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The Convergent Evolution of Agriculture in Humans and Fungus-Farming Ants

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Leaf-cutter ants are the preeminent herbivores of the New World tropics. Below ground, their colonies contain millions of worker ants that occupy thousands of chambers. Above ground, the soil they excavate forms huge mounds that dominate the forests and grasslands of Central and South America. Hundreds of thousands of ant foragers stream outward from these mounds, sharing the radiating, well-worn paths with equal numbers of inward-streaming sisters, the latter returning with cut leaf fragments held aloft in their mandibles like miniature pennants. Marveling at this spectacle, generations of humans have reasoned that leaf-cutter ants were vegetarians, consuming the cuttings in subterranean dining halls. It remained for the nineteenth-century naturalist Thomas Belt to discover and record the unexpected truth about the purpose of the leaves: “I believe the real use [the ants] make of [the leaf fragments] is as a manure, on which grows a minute species of fungus, on which they feed;—that they are, in reality, mushroom growers and eaters” (Belt 1874, 79). Belt’s description of the ants as “mushroom growers” so concisely communicated the behavior he observed that ant researchers have continued to use similar agricultural terminology ever since.

The attribution of agriculture to a nonhuman animal was paradigm-shifting and has been the subject of occasional skepticism. It has been challenged as anthropomorphic (Kermarrec, Decharme, and Febvay 1986; Rodgers 2008). It has also been challenged on the basis that it is more likely that the fungi are cultivating the ants than vice versa (Ridley, Howse, and Jackson 1996; North, Jackson, and Howse 1997; see also below). In this book, we regard agriculture as a special subset of the more general phenomenon of symbiosis. Under this view, it is appropriate to extend the aforementioned skepticism to the unique status traditionally afforded to human agriculture, which, like fungus-farming ant agriculture, is also a symbiosis and about which we might also reasonably question which of the symbionts is in control. Although it has been accelerated by intent, learning, and cultural transmission of information, human agriculture is at its core a biological phenomenon, and, as such, it is subject to the rules of Darwinian natural selection (Rindos 1984, 1989; Allaby 2010; chapter 10, this volume). All agricultural symbioses may therefore prove to share analogous elements, and those elements may in some cases be the results of convergent evolution. If so, then the comparative study of multiple agricultural symbioses may reveal common evolutionary mechanisms that influence the origins, population-genetic

and coevolutionary dynamics, and genomic architectures underlying agricultural evolution. The purpose of this chapter is to summarize what is broadly known about human agricultural evolution and to explore parallels, if any, with the evolution of fungus-farming ant agriculture.

Agriculture is a form of symbiosis in which one symbiont (the “farmer”) benefits by cultivating the other symbiont (the “crop” or, if the crop is genetically modified due to the symbiosis, the “domesticate”). Symbioses between two organisms can be broadly classified as commensalism (in which neither party benefits or incurs a cost), parasitism (in which one party benefits at the expense of the other), and mutualism (in which both parties benefit). The seeming straightforwardness of these categories is complicated by their context-dependency—that is, the nature of a symbiotic interaction can change depending on multiple factors, one of which is number of participating symbionts. As knowledge about symbioses increases, we are realizing that multipartite symbioses are common and are likely the rule, so that at some point symbiology grades into community ecology. This is proving true even for human agriculture (Fuller and Stevens 2017; chapter 10, this volume).

In this chapter, agricultural terminology will be used to refer to the full range of human cultivation and domestication of plants, animals, fungi, eukaryotic microorganisms, and bacteria. It will focus mostly on nutritional agricultural symbioses, or those that benefit the farmer by providing nutrition, but it is important to bear in mind the many agricultural symbioses that serve nonnutritional needs such as protection from other organisms (guard dogs, *Streptomyces*), production of materials (trees, bottle gourds, cotton, silkworms, alpaca), generation of physical labor (horses, oxen, camels, elephants), induction of pleasure and enlightenment (yeast, coffee, kava, tobacco, *Cannabis*), aesthetics (diverse ornamental plants, goldfish), and so on.

In the introduction to this book, *agriculture* is defined as large-scale cultivation upon which the farmers have become economically (i.e., obligately) dependent. In the first two sections below I will briefly introduce the fungus-farming ant agricultural symbiosis and summarize the differences between human and ant agriculture. In the remaining sections I will take advantage of research on the convergent features of multiple, diverse human agricultural systems to show that many of the evolutionary stages shared by human agricultural symbioses are also shared by the fungus-farming ant agricultural symbiosis. These stages include (1) preagricultural hunting-gathering and niche construction by central-place foraging social groups; (2) preagricultural incidental and, subsequently, intentional cultivation; (3) domestication; (4) the parallel rise of biodiverse agroecosystems; and (5) the postagricultural rise of highly complex societies.

The Fungus-Farming Ants

Fungus-farming, or “attine,” ants (subfamily Myrmicinae, tribe Attini, subtribe Attina) are a clade of (as of this writing) 246 species, including five fossil species, in 20 genera. They are descended from a common ancestor that lived in South America around 55–65 Mya, shortly after the end-of-Cretaceous mass-extinction event that briefly shut down photosynthesis (Janzen 1995; Kaiho et al. 2016). All attine ants are native to the New World and all obligately depend on fungus-farming for food. When departing from the maternal nest on her mating flight, a daughter queen carries a pellet of fungus from her mother’s

garden to use as the starting culture for her new garden. The conspicuous leaf-cutting ants, which make up 20% of attine ants, have received the great majority of scientific study because they are the primary pests of human agriculture in Central and South America (Cherrett 1989; Della Lucia 2011). The remaining 80% of fungus-farming ants are mostly cryptic species with small colony sizes that are rarely encountered by humans and about which, with few exceptions, we know very little (Weber 1972; Mehdiabadi and Schultz 2009; Hölldobler and Wilson 2010).

The Five Ant Agricultural Systems

As mentioned above, the definition of “agriculture” used in this book is large-scale cultivation upon which the farmers have become economically (i.e., obligately) dependent. Because all fungus-farming ants must cultivate fungi in order to survive, the term “agriculture” is used here to refer to the entire diversity of attine-ant fungus farming. However, as will be discussed below, the scale on which such cultivation takes place varies dramatically across attine-ant species. All fungus-farming ants grow fungi in the order Agaricales. Most grow fungi in the family Agaricaceae, which also includes the fungus most cultivated by humans for food, the button mushroom *Agaricus bisporus* (Miles and Chang 2004). Based largely on ant-fungal associations, ant agriculture is divided into five systems (figure 14.1): (i) lower agriculture, the ancestral agricultural system, (ii) coral-fungus agriculture, (iii) yeast agriculture, (iv) higher agriculture, and (v) leaf-cutter agriculture, a derived subset of higher agriculture (Schultz and Brady 2008; Mehdiabadi and Schultz 2009; Hölldobler and Wilson 2010; Della Lucia 2011; Branstetter et al. 2017).

In lower agriculture, 84 species of ants in 11 genera cultivate multiple species of parasol mushrooms currently assigned to the genera *Leucocoprinus*, *Leucoagaricus*, and *Lepiota* in the tribe Leucocoprineae (family Agaricaceae) (figure 14.1A). In coral-fungus agriculture, a derived clade of 29 species in the attine-ant genus *Apterostigma* are the only fungus-farming ants that cultivate fungi outside of the Agaricaceae, multiple species of the genus *Myrmecopterula* in the coral-fungus family Pterulaceae (figure 14.1B). In yeast agriculture, a derived subset of 17 species in the attine-ant genus *Cyphomyrmex* cultivates a small clade of fungal species descended from a lower fungal ancestor that, when associated with ants, grow in a unicellular “yeast-like” phase otherwise unknown in the order Agaricales (figure 14.1C). In higher agriculture, 111 ant species (59 non-leaf-cutting and 52 leaf-cutting higher-attine ants) largely cultivate a clade of multiple fungal species descended from a lower fungal ancestor that became an obligate symbiont (figure 14.1D). Unlike their lower fungal ancestors, higher-attine fungi are never found living apart from ants, they are polyploid, and they consistently produce “gongylidia,” nutritious swollen hyphal tips that are preferentially harvested and eaten by the ants. Within higher agriculture, leaf-cutter agriculture is the product of a major evolutionary transition in which a non-leaf-cutting, higher-attine ant ancestor acquired the ability to cut, process, and utilize fresh vegetation (leaves, grasses, and flowers) as the substrate for its fungus gardens (figure 14.1E) (Hölldobler and Wilson 1990; Mehdiabadi and Schultz 2009; Hölldobler and Wilson 2010; Leal-Dutra et al. 2020).

Agricultural System Boundaries

As mentioned above, garden fungi are typically transmitted vertically from one generation to the next, carried by daughter queens when founding new colonies. Genetic data indicate

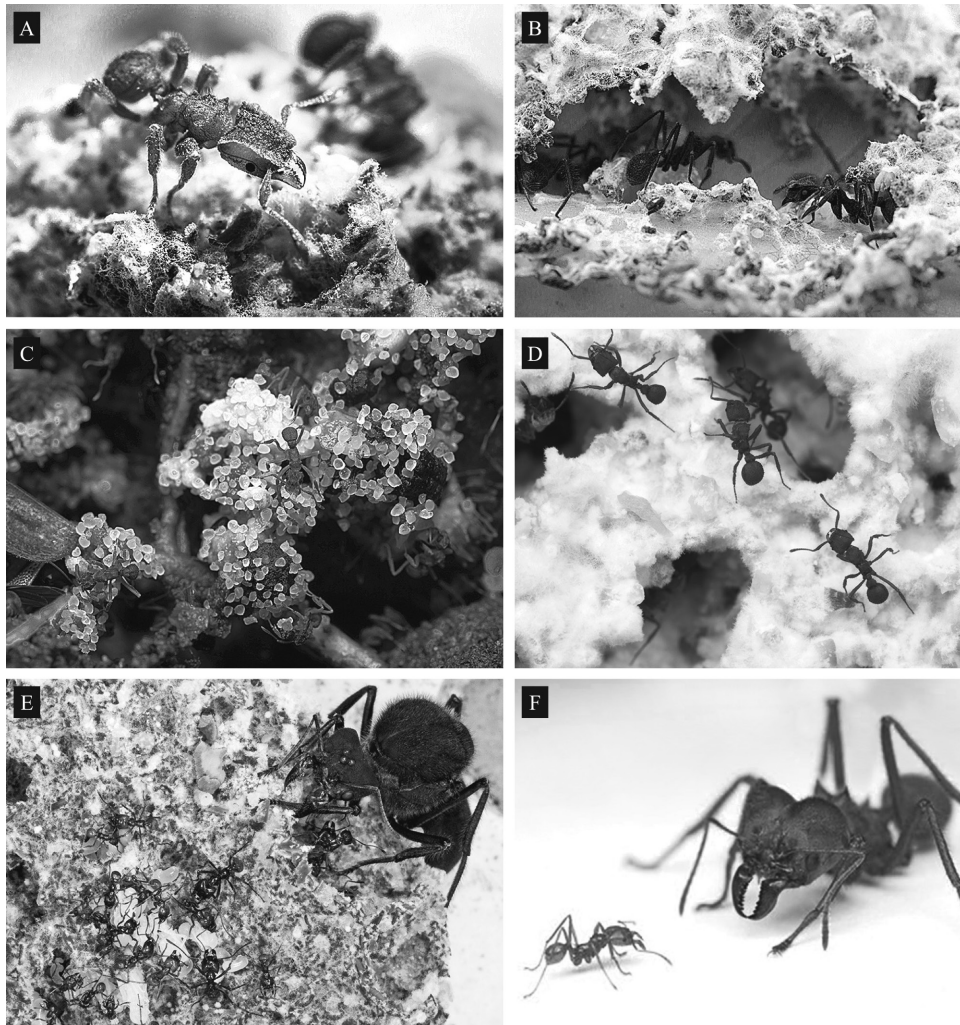


Figure 14.1

Representative ants and gardens of the five fungus-farming ant agricultural systems: (A) lower agriculture: *Mycetophylax asper*; (B) coral-fungus agriculture: *Apterostigma dentigerum*; (C) yeast agriculture: *Cyphomyrmex* sp. (*rimosus* group); (D) higher agriculture: *Trachymyrmex septentrionalis*; and (E) leaf-cutter agriculture: *Atta cephalotes*. (F) A minor worker (left) and a soldier (right), sisters from the same colony of *Atta cephalotes*, illustrating the extreme worker polymorphism of leaf-cutting ants. Reproduced with the permission of the photographers: Don Parsons (A); Alex Wild (B, C, D, F); Karolyn Darrow (E).

that horizontal transmission occurs frequently over evolutionary time periods, however, so that closely related ants may cultivate distantly related fungi and the same fungal species may be cultivated by distantly related ants. Horizontal transfer can occur when ants acquire fungal cultivars from each other (Adams 2000a; Green, Mueller, and Adams 2002; Howe, Schiøtt, and Boomsma 2018). It can also occur when ants acquire free-living conspecifics of cultivated fungi, which are known to occur in lower agriculture and yeast agriculture (Mueller, Rehner, and Schultz 1998; Vo, Mueller, and Mikheyev 2009). When cultivated by ants, fungi are propagated clonally, but when free-living, they reproduce sexually, so

at least in lower and yeast agriculture there is occasional sexual recombination due to genetic continuity between cultivated and free-living populations. Importantly, horizontal transfer events are constrained by the boundaries of the five agricultural systems, i.e., the cultivation of a fungus from one agricultural system by an ant species from a different agricultural system is rare. Violations of the boundaries defining yeast agriculture and coral-fungus agriculture are entirely unknown, i.e., all observed associations occur solely between ants and fungi within those groups. Only one lower-attine ant species is known to cultivate a higher-attine fungus (figure 14.2) (Schultz et al. 2015), whereas a few non-leaf-cutting higher-attine ant species have been found cultivating lower-attine fungi (Mueller, Rehner, and Schultz 1998; Mueller et al. 2018; Solomon et al. 2019). Finally,

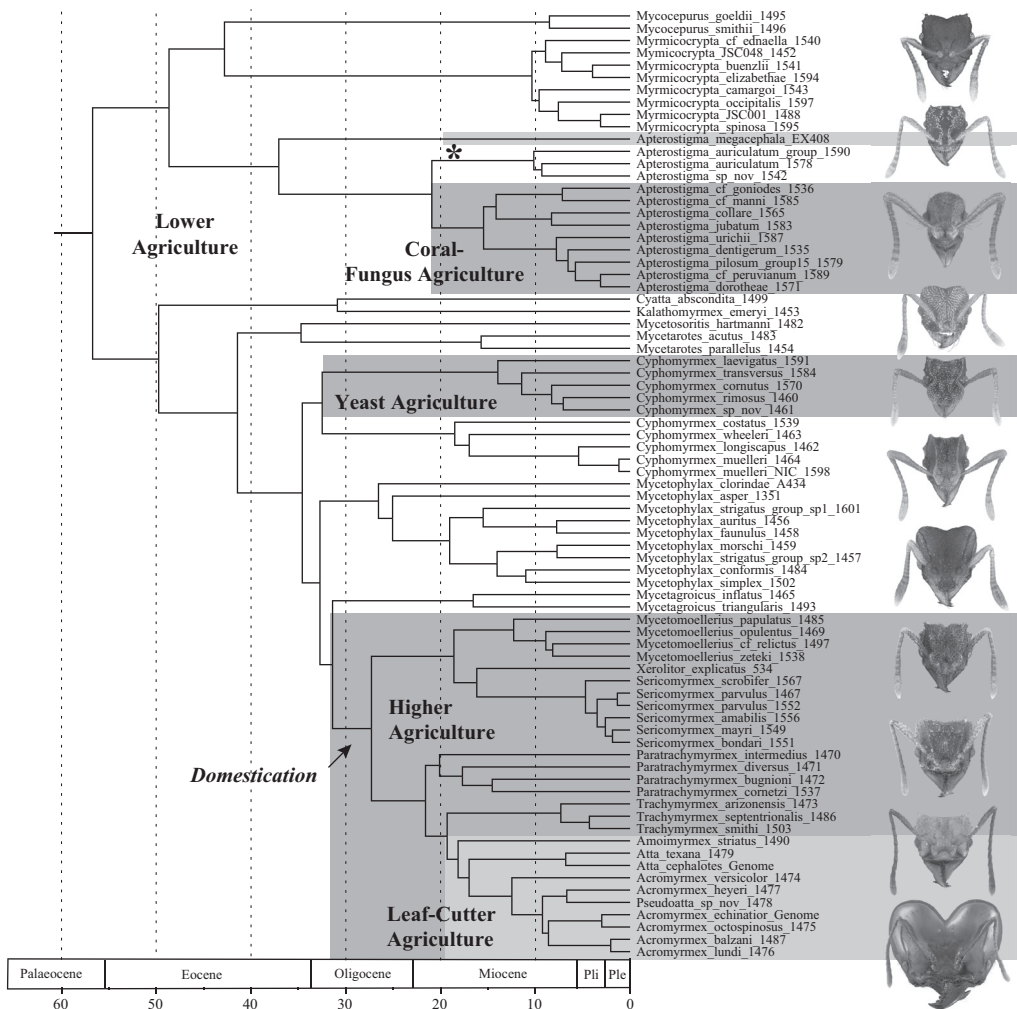


Figure 14.2 Time-dated chronogram of fungus-farming ants. Numbers at bottom indicate millions of years before present. The major agricultural systems (labeled) are characterized by the nearly monolithic fidelity of their component ants and fungi. The asterisk (*) indicates the only lower-attine ant species, *Apterostigma megacephala*, known to cultivate a higher-attine fungus. Adapted from Branstetter et al. (2017).

most leaf-cutting ants cultivate *Leucoagaricus gongylophorus*, a single species of higher-attine fungus, but a few leaf-cutting species have been found cultivating other species of higher-attine fungi (Mueller et al. 2018). The biological mechanisms constraining the agricultural-system boundaries remain unknown, but it has been suggested that they may be physiological, with ants in each agricultural system dependent on that system's fungi to supply an essential, system-specific combination of nutrients and/or micronutrients or, alternatively, that the mechanisms may be microbial-symbiotic, with each system hosting a system-specific, non-interchangeable consortium of microbes (Mueller et al. 2005; Seal and Mueller 2014; Schultz et al. 2015; but see chapters 3 and 4, this volume).

Crop Diseases and Biocontrol

Fungus-farming ant agriculture has crop diseases. Most notably, mycoparasitic ascomycete fungi in the closely related genera *Escovopsis* and *Escovopsioides* have been part of the symbiosis since its origin and have coevolved and codiversified along with the ants and their fungal cultivars (Currie et al. 1999a, 1999b, 2003; Gerardo et al. 2004; Meirelles et al. 2015b; chapter 11, this volume). The ants control them by weeding and by the application of antibiotics (i.e., “herbicides”), some of which originate in the ants, notably in their metapleural glands, antibiotic-producing glands that occur in almost all ants. In addition, most fungus-farming ants host actinomycete bacteria primarily in the genus *Pseudonocardia*, closely related to *Streptomyces*, the genus from which the majority of human antibiotics are derived. Housed in specialized crypts on the ants' integuments and nourished by glandular secretions, mutualistic *Pseudonocardia* produce antibiotics that are effective against *Escovopsis* (Currie 1999b, 2006; Li et al. 2018). The attine fungal cultivars also produce defensive antifungal chemicals (Worsley et al. 2018).

Differences between Human and Ant Agriculture

Before discussing possibly convergent traits in ant and human agriculture, it is important to point out the many differences between the two. Human agriculture is the result of diffuse coevolutionary processes that began with or even prior to the origin of *Homo sapiens* around 200 thousand years ago and domestication processes that began over ten thousand years ago. In contrast, ant agriculture is the result of processes that began as many as 65 Mya. Whereas human farmers represent a single species, fungus-farming ants comprise 246 known extant and five fossil species. Although much of human proto-agriculture (i.e., niche construction, ecosystem engineering, incidental cultivation, and early domestication, discussed below) occurred unintentionally (i.e., without conscious planning), intent has played an increasingly significant role in the evolution of human agriculture. Within the span of a single lifetime, humans observe, learn, and modify their behaviors in order to manipulate nature and obtain desired outcomes. They then transmit that information to the next generation. Fungus-farming ants have also “learned,” but changes in their hard-wired behaviors have occurred over evolutionary time spans through the trial-and-error process of natural selection. In the course of that evolution ants have become obligate farmers, unable to survive without their fungal crops. On a biological level humans are, strictly speaking, facultative farmers, individually able to return to hunting-gathering or another nonagricultural way of obtaining food. On economic and

cultural levels, however, modern humans are perhaps not quite so different from ants in their dependence on industrial-scale agriculture for maintaining current global population levels and infrastructure.

Humans cultivate thousands of species of plants, animals, fungi, and bacteria. Fungus-farming ants grow only fungi, and only fungi drawn from two subclades of two families in the order Agaricales, although they simultaneously host diverse microbes, a subset of which occur more or less consistently in their gardens (Pinto-Tomás et al. 2009; Aylward et al. 2012, 2014; Worsley et al. 2018). Ants grow their fungus gardens in climate-controlled chambers, usually underground, in a way that is similar to human greenhouse agriculture. Depending on the cultivar, humans use diverse cultivation techniques, although their highest-biomass crops are grown in open-plot, arable fields, which they may intensively prepare and to which they may add water, fertilizers, and pesticides. In contrast to human photosynthetic cultivars that derive nourishment from soil and sunlight, the heterotrophic attine fungal cultivars require living or dead organic matter for food, so, like their hunting-gathering ancestors, fungus-farming ants continue to forage outside the nest but, unlike those ancestors, they forage for food for their fungus gardens.

Hunting-Gathering, Niche Construction, and Cultivation

Humans

The end of the Younger Dryas near-glacial period around 12,000 years ago coincided with generally warmer and wetter conditions worldwide. Within a few thousand years, human agriculture had originated independently in the Near East, Mesoamerica, and South China, and by the mid-Holocene it had arisen in parallel in as many as twenty different locations (Smith 1998b; Diamond 2002; Fuller et al. 2014; Zeder 2018; chapter 10, this volume). Full-blown agriculture was not suddenly “invented” in each of these locations at a particular time in the past, however. It was preceded by hundreds of thousands of years of dietary evolution, during which humans broadened the plant-based portions of their diets, and by coevolution with plants, some of which would eventually become human domesticates (Rindos 1984; Hillman and Wollstonecroft 2014; Allaby et al. 2015). This protracted adaptive process required human genetic evolution (Mathieson et al. 2015) as well as the development of technologies such as fire and stone tools, the latter for grinding seeds and digging up roots (Hillman 1989; Hillman and Wollstonecroft 2014). Humans were cooking tubers at least 170,000 years ago (Wadley et al. 2020) and grass seeds (including the future domesticate sorghum) at least 105,000 years ago (Mercader 2009). Fifty thousand years ago, Neanderthals were cooking and consuming plants that would subsequently be domesticated by *Homo sapiens* (Henry, Brooks, and Piperno 2011, 2014).

Human Niche Construction

Paleolithic hunting-gathering humans lived in social groups and had strong impacts on their local biotic environments (Smith 2011a, 2011b; Petraglia 2017). Foraging individually or in groups, they transported desirable plants and animals back to their settlements to prepare, eat, and perhaps store for future use. As a result, without conscious planning or intent, hunting-gathering humans engineered ecological niches to which communities of plants and animals adapted (Smith 2011b, 2011a; Allaby et al. 2015; Zeder 2018). At

some point, beginning more than 45,000 years ago, this niche construction became a conscious goal and humans began to intentionally “domesticate” their environments (Roberts et al. 2017). They cleared the land around and otherwise defended favored plants such as fruit trees (Ames 1939; Rindos 1984; Anderson and Wohlgenuth 2012). They diverted water to enhance the growth of favored wild plants (Anderson and Wohlgenuth 2012). Perhaps most universally, they employed fire to alter their landscapes. They burned vegetation to encourage the growth of early-succession grasses and other food plants and to eliminate unfavored, post-fire-succession species (Smith 1998b; Anderson and Wohlgenuth 2012; Roberts et al. 2017). They also burned to drive out small game, which they hunted, and to increase small-animal hunting productivity (Bliege Bird et al. 2008). So-called “firestick agriculture” is still practiced by the Aboriginal people of Australia (Bliege Bird et al. 2008). Repeated burning coupled with deposition of organic matter over long periods of time created the nutrient-rich *terra preta* (black soils) of the Amazon (Denevan 2001).

Camp Followers

In addition to larger-scale niche construction, the immediate areas around human settlements were ideal habitats for a range of disturbance-adapted plant and animal species, which became increasingly associated with humans. Humans also incidentally imported plant species into their settlements when they returned with gathered food plants, dispersing the seeds (or other propagules) into the settlement area, particularly into refuse piles and waste middens. Camp-following species thus included a mixture of species useful, nonuseful, or even detrimental to humans. Among the useful species, future domesticates such as chenopods (e.g., quinoa), cucurbits (melons, squash, pumpkin, cucumber), sunflower, tomato, and chile pepper are thought to have arisen as camp-followers (Rindos 1984; Harlan 1992). Examples of ultimately useful camp-following animals include dogs, cats, and spiders, whereas examples of nonuseful camp-following animals include house mice, weevils, and fruit flies (Fuller and Stevens 2017; chapter 10, this volume). As will be discussed below for ants, camp-following species are not unique to humans; the cucurbit *Cucumis humifructus*, the “aardvark pumpkin,” is an obligate camp-follower of the African aardvark (Kirkbride 1993).

Interpreted retrospectively, in their daily encounters with thousands of species of plants and animals, including both camp-following and forage/prey species, preagricultural humans were unintentionally “auditioning” them as possible future domesticates, and, to avoid anthropomorphism, it should be said that those species were likewise auditioning humans as possible future domesticators. In evolutionary terms, some plants and animals were preadapted for agricultural symbioses whereas others were decidedly maladapted for that role (Diamond 1997, 2002, 2012; Smith 1998b; Zeder 2012). Interestingly, guilds of plants and animals not directly useful or sometimes even detrimental to humans have nonetheless persisted in human agroecosystems, in many cases carried along by the same initially unconscious artificial selection that humans applied to their cultivars (Harlan 1992; Spahillari et al. 1999; Howard, Archer, and Turley 2016; chapter 10, this volume). In an archaeobotanical study of a 23,000-year-old preagricultural site in Israel, Snir et al. (2015) report over 140 plant species gathered by humans, including the future domesticates wheat and barley and 13 well-known current weeds of human agriculture. In another study of three horizons spanning a 300-year period beginning 6,900 years ago and documenting

the early stages of rice domestication, Fuller et al. (2009) similarly report more than 50 species of plants, including what appear to be small-seeded future weeds of rice cultivation. One of the most widespread invasive plants on the planet, Johnsongrass, originated as a human food plant closely related to domesticated sorghum (Paterson et al. 2020).

Cultivation and Mixed Food-Acquisition Strategies

At various points in time and in different places, humans began to intentionally cultivate plants. For some vegetatively propagated plants, such as manioc (*Manihot* spp.), cultivation is no more complicated than sticking a cutting into the ground during the rainy season (Harlan 1992; chapter 10, this volume). The cultivation of yams and other root crops similarly requires little more than reburying the tuber, as is often done by hunter-gatherers as a method of storing surplus forage, or of cutting off and discarding the woody heads, which frequently resprout without further effort (Harlan 1992; chapter 10, this volume). For annual plants, rudimentary cultivation requires only the knowledge that seeds gathered in one year can sprout into plants in the following year and cultivation can consist of no more than broadcasting seeds into a suitable habitat without additional care. The Cocopa societies of the lower Colorado River, for example, broadcast panic-grass (*Panicum* sp.) seeds harvested in the previous year in muddy river bottoms recently exposed by receding flood waters, giving them no further attention until harvest (Smith 2001a).

Using such simple and non-time-consuming methods, hunter-gatherers added cultivation to their repertoires of mixed food-acquisition strategies. Tudge (1998) describes Paleolithic proto-farmers as “hobby farmers,” cultivating small plots of plants as a back-up while continuing to hunt for animals and gather wild plants for food. He points out the ecological advantage of nonreliance on a single food source, especially with regard to local overhunting. Indeed, the historical record suggests that mixed food-acquisition strategies represent stable states in a complex continuum that do not necessarily replace pure hunting-gathering or inevitably lead to domestication and agriculture (Harris 1989; Smith 1998a, 1998b, 2001a, 2001b; chapter 10, this volume).

Ants

Niche Construction

The common ancestor of all ants was a hunter-gatherer, taking prey as food primarily for the colony’s larvae and taking plant carbohydrates as food primarily for the adults. It lived in eusocial family groups consisting of the mother queen and her nonreproductive (worker) daughters, cooperatively rearing the next generation(s) of workers as well as reproductive (virgin queen) daughters/sisters and reproductive sons/brothers. (There are no worker males in ant colonies.) The familial colony occupied a semipermanent nest and, as a central-place forager, influenced the ecologies of the organisms living within its territory. This strategy, which originated ~103–124 Mya (Borowiec et al. 2017), was overwhelmingly successful, resulting in the estimated >25,000 extant species of ants (Ward 2014). Today, ants are keystone species in nearly every ecosystem on the planet and are universally recognized as premier niche constructors/ecosystem engineers (Folgarait 1998; Schultz and McGlynn 2000; Jouquet et al. 2006; Vandermeer and Perfecto 2007; Sanders and Veen 2011; Meyer et al. 2013; chapter 8, this volume). Their core hunting-gathering life-history strategy has repeatedly given rise to increasingly complex, mixed food-acquisition strategies in which

ants supplement hunting-gathering with, for example, honeydew “milked” from aphids, lipid-rich elaiosomes (food rewards) attached to ant-dispersed seeds, or carbohydrate and protein rewards supplied by plants that ants protect from herbivory (Beattie 1985; Hölldobler and Wilson 1990; Jolivet 1996; Rico-Gray and Oliveira 2007; chapter 8, this volume). Other ant lineages became specialized carnivores, in some cases adapted to very specific prey items such as spider eggs, polyxenid millipedes, termites, or other ants. The army ants have become both carnivorous and nomadic, managing arthropod prey populations across territories equivalent to those occupied by medium-to-large-sized vertebrate predators (Tobin 1994; Gotwald 1995; Brown 2000).

Camp-Following Fungi

Around 55–65 Mya in South America, the core hunting-gathering life-history strategy gave rise to fungus-farming ant agriculture. Although all extant attine ants obligately grow fungi for food, their ancestors almost certainly passed through a period of facultative fungivory—that is, they were hunter-gatherers with a diet that sometimes included fungi. Although previously thought to be relatively rare in ants (Tobin 1994), multiple new examples of fungivory have been discovered in the past two decades (Mueller et al. 2001; Witte and Maschwitz 2008; Blatrix et al. 2012; Beeren, Mair, and Witte 2014; Mayer et al. 2018; chapter 8, this volume). Based on the phylogenetics, behavior, and ecology of extant species, the ancestral attine ant lived and foraged in the leaf litter, where, like its modern descendants, it frequently encountered free-living leucocoprineaceous fungi (Vellinga 2004; Schultz et al. 2005; Vo, Mueller, and Mikheyev 2009). If the ancestral ant fed on them, the fungi could have benefited by being dispersed. All ants strain food through their infrabuccal pockets, a specialized organ in the mouth that filters out solid particles, including viable fungal mycelia and spores. The filtrate accumulates into “infrabuccal pellets,” which ants expel one or more times a day in colony refuse piles or in other locations inside or in the vicinity of the nest (Bailey 1920; Letourneau 1998; Mueller et al. 2001; Little et al. 2003). Some fungi are known to be dispersed in this way, including other ant-associated fungi (Bailey 1920; Wheeler and Bailey 1920; Mueller et al. 2001; Blatrix et al. 2013; Mayer et al. 2018).

Lower-attine fungi occasionally produce structures that appear to be homologous with gongylidia, the previously mentioned nutritious swollen hyphal tips that are consistently produced in domesticated higher-attine fungi (Möller 1893; Urich 1895; Weber 1972, 1979; Masiulionis et al. 2014). Ancestral leucocoprineaceous fungi may have recruited ants as dispersal agents by providing gongylidia as food rewards (Mueller et al. 2001; Schultz et al. 2005), a strategy evolutionarily convergent with the recruitment of vertebrates (including humans) by plants using fruits and the recruitment of ants by plants using elaiosomes (nutritious seed appendages) (Lengyel et al. 2010; chapter 8, this volume). If leucocoprineaceous fungi are camp followers of leaf-litter-dwelling ants, then we might expect to find them more generally associated with colonies of extant leaf-litter-dwelling, non-fungus-growing close relatives of fungus-farming ants. Of note is that unidentified fungi have been reported to grow consistently on ant-constructed walls of accumulated detritus in the nests of species in the genera *Wasmannia* and *Blepharidatta*, both closely related to fungus-farming ants (Wheeler 1901; Diniz, Brandão, and Yamamoto 1998; Brandao et al. 2001; Rabeling, Verhaag, and Mueller 2006; Schultz and J. Sosa-Calvo,

personal observation). Identifying these fungi will provide a first test of the camp-follower hypothesis for the origin of the fungus-farming ant agricultural symbiosis.

Domestication

Humans

In the introduction to this book, we define *domestication* as the genetic modification of one species by another in ways that benefit the modifying species (the farmer) but that would have reduced the fitness of the modified species (the domesticate) in its original niche. Note that this definition is neutral about genetic modifications in the farmer and that it is also neutral about the current fitness of the domesticate relative to its former fitness in the wild. It is possible that in the agricultural niche the domesticate has become more fit than, as equally fit as, or less fit than its undomesticated progenitor. Although they likely could not survive without humans, domesticated rice, wheat, and maize have become some of the most abundant plants on Earth (Collins 2015), and the worldwide population of cattle numbers over 1.4 billion (FAOSTAT 2020).

Domesticated plants possess suites of morphological traits that set them apart from their wild progenitors, some controlled by single loci, others multigenically controlled and producible via more than one developmental-genetic pathway. Depending on the plant (grass, legume, amaranth, cucurbit, and so on), this domestication syndrome includes increased seed size, decreased seed coat thickness, synchronous seed ripening, seed indehiscence, nondormant seeds, increased apical position of seeds on stalks, reduced stalk branching, and seed pod/spike/ear/panicle indehiscence (Smith 1998b; Bellwood 2005; Weiss, Kislev, and Hartmann 2006; Fuller 2007; chapter 10, this volume). Domestication traits in animals vary more widely across species, but include reduction in brain size (nearly universal), reduction in body size (common), reduction in female body size (common for managed herd animals), and reduction in tooth size (pigs) (Smith 1998b; Zeder 2012). Early evolving domestication traits are the products of unintentional artificial selection. For example, if preagricultural human cultivators harvested spikes from grasses when seeds were ripe, they would have missed seeds or spikes that had already fallen off (dehisced), and, if they sowed some of the harvested seeds the next year, those seeds would contain a higher frequency of indehiscent individuals. Repeated from year to year, such harvesting and sowing would result in an increasing frequency of the indehiscent trait over time, which is in fact what is observed in some well-preserved archaeological records.

Domestication is speciation. In the simplest case, what was formerly one population was subdivided into two populations, one of which, the wild progenitor, remained subject to the ancestral natural-selection regime whereas the other, cultivated population, was subjected to a human-mediated artificial-selection regime. Over time, the two populations diverged and a phenotypically and genetically distinct domesticated population was created. Whether one regards the domesticated population as a species, subspecies, race, variety, and so on, depends largely on one's species concept, but observed levels of genetic divergence separating human plant domesticates from their wild progenitors are typical of species-level differences (Dempewolf et al. 2012).

It has long been assumed that a high level of reproductive isolation (i.e., absence of gene flow) between the cultivar and its wild progenitor, coupled with strong artificial selection, were required—at least initially—to drive the fixation of domestication traits. In this intuitively simple scenario, a relatively small number of individual proto-domesticates was reproductively isolated from the wild population and interbred over multiple generations. Reproductive isolation could have been achieved by, for example, transporting the captive population beyond its ancestral range, cultivating self-pollinating species, or, in the case of an animal species, confining it in livestock pens. Undesirable phenotypes were (perhaps unintentionally) culled and desirable phenotypes retained until desirable traits became fixed in the domesticated population, a process that was thought to have proceeded relatively rapidly—that is, over the course of a few decades to a few hundred years. One problem with this scenario is that it entails a genetic bottleneck: depending on its size, genetic variability in the initial captive population would have been significantly reduced relative to that in the wild population. As a result, the population would have suffered from all of the problems associated with inbreeding depression (Barton and Charlesworth 1998), which would have affected its ability to adaptively respond to artificial selection for domestication traits and to natural selection for traits not directly associated with domestication, as in the case of transport by humans to a new and different environment.

At the other end of the gene-flow spectrum, the observed overlap in geographic distributions of some domesticates with their wild progenitors suggests that domestication may have occurred wholly or partly in sympatry. In this scenario, cultivars were subjected to artificial selection by humans while remaining in genetic contact with their progenitor populations, which, in contrast to the genetic-bottleneck scenario described above, would result in a domesticate with all or most of the background genetic variability present in the progenitor population. The problem with this scenario, which is shared with all sympatric-speciation scenarios (Bolnick and Fitzpatrick 2007), is that it requires genetic divergence to take place in the presence of unobstructed gene flow between the natural-selection and artificial-selection populations. Even if artificial selection on the captive population was strong, if the captive population size was small compared with the wild population size, then introgression from the parent population would be expected to have repeatedly diluted divergence, especially at domestication-trait loci where alternative alleles were favored in the captive versus the wild populations.

As in most biological systems, the population-level processes underlying domestication were far more complex than these contrasting allopatry/sympatry domestication scenarios in that they incorporated elements of both. Although the evolutionary histories of human domesticates differ in detail, the emerging convergent pattern, based on archaeological and archaeogenomic data, is that in most cases domestication took place over protracted time periods measured in many hundreds or in thousands of years—thus, for example >1,000 years for wheat and barley (Tanno and Willcox 2006), >4,000 years for maize (geographically divergent domestication lineages) (Kistler et al. 2018), ~3,000 years for rice (two Asian domestications) (Fuller 2007; Sweeney and McCouch 2007; Fuller et al. 2009; McCouch et al. 2012; chapter 10, this volume), and 1,000–2,000 years for pearl millet (Manning et al. 2011). In addition to long time spans, domestication also took place over large geographic distances and across a fragmented population-genetic landscape. At

any given point in time, multiple differently sized artificial-selection populations were in greater or lesser degrees of genetic contact with, or completely isolated from, each other and from multiple differently sized natural-selection populations. Over the same time spans humans transported domesticates to new localities, traded seeds, and exerted artificial selection, which, on average, was weakly applied across many loci (McCouch et al. 2012; Allaby, Smith, and Kistler 2018; Burgarella et al. 2018; Kistler et al. 2018). Although localized genetic bottlenecks probably did repeatedly occur in this temporally and spatially fragmented landscape, there is little evidence that bottlenecks played a significant role in the long-term evolution of most domesticates; instead, most domesticated crops have retained levels of genetic diversity comparable to those present in their wild progenitors (Allaby, Fuller, and Brown 2008; Purugganan and Fuller 2009; Allaby 2010; McCouch et al. 2012; Allaby, Ware, and Kistler 2019). This pattern holds even for self-pollinating crops such as wheat and barley, which in theory could have been domesticated in time spans measured in decades rather than centuries or millennia (Hillman and Davies 1990; Honne and Heun 2009). There is evidence that, in some domesticates (e.g., rice, the common bean), artificial selection has increased the frequency of domestication alleles in wild populations; in other words, rather than wild populations diluting the genetic profiles of artificial-selection populations, human-mediated artificial selection relentlessly (even if weakly) applied over thousands of years has instead altered the genetic profiles of wild populations (Kaplan 1981; Papa et al. 2005; McCouch et al. 2012).

In general, the evolutionary histories of domesticated animals conform to the same general pattern as that of plants, including lack of bottlenecks, large overall levels of gene flow between artificial-selection and natural-selection populations, and long histories of population fragmentation and intermittent contact through time. This has been complicated by frequent deliberate outcrossing with wild populations in more than a few species (Zeder 2012; Marshall et al. 2014), which has proven advantageous for maintaining desirable traits, and by multiple species-specific pathways to animal domestication (Zeder 2012).

Ants

As discussed above, early humans coevolved with plants and animals in human-constructed niches for many tens of thousands of years prior to the advent of agriculture. This resulted in genetic change in the various species, including humans. It is probable that lower-attine ants likewise diffusely coevolved with leucocoprineaceous fungi, albeit over far longer time spans measured in tens of millions of years, because (1) a comparison of ant and fungal phylogenies suggests that fungus-farming ants co-diversified with their fungal cultivars (figure 14.2) and (2) the previously discussed utilization of ants as dispersal agents by leucocoprineaceous fungi also suggests a prolonged coevolutionary interaction. With regard to our definition of domestication, the scant available evidence suggests that lower-attine fungi are undomesticated, attine coral fungi may be domesticated, and attine yeast fungi are undomesticated (but see below). In contrast, multiple lines of evidence unequivocally indicate that the higher-attine fungi are domesticated.

Lower-Attine Fungal Cultivars

The lower-attine fungal cultivars, consisting of dozens of species in the Leucocoprineae, are thought to be undomesticated and capable of living freely outside the ant-fungus sym-

biosis without any reduction in fitness. As previously mentioned, although they are typically vertically transmitted across ant generations and clonally propagated when associated with ants, cultivated lower-attine fungal populations are thought to be genetically continuous with free-living, sexually reproducing conspecific populations. This is because, over evolutionary time spans measured in, for example, hundreds of thousands of ant-colony generations (Mehdiabadi et al. 2012), lower-attine fungal cultivars frequently “escape” from the symbiosis into the wild, where they sexually reproduce and are frequently recruited from the wild by ant workers or by foundress queens that have lost their resident cultivars. Data in support of these assumptions include (1) the collection of free-living fungi that are, based on internal transcribed spacer (ITS) “DNA-barcoding” sequences, conspecific with ant-cultivated lower-attine fungi (Mueller, Rehner, and Schultz 1998; Vo, Mueller, and Mikheyev 2009) and (2) the fungal phylogeny, which indicates that lower-attine fungi belong to two phylogenetically disjunct clades that also contain fungi not known to be cultivated by ants (Schultz et al. 2015). Although the lower-attine leucocoprineaceous fungi are undomesticated, it is plausible that, due to millions of years of diffuse coevolution, at least some species are genetically modified to take advantage of their frequent associations with ants. The only available lower-attine fungal genome indicates that the fungal cultivar of the ant *Cyphomyrmex costatus* has more carbohydrate-degrading enzyme genes than three other fungal species in the order Agaricales for which there are comparable data. This genetic difference is consistent with the role of the fungal cultivar in degrading plant material (insect frass, flower parts) gathered by the ants for their fungus garden (Nygaard et al. 2016). Based on available evidence, the lower-attine cultivars might currently best be regarded as highly but diffusely coevolved attine-ant commensals, likely possessing numerous genetic modifications for prolonged associations with ants during which they are protected, increased in biomass, and dispersed, but not at the expense of being able to live independently from ants when necessary or advantageous.

Attine Coral-Fungus Cultivars

Genomic data for the attine coral-fungus cultivars are currently unavailable, but, based on reasonably good recent sampling, many close relatives but no free-living conspecifics of the coral-fungus cultivars are known (Dentinger et al. 2009; Leal-Dutra et al. 2020), suggesting that they may be domesticated. Although also in the order Agaricales, the pterulaceous cultivars (family Pterulaceae) are not closely related to the leucocoprineaceous cultivars (family Agaricaceae) grown by all other attine ants (figure 14.2), so the origin of coral-fungus agriculture necessarily involved an evolutionary leap in which an ancestral *Apterostigma* ant species transferred its fungus-growing behavioral repertoire to a species in a previously uncultivated fungal family. Although the application of previously acquired background knowledge to the cultivation of new, previously uncultivated species is a common theme in human agriculture, this is the only known example from ant agriculture.

Attine Yeast Cultivars

As mentioned previously, based on the occurrence of free-living conspecifics (Mueller, Rehner, and Schultz 1998; Vo, Mueller, and Mikheyev 2009), the attine yeast fungi grow in typical mycelial form while living in the leaf litter apart from ants but in a unicellular yeast-like form when associated with ants (figure 14.1C). Genetic continuity between cultivated and wild populations suggests that the yeast cultivars are equivalently fit whether

living with ants or growing in the wild (i.e., that they are undomesticated), but the occurrence of yeast-phase growth suggests genetic modification. Alternatively, yeast-phase growth could be induced entirely by the ants and the yeast cultivars could be genetically unmodified. As previously pointed out, however, unicellular yeast-phase growth is otherwise unknown in the order Agaricales, and the *Cyphomyrmex* yeast-cultivating ants are never found associated with—and are not known to be able to induce yeast-phase growth in—leucocoprineaceous species other than the yeast cultivars. Both the yeast cultivars and the ants that grow them belong to compact clades descended from a lower fungal and a lower-attine ant ancestor, respectively (figure 14.2) (Schultz and Brady 2008; Branstetter et al. 2017); this is consistent with ancestral species-to-species coevolution followed by an obligate association between fungal and ant descendants. Of note is that ambrosia-beetle-associated fungi in the phylum Ascomycota are also dimorphic (or “pleomorphic”), expressing yeast-like growth when growing in beetle mycangia or when actively tended by beetles but growing as mycelium in the absence of beetles (Batra and Michie 1963; Beaver 1989; Blackwell 2017; chapter 7, this volume). It thus remains possible that such fungi may be facultatively dimorphic, expressing one of two alternate phenotypes depending on their current environment. If so, this challenges our definition of domestication because it suggests a genetically modified cultivar that is equivalently fit in artificial-selection and natural-selection environments.

Higher-Attine Fungal Cultivars

The clearest case of domestication in attine-ant agriculture is the origin of the higher-attine fungi, which are never found apart from their ant farmers and which are genetically modified for life with ants. Unlike lower-attine fungi, higher-attine fungi are polyploid, they consistently produce gongylidia, and they express significantly different enzyme profiles, most associated with the degradation of fresh plant material. Higher-attine fungi sometimes produce sporocarps (mushrooms), such as on the surfaces of abandoned ant nests, but it is not known whether the spores are viable and therefore whether sexual recombination occurs (Kooij et al. 2015). When the ancestral higher-attine fungus was domesticated, a metabolic rate transition occurred. Unlike lower-attine colonies, which have metabolic rates lower than hunter-gatherer ant colonies, higher-attine ant colonies have significantly higher metabolic rates than hunter-gatherer colonies, even though the ratio of ant to fungal biomass remains the same as in lower-attine colonies. This difference may be due to the higher-energy chemical work performed by the fungus in order to produce a higher-value nutritional resource and/or to the requirement of the fungus to process a greater amount of substrate biomass with a greater amount of waste (Shik et al. 2014).

As mentioned, higher-attine fungi are polyploid (Kooij et al. 2015). This suggests that the putative benefits of polyploidy in human domesticates may also obtain in the domesticated higher-attine fungi, especially in *Leucoagaricus gongylophorus*, in which genetic variation significantly exceeds diploid levels, including (1) genome buffering (i.e., mitigation against the effects of deleterious mutant alleles), (2) increased allelic diversity and heterozygosity, and (3) generation of novel phenotypic variation (Udall and Wendel 2006). Kooij et al. (2015) suggest that, as in many human domesticates, such mechanisms may be responsible for the higher productivity of the higher-attine fungi, including their ability to degrade secondary plant compounds in the fresh vegetation substrates on which they grow.

Although gongylidia or gongylidia-like structures occur sporadically in lower-attine fungi (Masiulionis et al. 2014), these swollen hyphal tips are consistently expressed in higher-attine fungi and are preferentially harvested by the ants for food. Beyond nutrition, gongylidia serve to concentrate fungal enzymes (pectinases, proteases, and laccases) in the guts of garden-tending ants, which distribute them via their fecal droplets (Martin and Martin 1970; Schiøtt et al. 2010; De Fine Licht et al. 2014; Kooij et al. 2014). It can thus be said that the fungus uses the ants as vectors to transfer its digestive enzymes from the most luxuriant, gongylidia-rich middle layer of the garden to the most recently added and inoculated substrate in the upper layer of the garden. This allows for the rapid degradation of pectin, which makes starch and proteins accessible, and for the detoxification of toxic plant phenolic compounds (De Fine Licht et al. 2010; Schiøtt et al. 2010; Moller et al. 2011; Aylward et al. 2013; Grell et al. 2013; Kooij et al. 2014; Somera et al. 2015; Worsley et al. 2018). Although the *Leucoagaricus gongylophorus* cultivar genome encodes 145 lignocellulase enzymes (Aylward et al. 2013), these are generally expressed only in the older and least productive lower layers of the gardens, which are constantly being dismantled and discarded in the waste dumps. Higher-attine agriculture—particularly leaf-cutter agriculture—thus depends on considerable waste of substrate. It takes advantage of the increased levels of protein in fresh plant material by foregoing the digestion of recalcitrant polysaccharides and failing to utilize less accessible proteins (De Fine Licht et al. 2010, 2014; Schiøtt et al. 2010; Moller et al. 2011; Grell et al. 2013; Kooij et al. 2014; Worsley et al. 2018).

Climate Change

The desertification of the Sahara ~5000 years ago (Hély et al. 2009) and the resulting decreased access to free-living populations of food plants are hypothesized to have triggered the domestication of African rice, pearl millet, and possibly yams, the latter descended from a wet-forest-dwelling species (McKey et al. 2012; Burgarella et al. 2018; Cubry et al. 2018; Scarcelli et al. 2019). Climate change toward drier conditions has also been suggested as a possible cause of the domestication of higher-attine fungi and the origin of higher-attine agriculture. Higher-attine ants likely arose around 30 Mya (figure 14.2) in a seasonally dry habitat in South America following the Terminal Eocene Event, a period of global cooling that began 35 Mya, when drier habitats, including grasslands, greatly expanded globally (Prothero 1994; Graham 2011). As hypothesized by Branstetter et al. (2017), as fungus-farming ants dispersed out of wet forests and adapted to expanding grasslands and other seasonally dry habitats, they would have carried their wet-forest-adapted lower-attine fungal cultivars along with them into a geographic mosaic of populations in which gene flow between fungal cultivars and their wet-forest-dwelling wild progenitor populations would vary from strong to sporadic to nonexistent. Albeit occurring over a presumably vastly longer time span, these conditions are comparable to those described previously for the origins of many human domesticates: protracted periods of varying gene flow across a spatial and temporal mosaic of natural-selection and artificial-selection populations, the latter under generally weak but persistent selection across a large number of loci, ultimately producing new species dependent upon the farmers for survival. Some human domesticates can still outcross with their wild progenitors in spite of significant reproductive isolation and depressed hybrid fitness (Dempewolf et al. 2012; McKey

et al. 2012), but after tens of millions of years, higher-attine fungi have become obligate symbionts lacking any genetic connection with extant free-living progenitors, if such still exist. Perhaps not surprisingly, higher-attine fungi have also continued to speciate, but because species appear to be separated by differing ploidy levels (Kooij et al. 2015), it is possible that subsequent evolution in this group has been driven at least in some cases by polyploidization events.

Who Domesticated Whom?

Over hundreds of thousands of years, humans evolved to accommodate an expanding diet (Mathieson et al. 2015). Over the past ten thousand years, humans have continued to evolve in order to accommodate diets containing lactose and wheat, to resist diseases acquired from their animal domesticates, and to detect and/or tolerate a variety of plant secondary compounds (Jackson 1991; Johns 1996; Diamond 1997; chapter 12, this volume). According to our definition, none of these modifications qualify as the reciprocal domestication of humans by their domesticates. In contrast, it can credibly be argued that, rather than the ants domesticating the fungi, it was the fungi that initially domesticated the fungus-farming ants. Perhaps most persuasively, all attine ants are obligate fungus farmers that cannot survive without their fungi, whereas at least the lower-attine and yeast cultivars are able to survive without the ants. More like domesticates than domesticators, all fungus-farming ants have lost the ability to synthesize the amino acid arginine, which they obtain from their cultivated fungi, and they express high levels of a modified chitinase in their labial gland fluids in order to digest fungal chitin. Based on analyses of seven attine-ant genomes, fungus-farming ants have experienced rates of structural gene rearrangement (i.e., loss of synteny) far more rapid than in any animal group of comparable age. Early in fungus-farming ant evolution many gene families contracted. In the ancestor of the leaf-cutting ant genus *Atta*, however, major gene families expanded, producing 129 novel genes with no clear homologies to known genes (Nygaard et al. 2016).

Agriculture

Humans

In this book we define *agriculture* as large-scale cultivation upon which the farmers have become economically (i.e., obligately) dependent. Although the definition does not require the cultivated species to be domesticated, domestication preceded agriculture in the histories of all or most human agricultural origins (Rindos et al. 1980; Fuller et al. 2014; chapter 10, this volume). The rise of agriculture allowed Holocene human societies to accumulate surplus food supplies, which in turn gave rise, in a positive feedback loop, to increasing population growth and expanding settlements (Smith 1998b; Tudge 1998; Fuller et al. 2014). This then led to increasingly complex social systems, increasingly refined division of labor (chapter 2, this volume), and, ultimately, the emergence of world civilizations. The economists Gowdy and Krall (2014, 179) argue that postagricultural, global human society is the result of a major evolutionary transition that is rare in nature, which they call “ultrasociality”; it is characterized by “superorganisms exhibiting an unparalleled degree of division of labor and an economic organization centered around surplus production.”

Relevant to the subject of this book, the other examples they cite include fungus-farming termites and fungus-farming ants. The origins of human agriculture are consistently associated with major landscape modifications such as slash-and-burn clearing of forests (Neolithic Europe, New Guinea, China, Mesoamerica), excavation of irrigation ditches (northeastern Peru, New Guinea), raised fields, and anthropogenic “black soils” (Amazonia and eastern South America) (Denevan 2001; Fuller et al. 2014; McKey and Rostain 2014; Lombardo et al. 2020). With regard to nutrition, early agriculture was not necessarily superior to hunting-gathering, cultivation, and mixed food-acquisition strategies. Although human biological responses to agriculture varied considerably across agricultural origins (Pinhasi and Stock 2011; chapter 12, this volume), in at least some cases early agriculturalists were malnourished compared to hunter-gatherers due to overdependence on a limited range of foods, especially carbohydrates. For this reason and because of the accelerated population expansion that accompanied agriculture, early agriculturalists also suffered from increased exposure to pathogens, including newly evolved pathogens and pathogens vectored by their managed/domesticated animals (Larsen 1995; Mummert et al. 2011; Cordain, Hickey, and Kim 2012; Berbesque et al. 2014; Dyble et al. 2019; Larsen et al. 2019; chapter 2, this volume).

Agroecosystems

With the exception of microorganisms grown axenically in the lab, agriculture does not consist only of a farmer and a cultivar; rather, it is a multipartite symbiosis. Agricultural ecosystems provide reliable niches for diseases of farmers, for diseases of cultivars, for diseases of diseases, for pests of stored products, and for “weeds” (i.e., for organisms able to coevolve with and adapt to agroecosystems in order to directly or indirectly exploit the resources supplied by the farmers to their cultivars such as cleared land, tilled soils, fertilizers, and water) (Fuller and Stevens 2017). In many cases weeds have been unintentionally artificially selected by farmers to mimic their domesticates (Harlan 1992; Spahillari et al. 1999; Senda, Hiraoka, and Tominaga 2006; Thomas, Archer, and Turley 2011; Howard, Archer, and Turley 2016; Fuller and Stevens 2017; chapter 10, this volume). In some systems (e.g., maize, sorghum, rye, squash) even the ancestral progenitor may function as a weed (Wilkes 1977; Wilson 1990; Harlan 1992). Humans have developed many methods for excluding or controlling unwanted agricultural symbionts, including, in low-technology agriculture, the use of fire, mixed cropping, the cultivation of plant and animal biocontrol agents, and weeding (Denevan 2001; Anderson and Wohlgemuth 2012), and, in modern intensive agriculture, the use of herbicides, pesticides, biocontrol agents, and genetic engineering.

Ants

Around 55–65 Mya, an ancestral hunting-gathering ant became physiologically dependent on cultivating undomesticated leucocoprineaceous fungi and gave rise to lower-attine agriculture. In so doing, it was able to escape competition with other hunting-gathering ants by becoming fungivorous. Instead of competing with other litter-dwelling ants for arthropod prey and plant carbohydrates, it competed instead with microbes for bits of organic detritus, including insect frass, seeds, flower parts, wood particles, and dead insects (Weber 1972; Murakami and Higashi 1997; Leal and Oliveira 2000; Ješovnik,

Chaul, and Schultz 2018; Ronque, Feitosa, and Oliveira 2019). In terms of productivity, lower-attine ant agriculture is not superior to hunting-gathering. Lower-attine ants generate similar yields of ant biomass per unit foraging effort as equivalently sized colonies of non-attine hunting-gathering ants (Turner 1974; Quinlan and Cherrett 1979; Bass and Cherrett 1995). Most notably, by directly measuring whole-colony (ants plus fungus) metabolism (i.e., mass-specific CO₂ emission rate), Shik et al. (2014) show that, relative to hunting-gathering ants, lower-attine fungus-farming ant colonies have significantly lower mass-specific metabolic rates and that a significant part of the colony biomass is shifted into fungal (rather than ant) tissue. They hypothesize that transferring biomass from ants into a fungal mutualist may generate energetic storage advantages, paralleling a frequently-cited benefit of early human agriculture (Hayden 1995; Diamond 1997; Piperno and Pearsall 1998).

Around 30 Mya, following the Terminal Eocene Event, a lower-attine ant ancestor domesticated a lower-attine fungus and gave rise to higher-attine agriculture. As mentioned above, this domestication event may have been driven by the increase in grasslands and other seasonally dry habitats in South America, which separated fungal cultivars from continuous genetic contact with their free-living, wet-forest-dwelling conspecifics. Although extant non-leaf-cutting, higher-attine ants forage for substrates similar to those taken by lower-attine ants, some species additionally cut tender shoots, leaflets, and flowers (Leal and Oliveira 2000; Mehdiabadi and Schultz 2009; Ješovnik, Chaul, and Schultz 2018; Ronque, Feitosa, and Oliveira 2019). Unlike lower-attine ants, the colony-level metabolisms of higher-attine ants are higher than those of hunting-gathering ants (Shik et al. 2014). However, the colony sizes (around 3,000 workers maximum) and levels of social complexity of non-leaf-cutting higher-attine ants overlap with those of some derived species of lower-attine ants (Mehdiabadi and Schultz 2009).

Around 20 Mya, a non-leaf-cutting higher-attine ant ancestor acquired the ability to cut and process living plant material as the primary fungus-garden substrate. In so doing, it ceased to compete with (mostly microbial) detritivores that feed on the same substrates as lower-attine fungi and instead began to compete with vertebrate and invertebrate herbivores. In addition to the key adaptation of utilizing fresh vegetation, extant leaf-cutting ants in the genera *Amoimyrmex*, *Acromyrmex*, and *Atta* differ from non-leaf-cutting higher-attine ants in their vastly larger colony sizes and polymorphic worker castes (Mehdiabadi and Schultz 2009). In these traits *Amoimyrmex* and *Acromyrmex* species may be regarded as “transitional” or less derived than *Atta* species. For example, *Amoimyrmex* colonies contain approximately 5,000 individuals and *Acromyrmex* colony sizes approach a maximum of ~270,000 individuals, whereas standing populations of *Atta* colonies can reach 8 million individuals (Fowler et al. 1986; Wetterer 1995; Wetterer, Gruner, and Lopez 1998; Ferguson-Gow et al. 2014; M. P. Cristiano, personal communication). Likewise, the degree of physical caste differentiation in *Amoimyrmex* and *Acromyrmex* is less extreme than in *Atta* (Wetterer 1999; Cristiano et al. 2020). Following nest founding, an *Amoimyrmex* or *Acromyrmex* queen, like almost all other foundress ant queens, must forage for substrate until her first brood of adult worker ants emerges to take over that task, a period of 40–60 days during which she is exposed to very high risks of predation and disease. Nest-founding *Atta* queens, in contrast, found their nests “claustrally” by excavating a chamber in the soil, sealing off the entrance tunnel, and nourishing both the

fungus garden and the first brood of workers with trophic (nonviable) eggs generated by catabolized stored fat and wing muscle tissue (figure 14.1E) (Autuori 1956; Hölldobler and Wilson 2010).

Atta leaf-cutting ants are among the most highly eusocial of all organisms (Hölldobler and Wilson 2009, 2010) and are the obvious exemplars for comparisons with modern human industrial-scale agriculture. Leaf-cutter colonies, which Carroll and Janzen (1973) call “subdivided cows,” are the ecological equivalents of large herbivorous mammals in terms of collective biomass, lifespan, and plant material harvested (Herz, Beyschlag, and Hölldobler 2007). Peregrine (chapter 2, this volume) concludes that increasingly refined division of labor is one of a number of important components of agriculture, and this is certainly the case for *Atta*. Edward O. Wilson (1980) identified 29 discrete tasks performed by *Atta* workers, the majority involved in the assembly-line processing of fresh vegetation and performed by workers of specific size categories. *Atta* workers are highly polymorphic, spanning a broad range of sizes in which the smallest, the gardener-nurses, weigh 200 times less than the largest, the defensive soldiers (figure 14.1F). Unlike all other attine ants, *Amoimyrmex*, *Acromyrmex*, and *Atta* leaf-cutting ants are multiply mated: during their mating flights queens mate with an average of three males, storing and nourishing their sperm for life (Fjerdingstad, Boomsma, and Thorén 1998; Boomsma, Fjerdingstad, and Frydenberg 1999; Fjerdingstad and Boomsma 2000; Murakami, Higashi, and Windsor 2000; Villesen et al. 2002; Wirth et al. 2003; M. P. Cristiano, personal communication; chapter 5, this volume). In addition to supplying the sperm necessary for the many tens of millions of female offspring (males are the products of unfertilized, haploid eggs) produced by an *Atta* queen during her ~15-year lifespan, multiple mating serves to increase the genetic variability of the work force and thus overall resistance to disease (Hughes and Boomsma 2004). The disadvantage of multiple mating is that it decreases the genetic relatedness of workers in the colony, potentially decreasing the binding force of kin selection and increasing conflicts of interest over reproductive offspring. In leaf-cutter ants, however, the potential for conflict of interest has been largely or entirely removed both in the realm of sperm competition (den Boer, Baer, and Boomsma 2010) and in the realm of worker-worker reproductive conflict (chapter 5, this volume). Primitively, non-fungus-farming ant workers are able to lay haploid eggs that develop into males able to carry the worker’s genes into the next generation. Workers of most attine ants, including non-leaf-cutting higher-attine ants, retain this ability, which may be employed, for example, when the colony queen dies. Among the leaf-cutting ants, workers of at least some *Acromyrmex* species also retain the ability to lay haploid (male) eggs, whereas *Atta* workers are sterile (Dijkstra, Nash, and Boomsma 2005). In the rare, small subset of *Atta* workers that lay viable eggs, the eggs hatch into sexually dysfunctional “dwarf” males (Dijkstra and Boomsma 2006), which indicates that the ability to lay haploid eggs persists only as a vestigial trait. In the logic of kin selection, the highly eusocial *Atta* superorganism could not have evolved without a gigantic, polymorphic, genetically variable work force, which could not have evolved without multiple mating, which could not have evolved without the elimination of sperm and worker-worker conflicts over reproductive control. That all of these conditions are met in *Atta* species is the hard-wired ant equivalent of “increased social control,” cited by Peregrine (chapter 2, this volume), as one of the consistent components of human agriculture.

Agroecosystems

Like human agroecosystems, leaf-cutter agriculture provides a vast, reliable niche for thousands of symbiotic organisms, including arthropods, mollusks, annelid worms, nematodes, and reptiles (Autuori 1942; Weber 1972; Waller and Moser 1990; Schultz and McGlynn 2000). In the beetles (Coleoptera) alone, 411 species belonging to 25 families have been recorded from leaf-cutter nests (Navarette-Heredia 2001). Some species of non-leaf-cutting higher- and lower-attine ants are attacked by “agro-predatory” ants in the distantly related genera *Megalomyrmex* (subfamily Myrmicinae) and *Gnamptogenys* (subfamily Ectatomminae), which raid nests and consume both fungi and brood. In contrast, the semi-mutualistic *Megalomyrmex symmetochus* cohabits with non-leaf-cutting higher-attine ant hosts for many years as a social parasite, consuming resources but not at the expense of host reproduction and even protecting the host from *Gnamptogenys* raids (Adams et al. 2000b, 2013; Dijkstra and Boomsma 2003; chapter 8, this volume).

The gardens of leaf-cutter ants host an unknown but large number of bacterial species, including nitrogen-fixing bacteria (Pinto-Tomás et al. 2009; Aylward et al. 2012) and a cohort of three bacterial genera that consistently occurs in the gardens of fungus-farming ants, beetles, and termites (Aylward, Currie, and Suen 2012; Aylward et al. 2014; Barcoto et al. 2020). They also host hundreds of fungal species (Little and Currie 2007; Pagnocca et al. 2008; Rodrigues et al. 2008, 2013; Mendes et al. 2012; Pagnocca, Masiulionis, and Rodrigues 2012), including the consistently occurring mycoparasitic genera *Escovopsis* and *Escovopsioides* (Ascomycota: Hypocreales), which have co-diversified with attine-ant-associated fungi since the beginning of attine-ant agriculture (Currie et al. 2003; Gerardo, Mueller, and Currie 2006; Augustin et al. 2013; Meirelles 2015a; Meirelles et al. 2015b; Osti and Rodrigues 2018; chapter 11, this volume).

Conclusion

As pointed out by McGhee (chapter 1, this volume), the most likely reason for evolutionary convergence of human and insect agricultural symbioses is functional constraint: agricultural systems are bound to share similar elements because there is a limited number of ways to solve the problem of growing your own food. This chapter has summarized the many similarities as well as the obvious differences between human and fungus-farming ant agriculture. Here I will point out five broad similarities that are likely due to evolutionary convergence.

1. The ancestors of both human and ant agriculturalists lived in social groups that obtained nourishment through central-place hunting-gathering. They altered their local environments through niche construction/ecological engineering, creating reliable ecosystems for and coevolving with preadapted plants and animals. At some point they added incidental cultivation to their repertoires of mixed food acquisition. Central-place hunting-gathering is an ancestral trait in ants, most ants are premiere ecological engineers, and incidental fungal cultivation may be present in the close relatives of fungus-farming ants in the genera *Wasmannia* and *Blepharidatta*.

2. At some point a commitment to cultivation occurred in both human and ant agriculturalists. It occurred at the origin of fungus-farming ants, probably due to the reliability

of “stored” surplus in the form of fungus gardens rather than to superior productivity relative to hunting-gathering because fungus-farming ants continue to forage for garden substrate and their colonies have lower overall metabolic rates than those of equivalently sized hunting-gathering ant colonies. It is likely that commitment to agriculture occurred in human cultural evolution for similar reasons—namely, because of the environmental-buffering effect of stored surpluses and in spite of the longer-term positive feedback loop between increasing reliance on stored surpluses, population growth, and initial adverse effects on human health.

3. Human and ant cultivars became domesticated. Higher-attine fungi are genetically and phenotypically modified, polyploid, and more productive than lower-attine fungi. They have diversified into multiple species, and their wild ancestor is likely extinct. Higher-attine ant colonies have higher overall metabolic rates than those of equivalently sized hunting-gathering ant colonies. Most human domesticates are more productive than, and are essentially separate species from, their wild progenitors, most are polyploid, and some are arguably, along with their human farmers, the most successful species on planet Earth.

4. Both human and ant agriculture have produced large, complex societies with unprecedented levels of division of labor and social complexity. Colonies of leaf-cutting *Atta* species are among the most highly eusocial of all organisms, possessing a range of physical castes unparalleled among social insects and having evolved a suite of biological traits that together reduce conflicts of interest among colony members and bind them and their resident fungal clone into a cohesive superorganism (chapter 5, this volume). Hölldobler and Wilson (2010) refer to this extreme social cohesion as “civilization by instinct.”

5. Human and ant agriculture have produced agroecosystems consisting of hundreds or thousands of species of animals, plants, fungi, and bacteria. In both systems, in addition to farmers and cultivars, large numbers of species have come to rely on the huge, predictable niches produced by agriculture, including many species that have coevolved with the farmers and cultivars. Because some of them feed on or compete with their cultivars, farmers have evolved methods for controlling these “parasites”; some of these methods involve promoting the growth of predators/pathogens of the parasites.

If these similarities are due to evolutionarily convergent solutions to shared ecological problems, then it is very likely that, via a process of reciprocal illumination, we can discover the set of shared evolutionary and ecological rules that have produced and that govern both human and ant agriculture (Schultz et al. 2005). A similarly comparative study of convergence in strictly human agricultural evolution is underway due to a renaissance in synthesizing and analyzing new knowledge from archaeology, genomics, archaeogenomics, and population genetics (Allaby, Fuller, and Brown 2008; Fuller et al. 2014; Larson et al. 2014; chapter 10, this volume). Perhaps knowledge gained in that endeavor can inform the search for similar patterns in the comparative population genetics and genomics of higher-attine fungi, lower-attine fungi, and free-living leucoprineaceous fungi. During their evolution from wild progenitors to human domesticates, our plant and animal symbionts traveled down fragmented temporal and spatial population-genetic pathways that, in spite of their complexity, produced convergent phenotypic traits and genomic architectures. Did similar patterns of population-genetic evolution produce ant-cultivated domesticated fungi? Although the vastly greater time spans involved could make answering this question challenging, there are many extant species of lower-attine and higher-

attine fungi cultivated by many extant species of ants that provide dozens of comparative microcosms for exploring population-level ant-fungus agricultural evolution, including domestication, which may be in progress in a number of extant systems (Gerardo et al. 2004; Mehdiabadi, Hughes, and Mueller 2006; Mehdiabadi et al. 2012).

Boomsma (chapter 5, this volume) points out a fundamental difference between human and leaf-cutter agriculture: the latter requires a lifetime “matrimonial” commitment between the ant colony and its single clonal fungal cultivar in order to ameliorate potential conflicts of interest between them. Humans, in contrast, retain the ability to recruit new cultivar strains or species, whereas their cultivars, which are obligately dependent on them, are under the asymmetrical control of their human farmers. Although this may be true of human agricultural symbioses in principle, during the past century humans have become increasingly reliant on the large-scale cultivation of monocultures of genetically monotonous strains of a very few plant and animal species (Harris 2012; US Department of Agriculture 2020a, 2020b). This increasing dependency is so far associated with only a few known human genetic adaptations, none of which is fixed across all human populations, but that seems unlikely to remain the case. As we contemplate the long-term future of the human species, it might be useful to do so with a better understanding of the industrial-scale agriculture practiced by leaf-cutting ant species in the genus *Atta*. Given current concerns about preserving genetic diversity in our domesticates and about maintaining biodiversity in our agroecosystems, how is it that, possibly for as many as 20 million years, leaf-cutting ants have managed to sustainably propagate a single, possibly asexual, fungal species; manage an ever-present, ever-evolving microfungus crop disease; manage a diverse array of other macro- and micro-organismal parasites and commensals; and manage the trees and grasses on which they forage for substrates in their local environments? In spite of considerable research, the answers to these questions are not at all well understood and their implications for human agriculture, if any, are almost entirely unexplored.

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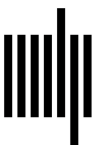
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