsuta* (family Rubiaceae) (Morawetz, Henzl, and Wallnofer 1992; Renner and Ricklefs 1998; Frederickson, Greene, and Gordon 2005; Salas-Lopez, Talaga, and Lalagüe 2016). *Myrmelachista* ants nest in domatia within *D. hirsuta* and systematically kill all other plants in the vicinity by injecting them with formic acid (Frederickson, Greene, and Gordon 2005). By killing competing plants, *Myrmelachista* ants promote the growth and spread of their host plant, which in turn expands the number of nesting sites for their colonies. Such colonies can become very large and contain up to 3 million workers and 15,000 queens distributed across monocultural stands of up to 600 *Duroia* trees (Frederickson, Greene, and Gordon 2005). Such stands are known colloquially as “devil’s gardens” and are believed by local people to be inhabited by evil forest spirits. Until recently, devil’s gardens were attributed solely to allelopathic compounds produced by the *Duroia* plants (Campbell, Richardson, and Rosas 1989; Pfannes and Baier 2002). It has alternatively been suggested that, rather than produced by *D. hirsuta*, the “domatia” are in fact the products of galling by the *M. schumanni* ants (Edwards et al. 2009).

A similar system is that of the ant *Pseudomyrmex triplarinus* and the host plant *Triplaris americana* (Polygonaceae), which provides the ants with domatia but no nutrition such as extrafloral nectaries. The *P. triplarinus* ants, which feed on homopteran honeydew, remove seeds and prune seedlings, producing cleared areas around their host plants (Larrea-Alcázar and Simonetti 2007). Given that there is a cost of increased herbivory in both systems (Pfannes and Baier 2002; Frederickson and Gordon 2007), that there are no plant-generated food rewards, and that the *D. hirsuta* “domatia” may instead be ant-induced galls, it remains unclear whether or not the plants in these systems receive any net benefits or are domesticated. Given this uncertainty, “devil’s gardens” may be interpreted as cultivation rather than agriculture.

Ants and Fungi

Symbiotic associations between ants and fungi are far less frequent than the associations of ants with animals and plants. As far as is known, ants rarely feed on fungi (Orr and Charles 1994; Tobin 1994; Epps and Penick 2018) or disperse them (Schultz and McGlynn 2000), although fascinating and poorly investigated exceptions exist (Witte and Maschwitz 2008; Von Beeren, Mair, and Witte 2014). Indeed, ants, which live mostly in the soil, limit their exposure to fungi via antibiotic secretions from the metapleural, mandibular, and other glands and via behaviors such as self- and allogrooming. In spite of this general avoidance of fungi, ant-fungus symbioses include some of the most remarkable examples of agriculture in ants.

Carton-Nest Builders

Similar to shelter-providing symbioses seen in most ant gardens, some carton-building ant species use fungal hyphae for structural reinforcement of carton nests (figure 8.1G) (Hölldobler and Wilson 1990; Schlick-Steiner et al. 2008; Mayer et al. 2014) and carton galleries that are used as prey traps (Dejean et al. 2005; Mayer and Voglmayr 2009). One such example is the European ant species *Lasius fuliginosus*, which lives in symbiosis with a fungus that is found only in ant nests and is most commonly referred to as *Cladosporium myrmecophilum* (Maschwitz and Hölldobler 1970; Hölldobler and Wilson 1990; Seifert 2018). Interestingly, genetic data from Eastern Austria suggests that *Lasius fuliginosus* and three other *Lasius* species can host in their colonies at least two fungal species at the same time and that a total of four fungal species are associated with *L. fuliginosus* nests (Schlick-Steiner et al. 2008). The carton nests are built in soil cavities and tree trunks from chewed-up particles of wood, soil, and plant matter mixed with ant saliva, excretions, and aphid honeydew (figure 8.1G). The fungal hyphae grow inside of the walls of the carton nest, providing scaffolding and reinforcement for the sponge-like carton galleries. Ants manure the walls with their fecal droplets and with collected honeydew, providing nutrition for the fungus. They also continuously crop the fungus to prevent it from overgrowing the nest. At least one of the fungal species they grow is transmitted vertically: when virgin daughter ant queens fly out to mate and start new colonies, they carry a small fungal inoculum from the parental nest inside their infrabuccal pockets (Hölldobler and Wilson 1990; Schlick-Steiner et al. 2008). Because ants disperse, inoculate, manure, provide nutrients for, and crop the fungus, we consider the *Lasius*-wall fungus mutualism to represent an obvious example of cultivation, and, because the fungus is obligately dependent on the ants (and, apparently, the ants are also dependent on the fungus), the association fulfills our definition of domestication. It does not constitute a nutritional agricultural symbiosis, but instead is akin to human non-nutritional, “material-goods” agricultures such as the cultivation of bottle gourds, lumber, and cotton. The symbioses between carton-building ants and fungi can also be viewed as an extension of the ant-aphid farming mutualism. The honeydew collected from tended aphids is used as a food source both for the ants and for the ants’ structural symbiont, the fungus.

Black-Yeast Growers

Few ant-fungus nutritional agricultural systems are known. One broad category, the product of multiple independent evolutionary origins, involves domatia-bearing plants, domatia-inhabiting ants, and ascomycete “black yeast” fungi from the order Chaetothyriales (figure 8.1H). The most well-known example was first observed more than a century ago (Miche 1911; Bailey 1920), but properly described and recognized as a nutritional mutualism only recently (Defosse et al. 2009, 2011; Blatrix et al. 2012). In this system, the African ant species *Petalomyrmex phylax* participates in a mutualism with the domatia-forming plant *Leonardoxa africana*. A small patch of black-yeast fungus grows on the inner surface of most domatia, where it is apparently nourished by the ants with feces and arthropod parts. The ants, in turn, use the black yeast as a food source, at least for their larvae (Blatrix et al. 2012). Similar domatia-inhabiting black-yeast fungal species are now known to associate with at least 19 plant and 10 ant genera, and these associations have apparently arisen independently in at least three geographically distinct plant-ant lineages,

including a subset of Neotropical *Cecropia-Azteca* symbioses, in which the fungi are transmitted vertically by *Azteca* foundress queens (Voglmayr et al., 2011; Blatrix et al., 2012, 2013; Mayer et al., 2014; Nepel et al., 2016; Mayer et al. 2018). Each domatia-inhabiting black-yeast species seems to be specific to a particular ant-plant symbiosis (Defosse et al. 2011; Voglmayr et al. 2011). This potentially widespread and complex system clearly needs to be further studied, especially the nutrient flow between ants, fungi, and plants. The current limited data indicate that the *Petalomyrmex-Leonardoxa* and *Azteca-Cecropia* systems involve most of the traits of cultivation, domestication, and agriculture (Voglmayr et al. 2011; Mayer et al. 2018).

The Fungus Farmers

The best known fungus-farming ants are the 245 extant species belonging to a single Neotropical clade, subtribe Attina (so-called attine ants) (Schultz and Brady 2008; Branstetter et al. 2017; chapter 14, this volume). All attine-ant species are obligate fungus-farmers, unable to live without their fungus gardens (figure 8.11). The cultivated fungi (phylum Basidiomycota, order Agaricales, families Pterulaceae and Agaricaceae) are grown in monocultures inside ant nests, in most species in underground nest chambers, on substrates of organic materials collected by the ants (Möller 1893; Weber 1972b; Mehdiabadi and Schultz 2010). Attine ants disperse their fungal crops; when leaving from the maternal nest to mate and start a new colony, daughter queens carry in their infrabuccal pocket a fungal pellet from the maternal garden. Attine ants also nourish their fungal cultivars, manure them with their fecal droplets, weed out microbial pathogens, and practice biochemical pest control by culturing antibiotic-producing bacteria in specialized crypts on their bodies (Weber 1972b; Bass and Cherrett 1996; Currie and Stuart 2001; Li et al. 2018). Attine-ant agriculture can be broadly divided into “lower” and “higher” ant agricultural systems. In lower ant agriculture, the fungal cultivars are facultative symbionts that can apparently live freely without the ants. Although it remains possible that lower-attine fungi possess adaptations for life with ants, this is a poorly explored area of inquiry, and so, in the case of lower ant agriculture, there is currently no evidence for domestication of fungi by ants (Mueller et al. 1998; Schultz and Brady 2008). In higher ant agriculture, practiced by 110 species of attine ants, the fungal cultivars are obligate symbionts, never found outside of the symbiosis (Mehdiabadi and Schultz 2010). Higher-attine fungi possess clear adaptations for life with ants: they are all polyploid, they consistently produce nutritious food bodies called “gongylidia” that are preferentially eaten by the ants, and they are significantly different from lower-attine fungi in expressed enzyme and amino acid profiles (Möller 1893; De Fine Licht and Boomsma 2014; Kooij et al. 2014, 2015). Higher-attine agriculture possesses all of the traits of domestication and agriculture (Schultz et al. 2005). The scale of agriculture practiced by the leaf-cutting ants, a subset of the higher-attine ants, is comparable to human industrial-scale agriculture (chapter 14, this volume), and, in terms of number of agricultural adaptations, more complex (chapter 1, this volume).

Leaf-cutting ants, unlike all other fungus-farming ants, have evolved the ability to cut and process fresh vegetation (living leaves, flowers, and grasses) as a fungal substrate. This ability has enabled leaf-cutter ant colonies to evolve into “superorganisms,” consisting of 5 million or more individuals and dominating New World grassland and forest ecosystems (Schultz and Brady 2008). A mature nest of a leaf-cutting *Atta* species is the

ecological equivalent of a large vertebrate herbivore in terms of biomass, life span, and consumption: a medium-sized colony collects almost one ton of leaves per year (Wirth et al. 1997, 2003; Hölldobler and Wilson 2010). *Atta* nests can be up to 7 meters deep and include more than 7,000 garden chambers, separate waste-disposal chambers, and a ventilation system (Moreira et al. 2004; Forti et al. 2017). Leaf-cutter nests alter the chemical and physical properties of the soil, contribute substantially to carbon turnover in Neotropical ecosystems, and represent an important resource for many other symbiotic species (Navarrete-Heredia 2001; Ballari, Farji-Brener, and Tadey 2007; Farji-Brener and Werenkraut 2017). As in human industrial-scale agriculture, leaf-cutter agriculture is achieved through finely scaled division of labor, accomplished through a highly polymorphic worker-caste task force in which the largest individuals (the “soldier” caste) weigh 200 times more than the smallest individuals (the gardener-nurses) (Wilson 1980; Hart and Ratnieks 2001; Garrett et al. 2016).

Remarkably, in at least some higher-attine ant species, it appears that higher agriculture has produced an agricultural surplus that ants can “trade” for other goods, similar to exchanges in human societies and to the earlier example in which the ant species *Lasius fuliginosus* uses surplus honeydew collected from aphids to nourish its structurally beneficial fungal symbiont. Relative to when it is not supporting a commensal ant symbiont, when it is hosting a colony of the socially parasitic, non-fungus-growing ant *Megalomyrmex symmetochus*, a colony of the higher-attine ant species *Sericomyrmex amabilis* increases the productivity of its fungus gardens by foraging for higher-protein substrates (Shik et al. 2018). Most of the time, *Megalomyrmex symmetochus* parasitizes the *S. amabilis* nest, feeding on its fungus garden and brood (Adams et al. 2000). *Sericomyrmex amabilis* is not very effective at colony defense, whereas *M. symmetochus*, which possesses volatile alkaloid venom, is very efficient at defense. When the *S. amabilis* colony is attacked by other ants, particularly by the raiding “agro-predatory” species *Gnamptogenys hartmani*, *M. symmetochus* defends the nest and usually rescues the colony from complete devastation (Adams et al. 2013). The ability of *Sericomyrmex amabilis* to upregulate the nutritional content of its fungus garden provides it with excess agricultural goods that are used to compensate *M. symmetochus*, which can behave as a simple social parasite or an efficient mercenary defender, depending on context.

Conclusion

Ants are one of the nine phylogenetic lineages of animals that have independently evolved similar sets of agricultural behavioral traits, although with varying levels of complexity (chapter 1, this volume). The specific ant behaviors that have converged on human practices of cultivation, domestication, and agriculture have been discussed throughout this chapter. In general, ants most commonly display behaviors comparable to human cultivation practices, such as fertilizing, planting, protecting, harvesting, and sheltering, while examples of convergence on domestication and agriculture are less common. In terms of kingdoms of life, ants frequently associate with animals and plants, and those associations range from facultative cultivation, such as tending homopteran insects or weeding and manuring epiphytic plants, to obligate dependence on domesticates, such as the ant *Dolichoderus cuspidatus* converging on the behavior of human nomadic herdsman, which

migrate because of their cattle, and *Philidris nagasau* ants planting their obligate crop plants closer to the sun, convergent with various human practices to maximize crop yield. The known agricultural symbioses of ants and fungi, less common than those with plants, are apparently obligate for the ant species engaged in them. They also share similarities with human agriculture: *Lasius fuliginosus* obligately cultivates its fungus for a structural rather than a nutritional purpose, similar to human cultivation of wood as a building material, while the fungus-farming attine ants independently evolved planting, substrate preparation, manuring, weeding, harvesting, and elaborate division of labor, as well as economic (i.e., obligate) reliance on their crop.

To conclude this review of the diversity of ant symbioses and the degree of convergence with human agricultural practices, we wish to consider if there are any lessons to be learned from ant-farming systems in the light of the urgent agricultural crisis currently experienced by humans. Unsustainable human agricultural practices on a global scale have altered planetary-level ecological processes through land-use change, carbon release, chemical pollution, biodiversity loss, and soil erosion (Skinner et al. 1997; Stoate et al. 2001; German, Thompson, and Benton 2017; IPBES 2019). Because of our reliance on industrial-scale monocultures, our crops are genetically less diverse and subsequently less resilient to unpredictable random catastrophic events (Dunn 2017; Nabhan et al. 2012). In our comparisons of traits of ant and human agriculture, an obvious lack of convergence exists in some of the traits relevant to agricultural sustainability. For example, colonies of *Atta* leaf-cutter ants, which harvest large amounts of plant material (e.g., 132 kg of biomass/ha/year), rarely exhaust local resources of native vegetation (Cherrett 1968; Wirth et al. 2003; Herz, Thompson, and Benton 2007), have positive impacts on the productivity of their local environments, and occupy keystone positions in local ecologies (Farji-Brener and Illes 2000; Farji-Brener and Werenkraut 2015). Also, despite growing a single fungal clone in a monoculture, vulnerable to the specialized, coevolved parasitic fungus *Escovopsis*, attine ants practice efficient pest management (Currie 2006; Mehdiabadi et al. 2010; chapter 11, this volume) by growing antibiotic-producing bacteria in specialized structures on their cuticles (Li et al. 2018). As a consequence of 60 million years of coevolution with their crops, crop pathogens, and antibiotic-producing bacteria, ants have developed efficient methods of biocontrol that do not adversely affect the sustainability of the system (Pathak, Kett, and Marvasi 2019).

Fungus farming in ants originated shortly after the end-of-Cretaceous mass-extinction-event known as the KT boundary (Branstetter et al. 2017). This was a period in earth history when organisms that depended on photosynthesis and those that depended on those organisms were threatened with extinction (Janzen 1995). Because fungi are saprobes, which can grow on dead plant and animal matter, this was also a period when fungivory and associating with fungi provided a stable food source for the ancestors of attine ants. From environmentally catastrophic conditions and in the midst of mass extinction, fungus-farming attine ants emerged as an ecologically successful radiation.

For human agriculture to survive analogous climate-related changes, we likewise need to find ways to diversify our resources and use them sustainably, rather than continuing to rely on those that are likely to be highly sensitive to climate change and associated natural disasters and that are dependent on large quantities of chemical pesticides and fertilizers (Dunn 2017; Poux and Aubert 2018). Our current approach to agriculture is

much less resilient than those of the various ant farmers considered in this review. A shift to sustainable agricultural practices such as organic, conservation, or regenerative agriculture will require radical changes to present agricultural policies, a strong emphasis on conservation of wild relatives of cultivated plants and on the genetic diversity of existing cultivars, a shift in human diet, and mainstreaming of biodiversity-oriented policies into nonagricultural sectors (IPBES 2019). As the authors of this review find ants to be a continuous source of inspiration, we hope that the diversity and complexity of the most successful organisms on earth will inspire the reader to reconsider the ways of the ants (King Solomon, Proverbs 6:6), to discover in their study the motivation for much-needed change, and to continue to look for new solutions in nature.

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