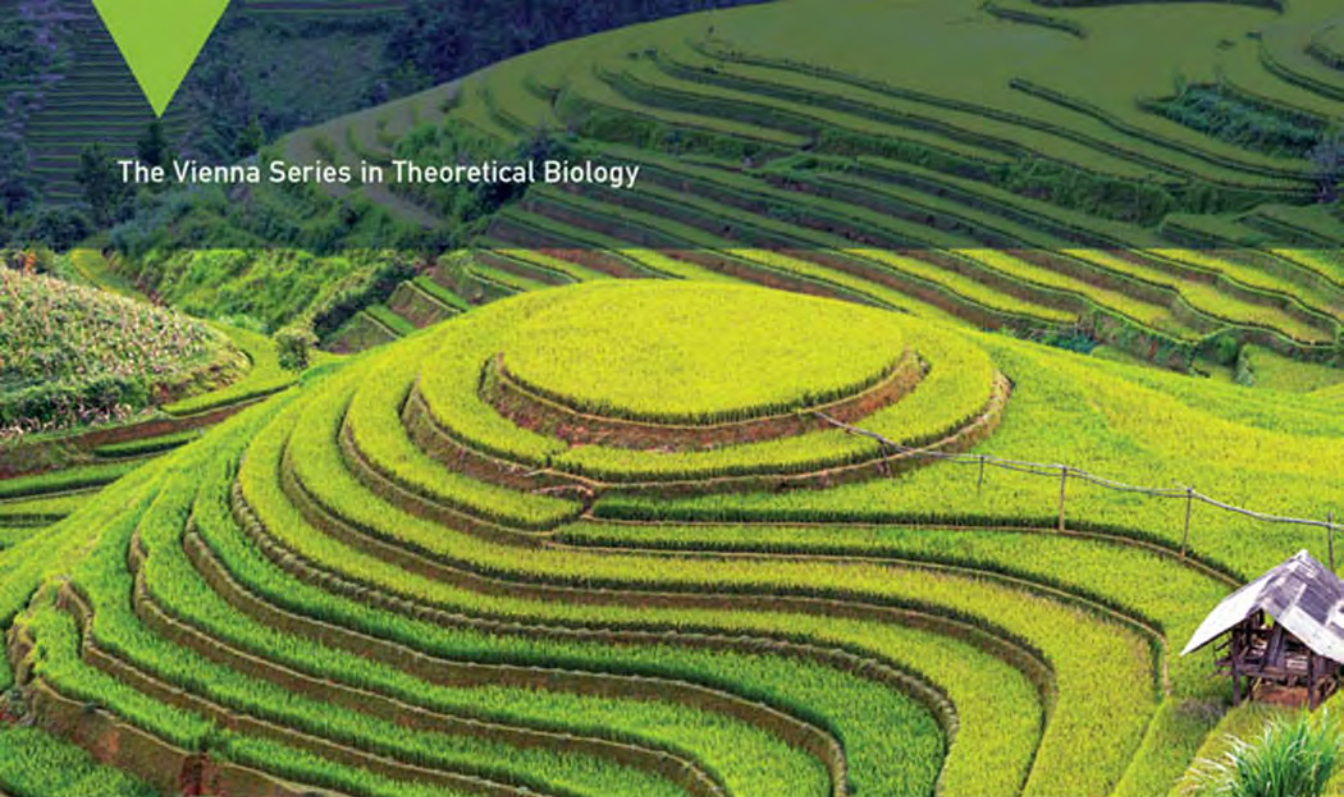


The Vienna Series in Theoretical Biology



The Convergent Evolution of Agriculture in Humans and Insects

edited by Ted R. Schultz, Richard Gawne, and Peter N. Peregrine



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Introduction

Ted R. Schultz, Richard Gawne, and Peter N. Peregrine

Agriculture originated at least 14 times—and perhaps as many as 23 times—in human history (chapter 10, this volume). Agriculture also originated a minimum of 20 times in nonhuman animals, including at least 15 times in insects (chapters 1, 6, 7, and 8, this volume). In humans, agriculture has dramatically increased the numbers of both farmers and domesticates as compared to their nonfarming, undomesticated close relatives. For example, the biomass of extant humans and their mammalian and avian livestock outweighs that of all wild mammals and birds by over 17 times (Bar-On, Phillips, and Milo 2018). Insect agriculturalists likewise dominate the biosphere. The colonies of fungus-farming termites and leaf-cutting ants are highly eusocial “superorganisms” consisting of many millions of individuals divided into physically differentiated castes, enabling highly refined division of labor that has been called “civilization by instinct” (Hölldobler and Wilson 2010). The multiple origins of agriculture in both humans and nonhumans represent remarkable, repeated cases of convergent evolution that deserve to be carefully examined in a comparative context. Moreover, the demonstrable success of human and insect agriculturalists raises the question of why, in the history of life on Earth, agriculture has only arisen dozens of times instead of hundreds or thousands of times. In other words, why is agriculture so rare in animals?

To explore such questions, two previous working groups of anthropologists, archaeologists, and entomologists were convened at the Santa Fe Institute in 2014 (August 28–29) and 2016 (April 10–12). These working groups concluded that the convergent evolution of agriculture may be explained, at least in part, by energetic benefits that include increased buffering against environmental variability due to dependable food resources and reduction of time spent foraging, especially for wild sources of protein for which competition from other species is fierce. The groups also identified a set of specific preconditions that likely must be present for agriculture to evolve, including (1) future farmers must be generalized foragers that create central places for food storage, distribution, and consumption; (2) future farmers must interact with a plant or animal species that is genetically or behaviorally pre-adapted for domestication; (3) future farmers must be highly social and capable of communicating in a manner that spans generations and allows for social learning or conditioning; (4) favorable mutations or innovations must be replicated rapidly across generations; and (5) the climate must be relatively stable. These preconditions may

be quite rare, which thus explains the relative rarity of agriculture. Although these conclusions were intriguing, they were judged to be preliminary, and so, on June 13–16, 2019, the 38th Altenberg Workshop in Theoretical Biology was convened at the Konrad Lorenz Institute in Klosterneuburg, Austria, in order to more thoroughly explore the topic of “The Convergent Evolution of Agriculture in Humans and Insects.”

This volume contains the products of that workshop. In part I, two different analyses codify and quantify the traits held in common across human and animal agriculturalists, one more broadly, spanning the entire animal kingdom (chapter 1), and one more narrowly, focusing on multiple human groups and a subset of insect agriculturalists (chapter 2). In part II, various authors examine both human and insect agriculture from a group-versus-individual-selection perspective, reasoning that it is unlikely that natural selection will generate an evolutionarily stable agricultural mutualism when farmers and cultivars—as well as individual cultivars—have conflicting interests. These chapters provide insights about the limited conditions under which we might expect agriculture to evolve and, thus, why it may be rare. The chapters in part III summarize the biology and evolution of the major groups of insect agriculturalists, including aspects of their biologies that have never before been reviewed. In part IV, chapters 10 and 12 explore different aspects of convergent evolution globally across human agricultural systems; chapter 11 compares fungal parasites of ant agriculture with fungal parasites of human agriculture; chapter 13 explores a general developmental mechanism for generating morphological form that provides insights into the rapid evolution of human and possibly nonhuman plant and animal domesticates; and chapter 14 provides an in-depth comparison of the evolution of agriculture in humans and in a single, relatively well-studied insect group, fungus-farming ants.

The evolution of agriculture is studied by scholars working in many different fields. For the most part, research on this topic has been conducted in relative isolation, discipline by discipline. The isolation of students of human and nonhuman agriculture, respectively, is particularly dramatic. To date, there has been remarkably little contact between researchers in these fields, and as a result many opportunities for fruitful interactions have been missed. The aim of this volume is to bring researchers working on human and insect agriculture together for the first time, with the goal of promoting an interactive dialogue that has the potential to bring about new empirical and theoretical advances. Ultimately, we hope that this book will serve as a foundation for future studies of agriculture from a comparative point of view.

Definitions

Throughout this book, the authors use the terms “cultivation,” “domestication,” and “agriculture.” Unless otherwise stated in a specific instance, these terms are defined as follows:

cultivation: Targeted intervention in the life cycle of a particular species in order to promote its growth, including practices such as tillage, planting, and harvesting.

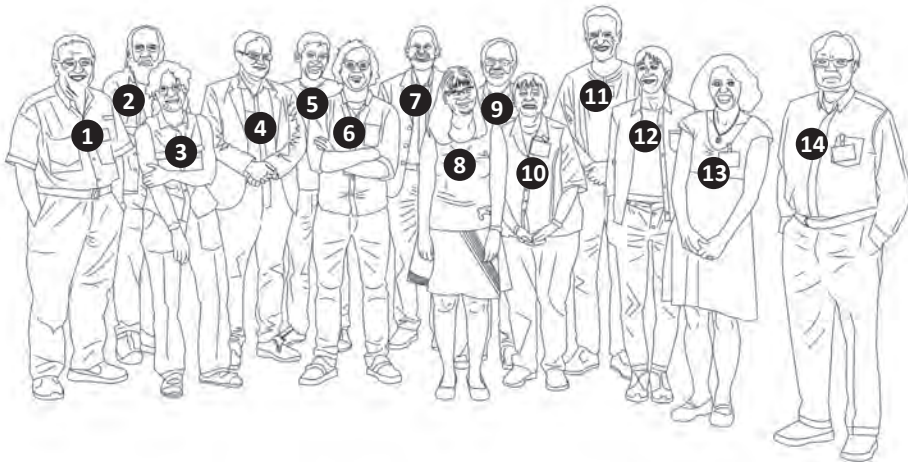
domestication: Genetic modification of one species (the domesticate) by another (the farmer) in ways that benefit the farmer but that would reduce the fitness of the domesticate in its original niche.

agriculture: Cultivation on a large scale in which the farmer has become obligately dependent on the cultivated species for nutrition.

Workshops

2014 Santa Fe Institute Working Group: Jennifer A. Dunne, David C. Krakauer, George R. McGhee, Ulrich G. Mueller, Peter N. Peregrine, Ted R. Schultz, Bruce D. Smith, Melinda A. Zeder

2016 Santa Fe Institute Working Group: Duur K. Aanen, Richard Gawne, Marcus J. Hamilton, Jiri Hulcr, George R. McGhee, Ulrich G. Mueller, Peter N. Peregrine, Ted R. Schultz



Participants in the 38th Altenberg Workshop in Theoretical Biology, “The Convergent Evolution of Agriculture in Humans and Insects,” June 13–16, 2019, Konrad Lorenz Institute, Klosterneuburg, Austria. (1) Ted R. Schultz, (2) R. Ford Denison, (3) Judith Korb, (4) Dorian Q. Fuller, (5) Peter H.W. Biedermann, (6) Rick Gawne, (7) Peter N. Peregrine, (8) Hanna Kokko, (9) Jacobus J. Boomsma, (10) Susan Milius, (11) Duur K. Aanen, (12) Ana Ješovnik, (13) Nicole Gerardo, (14) George R. McGhee. Not pictured: Jiri Hulcr.

10 **Coevolution in the Arable Battlefield: Pathways to Crop Domestication, Cultural Practices, and Parasitic Domesticoids**

Dorian Q. Fuller and Tim Denham

This chapter is about domestication of various plants by *Homo sapiens*, the novel ecosystems that such domestication processes created, and other taxa that benefited from these anthropic environments. The coevolution of symbioses of different phyla is by no means unique to the domesticatory relationships of humans and their crops. Indeed, “agriculture” by ants, termites, and beetles are far more ancient in evolutionary terms and widespread across phyla and habitats (Mueller et al. 2005; McGhee 2011; see also chapters 1, 2, and 14, this volume). The parallels between humans and some insects raise fundamental questions about what is meant by terms such as “cultivation,” “domestication,” and “agriculture.” For anthropologists and archaeologists these terms are often taken to be self-explanatory. Cultivation is something that people do—namely, learned cultural behaviors and labor investments whereby people plant crops in prepared plots of land. Domestication refers to the resultant changes, genetic and/or morphological, in the targeted plant taxa that become adapted to cultivation and provide a yield that is economic, often caloric, for the human cultivators. Agriculture is often distinguished based on scale, whether in terms of the degree of dependence on cultivated food for diet or in terms of the level of investment in agricultural activities, which is associated with the importance of cultivated food both to the human economy and ecology and as an obligate part of sustaining human communities and populations. Agricultural societies require cultivation to persist, whereas cultivation and use of domesticates may be undertaken on a variable scale by economies that could still be largely reliant on fishing, hunting, and/or gathering. Economies with a smaller reliance on cultivation, including many in which domestication traits were evolving in the crops, have often been recognized as distinctive and variously termed “intermediate economies” practicing “pre-domestication cultivation” (Hillman 1975; Harris 1989, 2012), low-level food production (Smith 2001), or food production with/without domesticates (Harris 1996; Fuller et al. 2018). In the general terms laid out by Mueller et al (2005), agriculture as we define it here requires “nutritional dependency” and the reorientation of social life to the production of food, whereas habitual planting, improvement of growth conditions, and harvesting without nutritional dependency constitutes nonagricultural cultivation.

One of the striking features of agriculture is that it has evolved in parallel in different places and at different times, offering the opportunity to consider commonalities in process and causal variables. Mueller et al (2005) concluded that there were seven separate origins

of agriculture among beetles, as well as one each among termites (in the Old World) and ants (in the New World). Similarly, among humans, agriculture developed independently at least 14 times, and perhaps as many as 23 times—in different regions, in different cultural traditions, and based on different crop plants (Purugganan and Fuller 2009; Larson et al. 2014; Denham et al. 2020). Our updated understanding of these geographically and culturally separate origins of crop domestication and agriculture are mapped in figure 10.1, which distinguishes centers focused on the cereal domestication pathway (figure 10.1A) and the vegetocultural pathway (figure 10.1B).

In comparative terms three things are striking about the human development of agriculture that we wish to explore here. First, the nature of crop types and practices of reproduction vary and are linked to different forms of domestication. We can therefore break human-plant domesticatory relationships into a series of alternative domestication pathways. There is a coherent set of convergent traits for species within each pathway, but there are differences in the kinds of domestication traits between each pathway. Here we explore these pathways for the evolution of grain crops; the weeds of grain crops, some of which were selected as secondary domesticates; vegetocultural crops (roots, tubers, and so on); and fruit trees. Each of these pathways has its own distinctive syndrome of domestication traits and tends to be associated with different kinds of agricultural system.

Second, human agriculture has tended to be diverse and diversifying in the sense that the number of plant species that have coevolved with humans to become domesticates has increased over time. We highlight this in the sections below with regional examples of diversification trajectories. This contrasts with insect agricultures, which tend to be an obligate mutualism between a specific insect species and a specific fungal crop (Mueller et al. 2005; chapter 5, this volume; chapter 14, this volume). In humans the range of crop species has progressively increased, and we suggest that this is driven by processes of cultural evolution that continued to increase productivity in order to support long-term population growth and increasing sociocultural complexity (Ellis et al. 2013, 2018). Even in cases where human agriculture may have begun with just a single crop, which is plausibly the case with early rice farming in the Yangtze basin (Fuller et al. 2014), agriculture subsequently diversified to include many more crops and various domesticate types (e.g., melons, peaches, soybeans, water chestnuts, and so on). This diversifying tendency may be unique to human forms of agriculture.

Third, the nature of evolutionary transmission among humans is primarily through cultural information rather than genetics, and this has allowed for a potentially more rapid process. The character of cultural transmission has probably fostered the many pathways to domestication and the long-term diversification of agricultural systems.

Defining the Arable Habitat: Target Crops and Weedy Taxa

Before exploring some of the archaeological cases of agricultural evolution, we will clarify how we understand the cultivated ecosystem of arable habitat. We take the *arable habitat* to refer to those areas of land that have been prepared and planted. Preparations normally include removal of some or most preexisting vegetation, through practices such as cutting, uprooting, digging, or burning, followed by some preparation of soil (tillage). The target

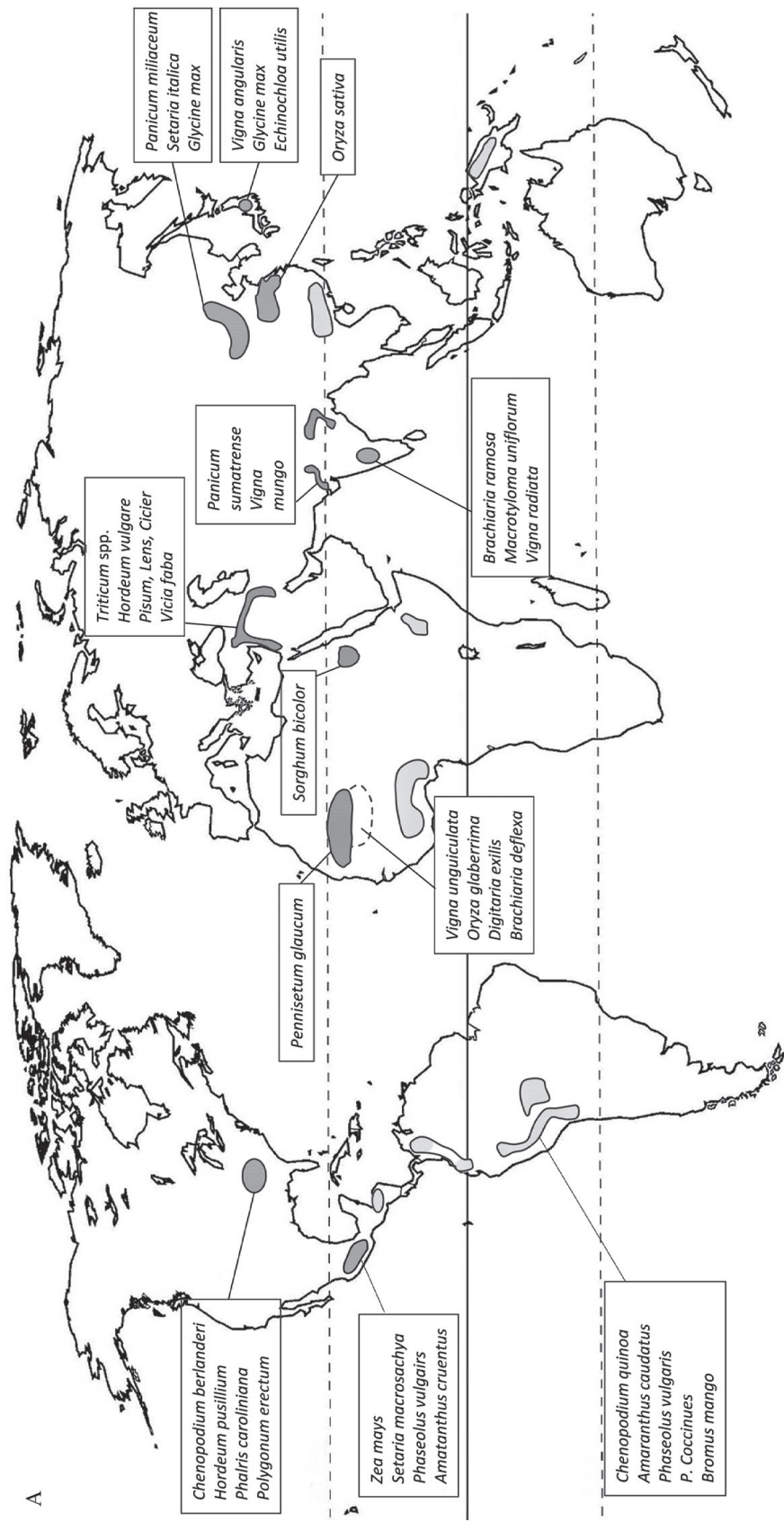
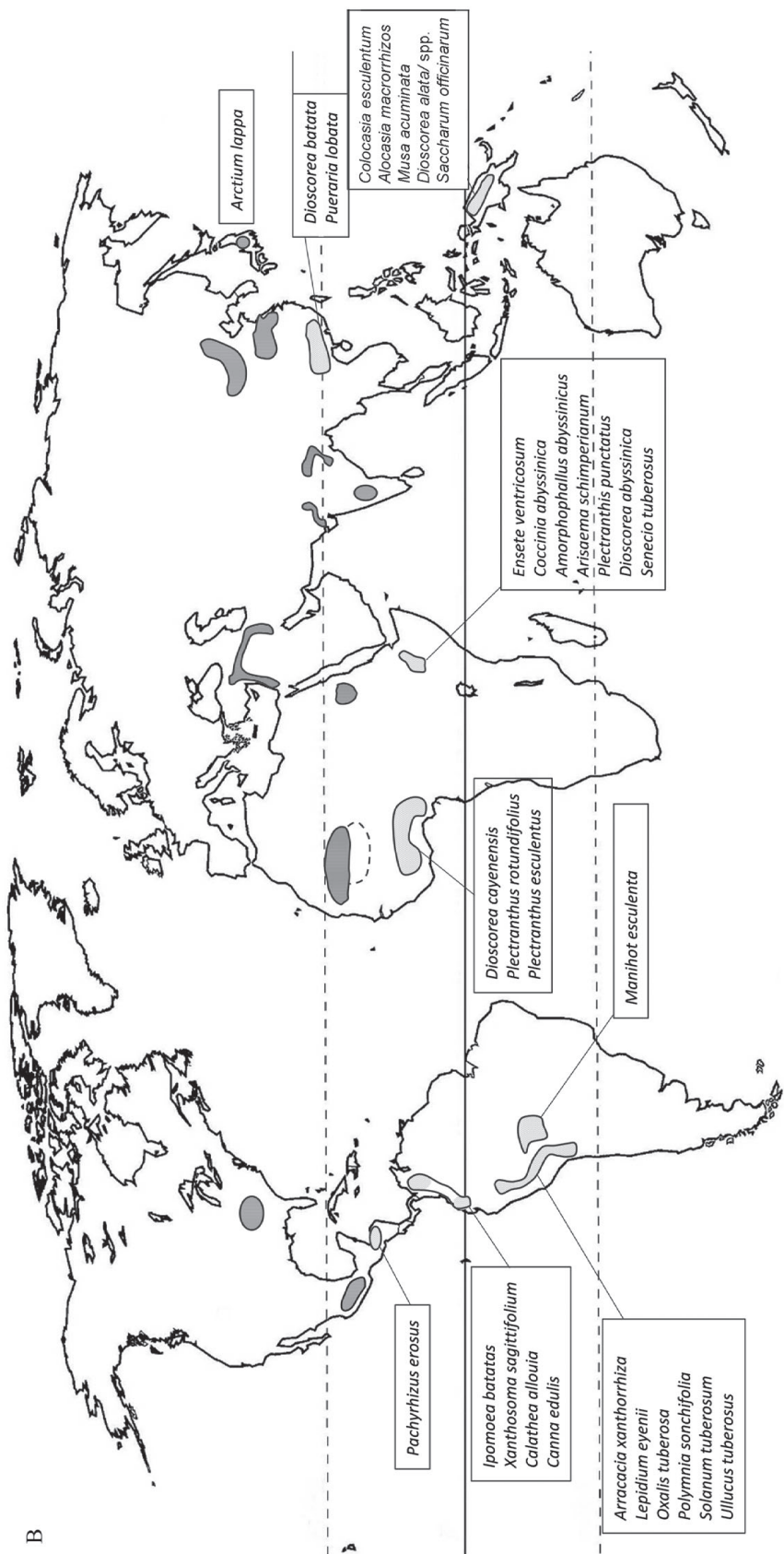


Figure 10.1 Centers of ancient plant domestication: (A) presents selected seed crops in relation to regions of domestication; (B) presents key vegetational crops in relation to regions of domestication. Adapted from Fuller et al. 2014; Denham et al. 2020.



B

Figure 10.1
(continued)

species of cultivation—namely, the crop—is then planted; planting may be by seed or vegetative organ (cuttings, tubers), and these alternative reproductive systems lead to different patterns in terms of domestication process and domestication traits, as we turn to below. In part, domestication is characterized by convergent evolution, in what botanists have long discussed in terms of a “domestication syndrome” (Harlan, De Wet, and Price 1973; Hammer 1984; Harlan 1995; Fuller 2007; Denham et al. 2020). However, as we explore in this chapter, the symptoms that recur across different crops and that distinguish them from their wild relatives tend to differ based on the mode of reproduction and what we term here *alternative domestication pathways*. In particular we consider four alternative pathways: a seed crop or cereal pathway; a secondary cereal pathway, in which weeds are turned into crops; a vegetative pathway; and, a long-lived perennial, or tree fruit, pathway. Recent years have seen archaeological progress in documenting examples for each of these pathways.

The arable habitat, however, is never restricted to the crop, but also provides a habitat for competing taxa, or what would commonly be termed “agricultural weeds.” Because these weeds compete with the crop for resources (soil nutrients, water, light) and success of the weeds tends to decrease the yields of crops, they can be regarded as parasitic upon the symbiotic relationship that is cultivation. Because weedy taxa have also been evolving adaptations to make them more successful as weeds of cultivation, they often possess some adaptations that overlap with those of the target crops. For this reason it has been suggested that they could be considered *parasitic domesticoids* (Fuller and Stevens 2017), inasmuch as they have evolved some traits that are shared with and similar to domesticated crops, but that aid them in parasitizing the resources of the cultivation symbiosis. It has long been noted that some agricultural weeds are today unknown from nonagricultural habitats, which indicates that these so-called obligate weeds have ancestrally evolved from species that originally occupied other habitats and have subsequently been extirpated from such habitats or those habitats have been replaced by anthropogenic habitats. Such obligate weeds are best known from those that evolved early in Southwest Asia as part of cereal agriculture there (Zohary 1950; Willcox 2012; Fuller and Stevens 2019a), but similar cohorts of weeds can doubtless be recognized in other regions too. Many of these weeds spread with agriculture to much greater geographical ranges than they had ever occupied as wild species, with some weeds becoming more globally widespread than many crops (Holm et al. 1977). The adaptations that many of these weeds possess often parallel crops in terms of changes in seed size, dormancy and germination, or growth habit.

The arable field has been regarded as a botanical battleground, where crops and their human cultivators wage an ongoing war with weeds (Jones 1988; Fuller and Stevens 2019a). A key adaptation on the human side of the battle occurs through sociocultural rather than genetic evolution. Human agricultural practices—in terms of various forms of tillage, soil preparation, intercropping, irrigation, weeding, and, in more recent centuries, the use of chemical herbicides—all represent innovations acquired and spread as cultural information in a process that has helped to push some weedy competitors out of the field and increase productivity. However, this battle is never won; as some weeds are pushed out of the segetal (growing within cultivated fields) and relegated to the ruderal (disturbed ground along paths and settlement margins), other weeds take their place. There are no weed-free cultivation systems. Take the example of rainfed rice compared to irrigated rice:

studies in traditional Indian fields recorded an average of 31 weed taxa in dry rice, compared with 13 in wet rice; wet rice has fewer weeds and is much more productive, yet it is not weed-free (Weisskopf et al. 2014). In any given region the long-term history of arable flora is a product of ongoing cultural evolution in agricultural practice, including the introductions of new crops and weeds via trade (Poschlod 2015a, 2015b; Pokorna et al. 2018; Stevens and Fuller 2019).

Other organisms, notably various animals, compete with humans for the calories derived from cultivation by infesting stores of harvested crops. Zoologists often refer to these as “commensal organisms,” although they should probably also be classed as parasitic domesticoids. These animal species compete for calories with human cultivators and in essence parasitize the symbiotic relationship of cultivation, while also evolving adaptations that tie them to the human ecology of cultivators, much like domestication traits. This category includes several small animals that dwell in human settlements and feed largely on grain stores or incidental waste from grain stores, such as house mice (*Mus musculus*) (Fuller and Stevens 2017; Weissbrod et al. 2017; Cucchi et al. 2020). In many cases, such as flightless grain weevils (e.g., *Sitophilus granarius*, *S. oryzae*; see Plarre 2013) and particular mouse subspecies (*Mus musculus domesticus*; see Cucchi et al. 2020), these taxa are reliant on human settlement habitats and human-mediated dispersal. Along with the coevolution of weeds in early fields of cultivation, various animal taxa coevolved to take advantage of human settlements and caloric stores of crops. Thus in addition to the botanical battleground that was the cultivated field, there was an ongoing battlefield in settlements focused on granaries. The diversifications of dogs and domestic cats generated allies for this conflict. The above discussion highlights how human agricultural ecosystems continually acquired and renewed taxonomic diversity.

Archaeological Evidence for Domestication of Seed Annuals: The Cereal Pathway to Agriculture

The best studied cases of agricultural origins involve cereals, or similar grain crops such as pulses. Much of the human world today is reliant on the production of cereal crops, especially a few key species (wheat, rice, maize, barley, and sorghum) that feed the most people. These crops also supported many of the earliest urban human settlements and have attracted the most archaeological attention. In some ways these are also much easier crops to study: the ability to be stored as hard dried seeds results in better archaeological preservation (usually through charring), and seeds are therefore readily recovered archaeologically when sampling for small organics, such as through flotation, is carried out. The greater wealth of evidence for grain crop domestication does not mean that its understanding is without controversy. One can find debate between those who assume that cereal domestication was exceedingly rare and thus posit centric models (e.g., Lev-Yadun, Gopher, and Abbo 2000; Abbo, Lev-Yadun, and Gopher al. 2011, 2014), and those who take a non-centric view that domestication took place numerous times in parallel (e.g., Willcox 2005; Fuller, Willcox, and Allaby 2012; Fuller et al. 2014). It is also the case that those who prefer a centric hypothesis tend to see domestication as a kind of “discovery” driven by human conceptualization of the domesticated as distinct from the wild, whereas multi-centric views tend to emphasize the operation of what Darwin (1868) termed “unconscious

selection,” meaning that domestication features evolved as the unintended evolutionary outcomes of human activities (Zohary 2004). We accept that the multi-centric and unconscious selection processes are more likely and are supported by the majority of archaeologists specializing in the emergence and transformation of early agriculture.

The domestication processes of these cereals result in parallel evolution of a *domestication syndrome* (Harlan, De Wet, and Price 1973; Hammer 1984; Fuller 2007). Domestication represents selection and fixation of genes and morphological adaptations of plants that were either absent or rare variants in preexisting wild populations. These traits evolved over a period of time, which we can define as a *domestication episode*, whereby populations of plants became genetically modified from their wild predecessors and gained adaptations to cultivation and human harvesting. These characteristics can be related to different aspects of cultivation in terms of what causes them to evolve. On the one hand there are traits that offer competitive advantages for the establishment of seedlings in cleared soil conditions within a cultivated field; on the other hand there are features that relate to human harvesting, thereby connecting cereal reproduction to dispersal by the farmer. Current archaeological data suggest that domestication traits evolved in crops over extended periods of time ranging between 2,000 and 4,000 years (see Fuller et al. 2014, 2018). This protracted domestication episode of a few millennia is often referred to as “pre-domestication cultivation” and represents a key period for understanding the origins of agriculture (Harris 1989; Hillman and Davies 1990; Willcox 2005, 2012). Recent work in Southwest Asia suggests that the domestication episode took place between 9500 and 7000 BC for a few species of wheat (*Triticum monococcum*, *T. dicoccon*, *T. timopheevi*), barley (*Hordeum vulgare*), lentil (*Lens culinaris*), pea (*Pisum sativum*), chickpea (*Cicer arietinum*), broadbean (*Vicia faba*), and flax (*Linum usitatissimum*) (Zohary, Hopf, and Weiss 2012; Fuller et al. 2018). Recent work in southern China suggests that the domestication of rice (*Oryza sativa*) occurred between ~7000 BC and 4000 BC (Fuller et al. 2014; Stevens and Fuller 2017) and might have also involved *Trapa natans* water chestnuts (Guo et al. 2017). Although there are still relatively few crop domestications that are fully documented through time series of archaeological data, some studies have increased evidence for parts of the sequences of change in several crops, such as indigenous seed crops of North America (Smith and Yarnell 2009; Fuller et al. 2014), sorghum (*Sorghum bicolor*) in Sudan (Winchell et al. 2018; Barron et al. 2020), various Indian Leguminosae (Murphy and Fuller 2017; Fuller et al. 2019), and Andean *Chenopodium* spp. (Langlie et al. 2011; Fritz et al. 2017), to name a few. What these examples have in common are both the protracted time period of change in the morphologies of these crops and the recurrence of morphological changes across species.

Key changes that relate to soil conditions include a trend toward increasing seed size and loss of germination inhibition. Crops tend to germinate as soon as they are wet and planted, in contrast to wild forms that often germinate after certain conditions have passed, such as in response to day length or temperature or after the seed coat is physically damaged. Loss of inhibition can be expected to be selected for under cultivation as seeds that do not germinate will not contribute to the harvest. Seed size increases are thought to relate to increasingly fit seedlings, which are better able to establish themselves quickly in the cleared ground of fields (Fuller 2007). Seed size change is readily studied from archaeological seed remains through the compilation of measurements (figure 10.2).

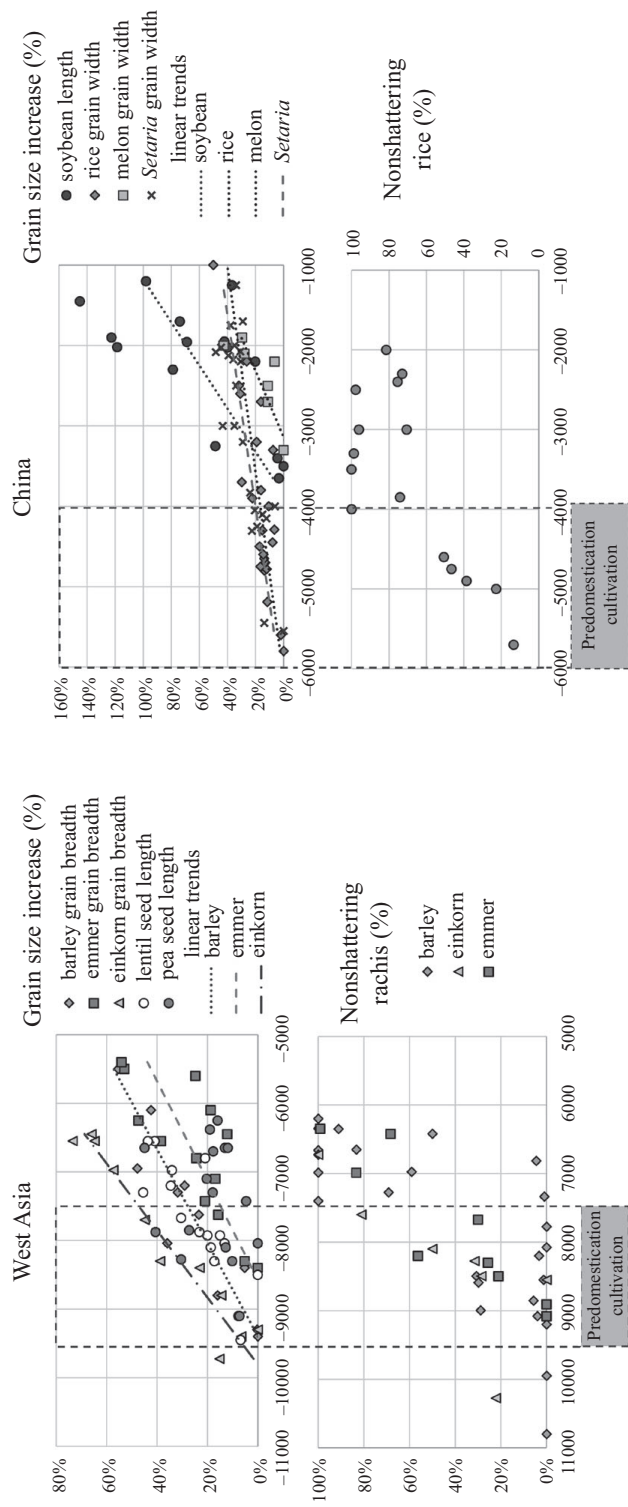


Figure 10.2

Domestication trajectories documented by morphological changes in seed crops: comparing China (right; Stevens and Fuller 2017; Fuller and Stevens 2017) and West Asia (left; Fuller et al. 2018). Archaeological data are plotted against the median calibrated radiocarbon age associated with the seed assemblage. Charts at the top indicate the increase in average seed size expressed as a percentage increase since the earliest/smallest assemblage. The stage defined as pre-domestication cultivation is indicated for each region; timescales are in years BC.

Although preservation through charring may change seed size, usually leading to shrinkage, this is expected to have similar effects across different archaeological samples, allowing comparisons between archaeobotanical assemblages to chart general trends. What is striking is that evidence for grain size increase in cereal crops is focused on the early millennia of domestication, with little significant or directional change afterward. Even modern breeding tends to work within the bounds of the size ranges established during early domestication in grains and grain legumes: the largest of modern wheat or rice grains are not significantly different from those at the end of the Neolithic (Gegas et al. 2010; Okamoto et al. 2012; Lu et al. 2013; Fuller et al. 2014, 2017).

A key change that related to cycles of human harvesting and sowing from stored harvests is the loss of natural seed dispersal, such as through the dehiscence of spikelets, or the “shattering” of cereal ears or panicles. This is often regarded as the single most important domestication trait (Zohary 1969; Harlan, De Wet, and Price 1973; Harlan 1995; Abbo, Lev-Yadun, and Gopher 2014). It makes a species highly dependent upon the human farmer for survival and means that instead of shedding seeds when they are mature, a plant retains them. Those retained seeds must be separated by processing (threshing)—thus, by the addition of human labor. Some of these seeds are further processed for human consumption while others are kept as a seed stock, to be dispersed later by farmers to create further crop generations. Over the era of domestication in Southwest Asia, human groups invested increasing effort in creating bespoke harvesting tools in the form of sickles, and thus technological evolution tracks the evolution of morphological change in wheats and barleys (Maeda et al. 2016). In the case of Chinese rice, specialized harvesting tools—hand-held knives or sickles—appeared around 3000 BC after nonshattering morphologies had already been fixed for some time (Fuller 2007; Stevens and Fuller 2017).

Other changes that are part of the domestication syndrome are either less necessary or harder to recover in the archaeological evidence (Fuller 2007). An increasing reliance on human harvesting also tended to lead to the reduction in seed dispersal aids. Plants often have a range of structures that aid seed dispersal, including hairs, barbs, and awns, and in grasses even the general shape of the spikelet. Thus domesticated wheat spikelets are less hairy, have shorter or no awns, and are plump, whereas in the wild they are heavily haired, barbed, and aerodynamic in shape. Awnless wheat, rice, and other cereals exist under cultivation and are absent from wild populations. While these changes can be regarded as having come about by the removal of natural selection for effective dispersal, allowing for less metabolic “expenditure” on these structures, there is often still much variation in the degree to which some of these structures are retained in some domesticated populations.

Another recurrent change is a shift to a more compact growth habit and increased apical dominance. Harlan (1995, 199) refers to this as the “sunflower effect.” Domesticated cereals in general have shifts from their wild progenitors, sometimes involving suppression of tillers (basal secondary stalks) or axillary branches higher up, but also often selecting for even maturation across different branches. For example, in maize, foxtail millet, and pearl millet (*Zea mays*, *Setaria italica*, *Pennisetum glaucum*), the domesticated form tends to have suppression of any lateral branches or tillers, whereas in wheat, barley, and rice lateral branching is reduced and tillers have been selected to mature more evenly (Doust 2007). These branching patterns are not only determined by genetic combinations, but also respond to environmental cues, conditions of soil, and shading. From the farmer’s point

of view, being able to pack more erect crops together in a field will increase potential production per unit of land, but it comes at a potential price because each individual plant has less soil space and therefore less “real estate” from which to derive soil nutrients and water (see also, chapters 3 and 4, this volume). Apical dominance may have evolved only after cultivation was established along with fertilizing practices. This in turn means that erect and more productive early crops required more human labor inputs in terms of soil maintenance, the so-called soil nutrient trap (Fuller, Allaby, and Stevens 2010).

While domestication evolved in the context of cultivation, the final shift to agriculture represented an economic reorientation in which time put into cultivation and its products became far more central to human societies. Where detailed data are available, wild foods remained important and even staples alongside cereals undergoing domestication, including in Southwest Asia, where wheat and barley were domesticated (Arranz-Otaegui et al. 2016; Fuller et al. 2018), and in the Yangtze basin in China, where rice was domesticated (e.g., Fuller and Qin 2010). Thus one of the correlates of domestication was a process of investing more in production of crops and divesting from efforts in hunting and gathering. In summarizing our conceptualization of the cereal pathway to agriculture (figure 10.3), we can think of this as a spectrum of stages that tend to move from wild plant exploitation through intermediate economies involving pre-domestication cultivation to agriculture, when the economy (human food web) is focused primarily on the cultivation of genetically transformed taxa. During the intermediate stages we can document the dynamic evolution of the target species in terms of those alleles that confer the adaptations of the domestication syndrome.

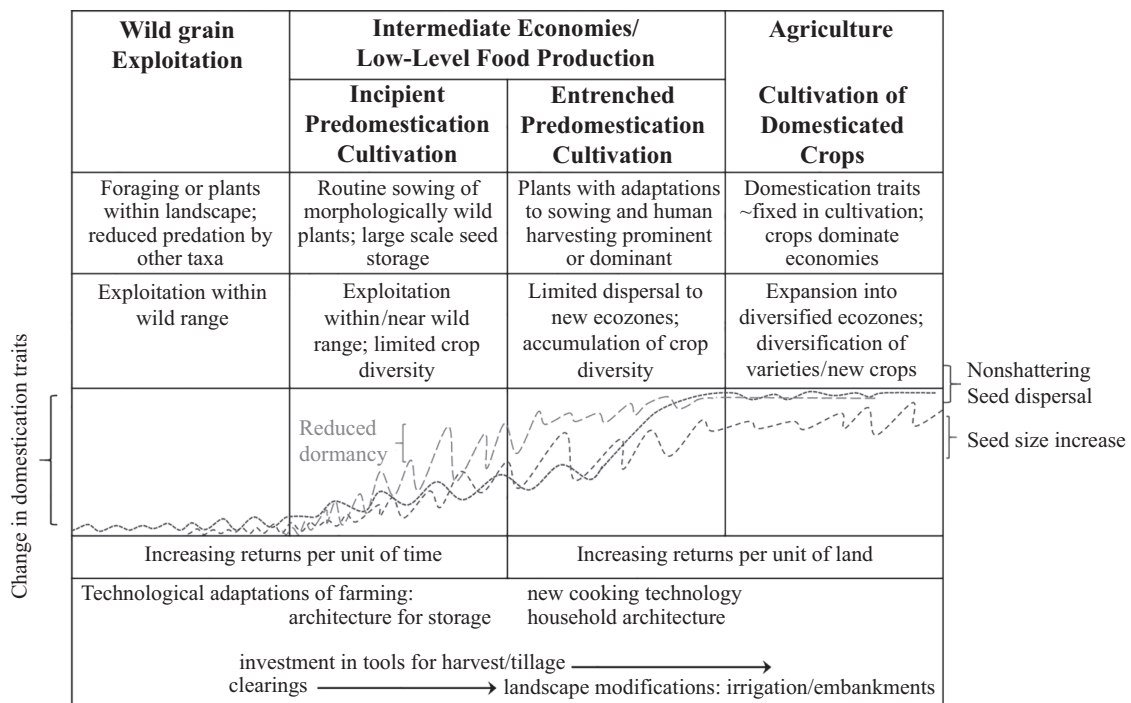


Figure 10.3
The schematic representation of a typical cereal/seed crop domestication trajectory and correlated changes in human economy and technology. This diagram revises and incorporates previous schema (e.g., Harris 1989; Fuller 2007; Fuller et al. 2018).

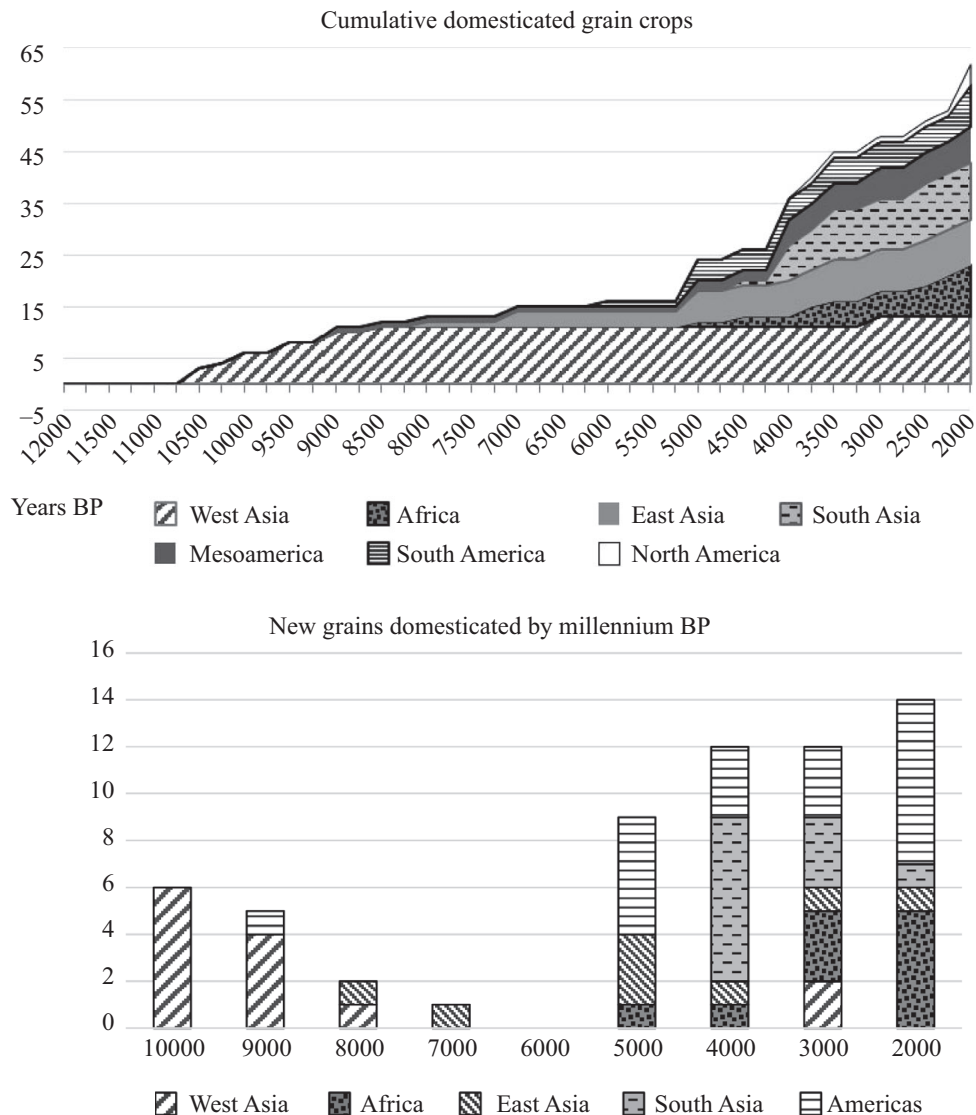
Diversification in Agriculture: Global and Regional Trends

Once cereals and associated seed crops were domesticated and regional agricultural systems were established, a number of tendencies for change in both the human and crop components of these systems can be recognized. Populations of humans practicing agriculture tended to grow in population density and eventually to disperse outward to additional territory (Bellwood 2005; Shennan 2018). The extent of local population growth and rate at which agriculturalists expanded by migrations varied, depending on factors such as the potential carrying capacity of the agricultural systems in question (Fuller, Champion, and Stevens 2019; Qin and Fuller 2019) and interaction with existing populations in adjacent regions (Donohue and Denham 2010). In some cases the expansion of agriculture into new geographical zones presented challenges, as crops were moved well beyond the ecological parameters that their wild ancestors had been adapted to. Some crops were less adaptable, leading to some loss of crop diversity farther away from places of origin. This was noticeable during the European Neolithic where western and northern areas had much reduced crop diversity, with crops such as lentil, chickpea, and einkorn wheat becoming progressively rarer (McClatchie et al. 2014; Fuller and Lucas 2017). Among the challenges that had to be overcome were changes in seasonal temperature and the distribution of rainfall, which led in many cases to adaptive changes in the sensitivity of photoperiodicity (Lister et al. 2009; Fuller and Lucas 2017; Liu et al. 2017).

Some declines in crop diversity during initial dispersal were, however, ultimately counteracted by large patterns of increasing crop diversity. The increase in crop diversity can be seen at two different scales. At a global scale and over the long term, the total number of grain/seed crops that people around the world domesticated increased, especially as crops were domesticated in more regions (figure 10.4). Thus while domestications of the Early Holocene, from 10,000 to 7,000 years BP, were dominated by Southwest Asian grain domesticates, those between 5,000 and 2,000 years BP involved many more geographical regions, from Africa and the Americas to South and East Asia. But another aspect of diversification is that the number of crops grown in any particular region and documented on a typical site from that region tended to increase over time. Based on a large database of crop presence and absence across the Old World (Stevens et al. 2016), it is possible to see how the average number of crops on a site and the maximum number of crops known in a region tend to increase over time (figure 10.5). Southwest Asia is an exception because there seems to have been a loss of diversity during early agriculture, after which diversity again increased. By contrast, data from China and sub-Saharan Africa show clear rising trends of crop taxa counts after 5000 BC. These differences highlight how the evolution of agriculture was never a single fixed adaptation; rather, it has continually evolved.

Secondary Cereal Domesticates: Crops from Weeds

Another source of new diversity was the expansion of the crop repertoire through additional, secondary crops evolved from weeds. As long as there has been cultivation, there have been weeds of cultivation. Some of those weeds have been extremely successful at adapting to anthropic environments, especially as agriculture was dispersed to an ever-greater

**Figure 10.4**

Long-term diversification in global seed crop repertoire (Old World data after Fuller, Champion, and Stevens 2019; New World data after Larson et al. 2014).

geographical range, and they increasingly challenged preexisting crops with variations in climate and soil. In some circumstances weeds outcompeted crops, and it was from among those highly successful weeds that some additional crops were domesticated. Following Vavilov (1926 [1992]), these can be defined as secondary cereals and include well-known species such as rye (*Secale cereale*) and various cultivated oats (*Avena sativa*, *A. byzantina*, *A. chinensis*, *A. abyssinica*). To this list can be added some of the millets of India, such as kodo millet (*Paspalum scrobiculatum*) (Fuller 2020) and probably some of the small millets (fonios) of western Africa (*Digitaria exilis*, *D. iburua*, *Brachiaria deflexa*) (Champion and Fuller 2018). Some pseudo-cereals (*Chenopodium* spp, *Amaranthus* spp.) and buckwheats (*Fagopyrum* spp.) may have evolved by this pathway, but in general these taxa are much less well documented. This is likely the major pathway for many fodder crops—species grown to provide food for domesticated livestock, such as alfalfa (*Medicago sativa*), common vetch (*Vicia sativa*), and red clover (*Trifolium pratense* var. *sativa*);

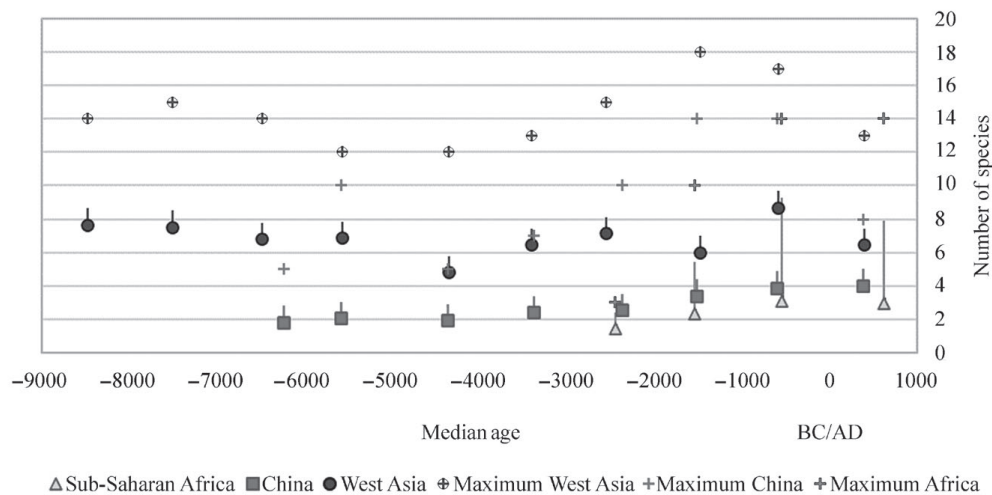


Figure 10.5

Trends toward increased crop diversity by region. Counts of crop species are averaged across sites within each region in millennium bins. Error bars indicate the standard deviation above the mean; maximum outlier values are also indicated. Total site counts: Western Asia=143, China=73, sub-Saharan Africa=41.

many domesticated oats are also grown mainly as fodder (e.g., *Avena strigosa*, *A. byzantina*). All of these domesticates come from species that had already become well-adapted segetal weeds in arable habitats (figure 10.6). Where genetic evidence is available, it suggests multiple domestications from geographically differentiated populations across the wild or weedy range, as reported for *M. sativa* (Muller et al. 2003, 2006) and likely for *V. sativa* (Erskine, Smartt, and Muehlbauer 1994; Potokina et al. 2002; Zohary, Hopf, and Weiss 2012).

Weeds can be thought of as having undergone partial domestication, as they became adapted to life in the cultivated field (as segetal weeds) (Baucom and Holt 2009). In some cases weeds have evolved crop mimicry in which their vegetative growth makes them more or less indistinguishable from crops (Barrett 1983; Fuller and Stevens 2019a). One source of particularly troublesome weeds are crops themselves, which have undergone *de-domestication* or *feralization* by re-evolving some aspects of wild adaptations (such as seed dispersal), but otherwise retaining adaptations of cultivation (e.g., Sukopp and Sukopp 1993; Londo and Schaal 2007; Thurber et al. 2010; Xia et al. 2011; Qi et al. 2015; Huang et al. 2017). Most major cereal crops, such as rice, barley, and sorghum, have weedy forms that are widespread in global agriculture, creating “crop-weed complexes” (Harlan and De Wet 1965; see also Barnaud et al. 2009; Viguiera, Olsen, and Caicedo 2013). In these cases segetal weeds have evolved as the feral forms of crops.

A simplified schema of thinking about how crops and weeds have mutually evolved is given in figure 10.6. Arrows indicate potential evolutionary (phylogenetic) relationships between taxa, and these are distributed across a grid demarcated by degrees of anthropic habitat modification and by degree of genomic divergence from ancestral, preagricultural, wild forms. Weeds can be divided between those that persist within active cultivation systems (i.e., segetals) versus those that persist in human disturbed ground, or “weeds of waste” (i.e., ruderals). Ruderals and segetals are closely entwined because species may switch between these kinds of habitats depending on the nature of cultivation practices. It

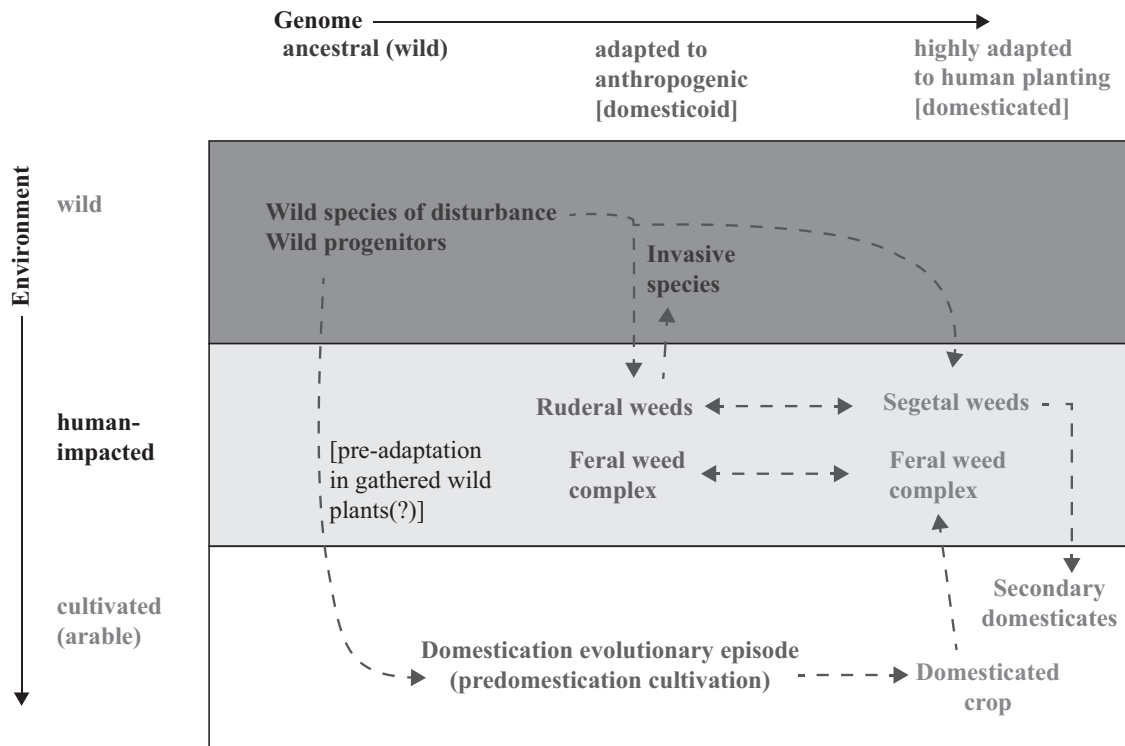


Figure 10.6

A schema of the potential evolutionary trajectories and phylogenetic relationships between crops, weeds, and wild relatives. These are charted in terms of degrees of habitat transformation by humans and in terms of degrees of genomic change (number of adaptive alleles) from hypothetical preagricultural wild populations.

is important to note that many species encountered as ruderals today were segetals in the past. This is a consequence of the ongoing coevolutionary battle between cultivators and weeds (Jones 1988; Poschlod 2015a, 2015b; Pokorna et al. 2018; Stevens and Fuller 2019).

The domestication syndrome in most secondary domesticates is the same as that described for the cereal pathway above, including increased seed size, reduced dormancy, changes in growth habit, and loss of natural seed dispersal. Some of these changes, such as in dormancy and growth habit, can be expected to have evolved in weeds. While minor changes in seed size and even a minor presence of nonshattering could arise in some weeds, a major increase in grain size and the loss of natural seed dispersal evolved rapidly among secondary domesticates once they became target cultivars. The domestications of many weed taxa are not as well documented as those of primary cereals. Nevertheless, with the oats, rye, and common vetch in Europe, domestication occurred just before or during the Iron Age (1000–1 BC) (Zohary, Hopf, and Weiss 2012). Cultivation of fodder crops of alfalfa date back to perhaps 400 BC in the Mediterranean (Rovira and Alonso 2018) and at least AD 100 in Chinese Central Asia (Chen et al. 2020), while *Vicia sativa* was certainly grown in Roman times 2,000 years ago (Erskine, Smartt, and Muehlbauer 1994; Zohary, Hopf, and Weiss 2012). Kodo millet (*Paspalum scrobiculatum*) domestication in India can be attributed to a similar period (Fuller 2020). The domestication episodes for these species took place during periods of well-developed and diversified agriculture, involving farmers with long-established cultural traditions of agronomy, in which crop diversity was an established strategy for coping with environmental variability. Conse-

quently, these secondary taxa evolved domestication traits much more rapidly than earlier cereal domesticates. It is also possible that conscious selection akin to artificial selection in modern times was involved in these processes (artificial selection as distinct from unconscious selection was defined by Darwin [1868]).

Vegetative Domestication of Root Crops

Although not as well documented as for cereals, the domestication of root crops has been almost as significant for subsistence in the past, especially in the wet tropics, mountainous regions, wetlands, and some deserts (Harris 1972). Early farming emerged in several regions based, at least in part, on the vegetative propagation of root crops that today are globally significant, most notably manioc (*Manihot esculenta*), potato (*S. tuberosum*), and sweet potato (*Ipomoea batatas*) in the Americas (Ugent and Peterson 1988; Piperno and Pearsall 1998); and aroids (Araceae) and yams (*Dioscorea* spp.) in the Indo-Pacific region extending from eastern India to New Guinea (Burkill 1935; Li 1970; Yen 1973). Thus, understanding vegetative propagation provides a truly global perspective on the long-term history of human selection and domestication of plants, practices of cultivation, and forms of agriculture.

The vegetative domestication pathway is primarily, although often not exclusively, asexual; that is, it is clonal and occurs through the planting of reproductively viable plant parts, such as fragments of underground storage organs, divided root mass, and vine/stem cuttings. In most root crops, the vegetative plant part harvested, stored, and then replanted is also the part eaten—whether corms in taro (*Colocasia esculenta*), rhizomes in ginger (*Zingiber officinale*), root tubers in manioc (*Cassava manihot*), or stolon tubers in potato (*Solanum tuberosum*) and yams (*Dioscorea* spp.). In other cases, vegetative reproduction can be enabled by another plant part, such as stem/vine slips in sweet potato (*Ipomoea batatas*).

Sexual reproduction still occurs in some cultivars, whereby new, spontaneously emergent sexually reproduced phenotypes are adventitiously incorporated into vegetatively propagated stock. Such practices were important generators of high varietal differentiation in manioc and sweet potato, as well as other root crops. Even in some vegetatively propagated crops that are considered almost exclusively asexual today, sexual reproduction is implicated in the early stages of domestication, such as in greater yam (*Dioscorea alata*; Lebot 2009). For most root crops, with the exception of some tap roots (e.g., carrots, *Daucus carota*) and bulbs (e.g., onions, *Allium* spp.), the primary practice of intervening in plant reproduction is vegetative, and prolonged clonal cultivation seems to have reduced sexual reproductive capacity in some crops (Denham et al. 2020).

Long-term domesticatory relationships can be envisaged for root crops that encompass plant management at the least intensive end of the spectrum to mechanized monoculture at the most intensive end (Harris 1972; Hather 1996). For instance, many nonfarming, foraging groups around the world practice vegetative propagation behaviors such as tending favored plants and replanting viable plant parts during gathering of tubers (Barton and Denham 2018). Over time, human-mediated selective pressures would have gradually increased as a result of preferential plant management and resource intensification through

burning, disturbance, and replanting, as well as adventitious growth from discarded and misplaced plant-parts around camps. These practices include both conscious and unconscious selective pressures on plants, yet they are conceptually distinct from other forms of cultivation because they do not involve planting in prepared plots or fields.

At some point in the domestication history of a crop, people started to transplant viable plant-parts of preferred phenotypes into prepared plots to cultivate them and eventually began to disperse them under cultivation (figure 10.7). A general loss of sex in clonal plants under cultivation, namely, a general lowering of sexual reproductive capacity, was stimulated through various mechanisms: some likely inadvertent (unconscious selection), such as movement into new environments (i.e., altitudes and latitudes) where sexual reproduction was not possible; some more conscious, such as preferential selection of sterile forms; and some highly deliberate, such as harvesting before flowering and seed-set. Thus, numerous practices worked to suppress sexual reproduction, with subsequent selection being driven primarily by clonal variation under cultivation.

Clonal propagation exerted greater selective pressure on field crops and allowed a higher degree of control over preferred phenotypes than sexual reproduction. However, in most vegetative crops the degrees to which domestication represents “morphogenetic” fixation, or a plastic response to growth environment, including cultivation practices, are unclear (Denham et al. 2020). It can be argued that plastic adaptation to growth environments in vegetatively propagated crops drives phenotypic variation, in contrast to sexually reproduced crops in which phenotypes are less plastic and more tightly regulated genetically. Nonetheless, even though plasticity may be more visible in clonally reproduced crops there

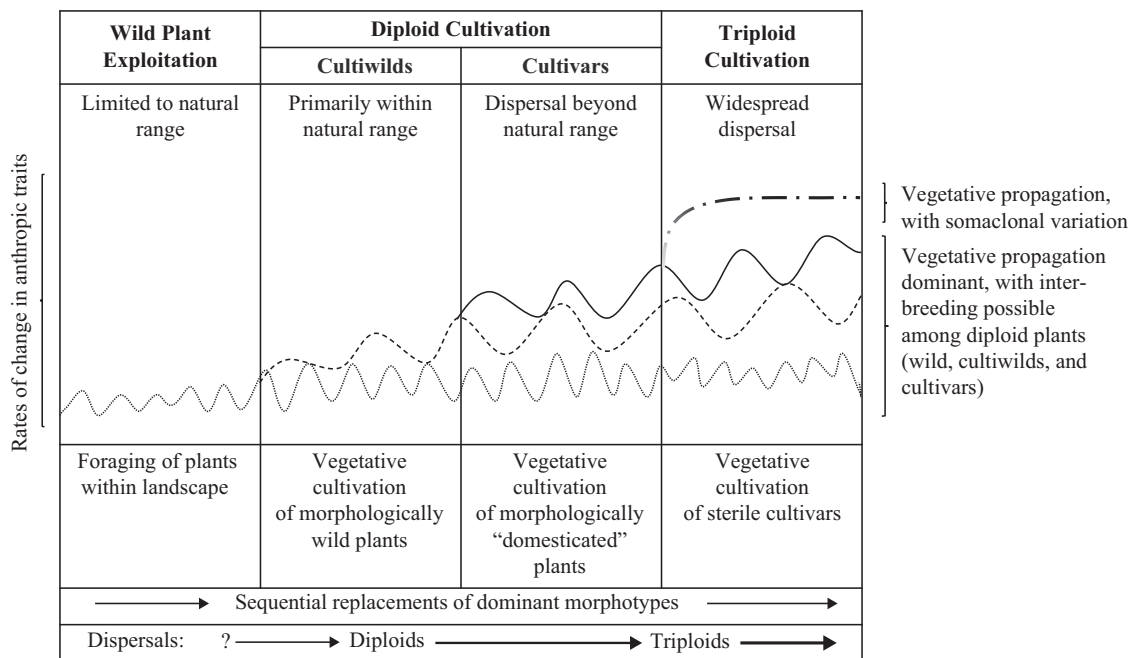


Figure 10.7

The schematic representation of a typical vegeticulture domestication trajectory for a root crop with triploid cultivars, such as taro (*Colocasia esculenta*). Exploitation of wild plants (dotted line) eventually led to the cultivation of morphologically wild plants, called *cultiwilds* (dashed line), with the subsequent generation and cultivation of diploid cultivars (solid line), from which triploid cultivars emerged, dispersed, and became the dominant cultivar groups (dotted-dashed line).

is still underlying genetic variation resulting from somaclonal mutations, introgression for sexually viable plants, and other phenomena.

Cultivation practices are intended to create growth environments that favor larger edible underground storage organs by increasing the friability of soils, maintaining soil water content, and reducing competition from other vegetation. Other practices are designed to foster specific phenotypic responses, whether sequential harvesting to prolong timing of production (e.g., many root crops), density of planting for apical dominance (e.g., manioc and some yams), or watering to reduce toxins (e.g., manioc). For many vegetatively propagated plants, though, it is hard to clearly determine domestication traits because either the wild progenitor is unknown, such as for greater yam (*D. alata*) and sweet potato, or little is known about the plant ecology, genetics, and cultivation history of related wild species.

Furthermore, most vegetative crops have low archaeobotanical visibility, principally because the key plant-parts exhibiting potential domestication traits are either soft tissues that preserve only rarely in burned, desiccated, or waterlogged form or are preserved as less diagnostic phytoliths and starch grains. Furthermore, much of the phenotypic variation in plant macrofossils, such as archaeological parenchyma, and in microfossils, such as phytoliths and starch grains, are poorly understood in terms of establishing domestication traits relative to wild populations. To exacerbate matters, these techniques are not routinely applied during archaeological investigations, aside from some noteworthy exceptions (for example, Piperno and Pearsall 1998; Mindzie et al. 2001; Denham et al. 2003; Iriarte et al. 2004).

Furthermore, in comparison with many cereals, the phylohistories and geodomestication pathways for most vegetatively propagated root crops are poorly characterized or are only beginning to be clarified genetically, as is the case for manioc (Wang et al. 2014), potato (Hardigan et al. 2017), sweet potato (Roullier et al. 2013a; Muñoz-Rodríguez et al. 2018), taro (Chair et al. 2016), and some yams (Malapa et al. 2005; Scarcelli et al. 2019). However, caution is needed when relying on genetic data from modern populations to infer plant domestication and dispersal histories. In recent times, as in the deep past, specific lineages have come to dominate cultivated assemblages following successive waves of dispersal and widespread adoption, resulting in the near-wholesale replacement or marginalization of preexisting genetic lineages (e.g., Roullier et al. 2013b). Limitations of the archaeobotanical and genetic data hinder a detailed reconstruction of the domestication histories for most root crops.

Taro (*Colocasia esculenta*) is a widespread aroid, exploited primarily for an underground corm, although its leaves are also cooked as a vegetable. Its natural range is poorly determined and potentially extends from the Indian subcontinent, mainland and island Southeast Asia, northward to East Asia and eastward to New Guinea–northern Australia, with multiple domestications potentially occurring within this range. Yams (*Dioscorea* spp.) are a pantropical genus utilized primarily for underground, edible tubers. Yam species were independently domesticated in tropical climates of the Americas, Africa, India, and Southeast Asia–New Guinea, where they are regionally significant subsistence crops. In the Island Southeast Asian–New Guinea region, archaeobotanical finds of several yam species (*D. alata*, *D. esculenta*, *D. bulbifera*) and taro, as well as other aroids (i.e., *Alocasia* spp. and *Amorphophallus* spp.), have been documented at Pleistocene- and Holocene-aged sites, yet few of these finds occur in contexts associated with agriculture. Exceptions include starch grain residues of yam and taro, as well as aroid seeds, from early and mid-Holocene contexts at Kuk Swamp in the highlands of New Guinea (Fullagar et al. 2006).

These findings do not indicate that these root crops were domesticated at Kuk; rather, archaeobotanical association with archaeological evidence of cultivation, pedological indications of digging, and palaeoecological evidence of montane forest disturbance suggest that they were cultivated there. Much more recent finds of taro corms, along with banana (*Musa* sp.) skin peelings and sugarcane (*Saccharum officinarum*) stem sections from archaeological contexts associated with the Islamic port at Quseir al-Qadim in Egypt, indicate westward movement of these plants to the Red Sea by at least AD 1040–1160 (Van der Veen and Morales 2011), although all three crops were likely introduced to Africa and the Mediterranean much earlier (Murdock 1960; Perrier et al. 2011; Grimaldi et al. 2018).

In a similar vein, the domestication histories of several major root crops in the Americas are relatively poorly documented archaeobotanically. Although mixed, food-producing economies have been proposed for the Americas during the early and mid-Holocene (Iriarte 2007), there are no clear signatures of domestication in the archaeobotanical record of vegetatively propagated crops for this period. Two globally significant crops, potato (*Solanum tuberosum*) and sweet potato (*Ipomoea batatas*), are discussed below as exemplars.

Potato (*Solanum tuberosum*) originally formed part of regionally important root crop assemblages in the Central Andes, where they were all vegetatively propagated and of variable importance at different altitudes, including oca (*Oxalis tuberosa*), ulluco (*Ullucus tuberosus*), and mashua (*Tropaeolum tuberosum*) (National Research Council 1989). Potato spread significantly only after its post-Columbian introduction to Europe. Desiccated macro-remains of potato (*S. tuberosum*) were excavated from 10,000-year-old contexts in Chilca Canyon, coastal Peru (Engel 1970), as well as from multiple sites dating from 4,250 to 3,500 years ago in the Casma Valley, coastal Peru (Ugent, Pozorski, and Pozorski 1982; Ugent and Peterson 1988). Although these finds are at a remove from the inferred loci of domestication in the Peruvian Andes, their significance varies: the early Holocene remains may not constitute dispersal under cultivation, especially since there are no comparable finds for several thousand years, whereas those dating to ~4,250–3,500 years ago are clearly part of a mixed farming economy.

Sweet potato (*Ipomoea batatas*) may have undergone two domestications in the Americas: a northern domestication in Central America/the Caribbean generated the *camote* and *batata* cultivar groups, and a southern domestication centered on Peru and Ecuador generated the *kumara* cultivar groups (Roullier et al. 2013a). It is an orphaned crop, which has no known wild progenitor. Sweet potato was widely cultivated up to mid-latitudes in North, Central, and South America, as well as in the Caribbean during pre-Columbian times. Sweet potato had also dispersed widely through Eastern and Central Polynesia from at least ~AD 1200–1300, eventually reaching the Hawaiian archipelago, Easter Island, and New Zealand—most probably due to human agency (Yen 1974; Roullier et al. 2013b), although natural seed dispersal cannot be completely discounted (Muñoz-Rodríguez et al. 2018). Archaeobotanical evidence for sweet potato is rare; the earliest comprises desiccated tubers dating to ~4,250 years ago in the Casma Valley, coastal Peru (Ugent, Pozorski, and Pozorski 1981).

The practices, locations, and timings for the domestication of most vegetatively propagated root crops are poorly known. Comparable geodomestication pathways for other types of vegetatively propagated field crops, such as bananas (*Musa* cvs.; Perrier et al. 2011)

and sugarcane (*Saccharum officinarum*) (Grivet et al. 2004), are variable in terms of the coverage and consilience of archaeobotanical and genetic evidence. Furthermore, there appears to be considerable variation among clonal plants in the degree to which observed phenotypic change may be considered plastic (i.e., that which is environmentally induced) or nonplastic (i.e., that which is under direct genetic control).

As in grain-based agriculture, vegetative systems also attract weeds, which have generated parasitic domesticoids, although these are less well studied. In vegetational systems in Southern Ethiopia, for example, weeding is a routine practice to reduce competition from perennial monocots such as *Cynodon* grasses and *Cyperus rotundatus* sedges, which compete with younger *Ensete ventricosum* (Ethiopian banana) cultivars (Tsegaye and Struik 2002). Among the common weeds in Southern Ethiopian fields and gardens are several Araceae species, which are tolerated as their tubers can be processed for edible starch, and in some cases they have come to be cultivated as crops in their own right, as in the case of *Arisaema schimperianum*, *Amorphophallus abyssinicus*, and *Sauromatum nubicum* (Westphal 1975; Engels and Goettsch 1991). Vegetative agriculture in Island Southeast Asia and the Pacific also features several species that span the spectrum from weed to crop. Examples include the kudzu vine (*Pueraria montana*, syn. *P. lobata*) and Polynesian arrowroot (*Tacca leontopetaloides*), both of which are widespread as weeds (Holm et al. 1979), although occasionally they are intentionally planted. Nevertheless these taxa may sometimes be processed for the starchy tubers or for medicine (Barrau 1958; Kirch 1978; Spenneman 1994) and were translocated with the spread of agriculture in the Pacific. It has been speculated that kudzu was originally a major crop and later became a feral weed (Barrau 1965). Kudzu is native to parts of mainland East and Southeast Asia, as well as some islands (Philippines), but it is now ubiquitous in anthropogenic habitats in Melanesia and is known as an invasive clonal weed elsewhere in Polynesia, North America, and Australia (Van der Maesen 2002; Bodner and Hymowitz 2002). Polynesian arrowroot is thought to be native to sandy coastal habitats in Island Southeast Asia and was introduced to the isolated island of Palau around 3,000–2,000 years ago (Farley et al. 2018).

Despite limitations of record and the confounding effects of plasticity, some general trends in the character of vegetative crop plant domestication have been elicited (Denham et al. 2020). There seem to be convergent tendencies to lessen sexual reproductive capacity and increase the size of the edible portion. Other traits seem to be more plastic, including yield, ease of harvesting, timing of fruit production, some aspects of plant architecture, and some defensive adaptations.

Whereas in sexually reproduced crops phenotypic and genotypic transformations associated with early domestication are often portrayed as occurring in lockstep, the considerable variation exhibited by vegetatively propagated plants probably represents phenotypic plasticity resulting from active and recurrent practical management of the plant and its growth environment by people. In some ways, the domestication of sexually reproduced cereals and legumes is articulated primarily in terms of Darwinian adaptation to anthropic environments and human selection under cultivation, whereas vegetatively propagated plants exhibit a greater degree of plastic adaptation to growth environments, in a Lamarckian-type mechanism to drive phenotypic variation.

Archaeobotanical Evidence for Domestication of Long-Lived Perennials

A fourth category of domestication pathway is represented by most fruit and nut trees and long-lived vines. These taxa are woody perennials that have long generation times (5, 10, or 15 years) and lower productivity per year than most annual crops. This is thought to make it harder for them to undergo selection, in contrast to large populations of each annual generation (Zohary, Hopf, and Weiss 2012). An added factor affecting productivity is that most fruit trees have high interannual variability in production, with off years of low productivity (Goldschmidt 2013), which fall on the spectrum of mast-fruiting patterns known for many nuts (Vander Wall 2001). Added complications are that most of these species have insect pollination and therefore regular cross-pollination, in contrast to the high selfing rate in most cereals or other annual crops. Selfing should make it easier to fix favored traits in cereals than would be the case in tree crops (Zohary 2004). Since ancient times most reproduction has been by vegetative means, that is, cloning from cuttings, which is a common practice in orchards and vineyards today. Vegetative cuttings have the advantage of preserving favored traits and reproducing varieties (Zohary and Spiegel-Roy 1975; Zohary, Hopf, and Weiss 2012) and involve a high degree of conscious selection because people deliberately favor phenotypes. The diversity represented by varieties must have originated from cycles of sexual reproduction, as well as the occasional case of somatic mutation—which is well-known in citrus fruits, for example. Our current understanding is that after initial domestication involving sexual reproduction and planting from seed, cloning and vegetative plant propagation became the predominant mode of cultivation; grafting developed later (figure 10.8).

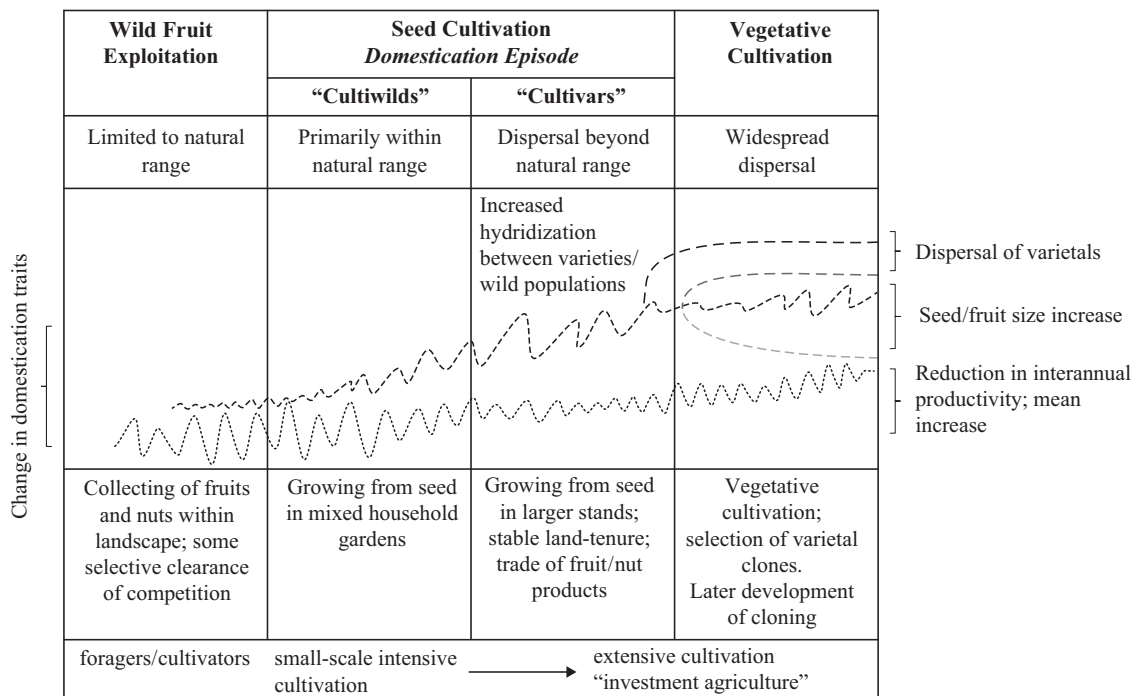


Figure 10.8 The schematic representation of a typical tree fruit crop domestication trajectory indicating how phenotypic changes are expected to correlate with changes in human economy and technology.

Archaeobotanical evidence, however, has made clear that initial cultural uses and domestication must have involved a predominance of reproduction for seed for some millennia (Weiss 2015; Fuller 2018). This is indicated by evidence across several crops, from several different world regions, for directional change in seed size, in particular increasing seed/endocarp length, which is linked to larger fruit sizes with a higher proportion of edible flesh (Liphschitz and Bonani 2001; Zheng, Crawford, and Chen 2014; Dighton et al. 2017; Fuller 2018; Bonhomme et al. 2020). This is well documented in several Mediterranean fruits (grapes, olives, dates), as well as in East Asian peaches, Japanese chestnuts, Pacific nuts such as *Canarium*, Indian mangos, and Mesoamerican avocados, which demonstrates convergent evolution across different cultural traditions and phylogenetically distant taxa (Fuller 2018). It is unclear to what extent this selection for larger fruits might have involved a conscious element on the part of cultivators, but it can be estimated that the rate of phenotypic change, when corrected for generation length, was at least as fast and often faster than evolutionary rates recorded in early seed crops (Fuller 2018). Alongside selection for increased seed size is contemporaneous evidence for the translocation of cultivated fruit trees beyond their regions of origin, with a major period of range expansion coinciding with the era of most marked morphological change in seed/fruit size. This can be illustrated with current data from peaches domesticated in China (figure 10.9) and date palms from western Asia (figure 10.10). Of interest is that after a period of largely directional change in seed morphology, such changes stop and then further variation can be documented between regions and assemblages. This is likely to coincide with the dominance of vegetative propagation of particular varieties of these fruits.

Some generalizations can be offered about how tree fruit impacted human ecology and the organization of land use. Where such crops were added to agricultural traditions that

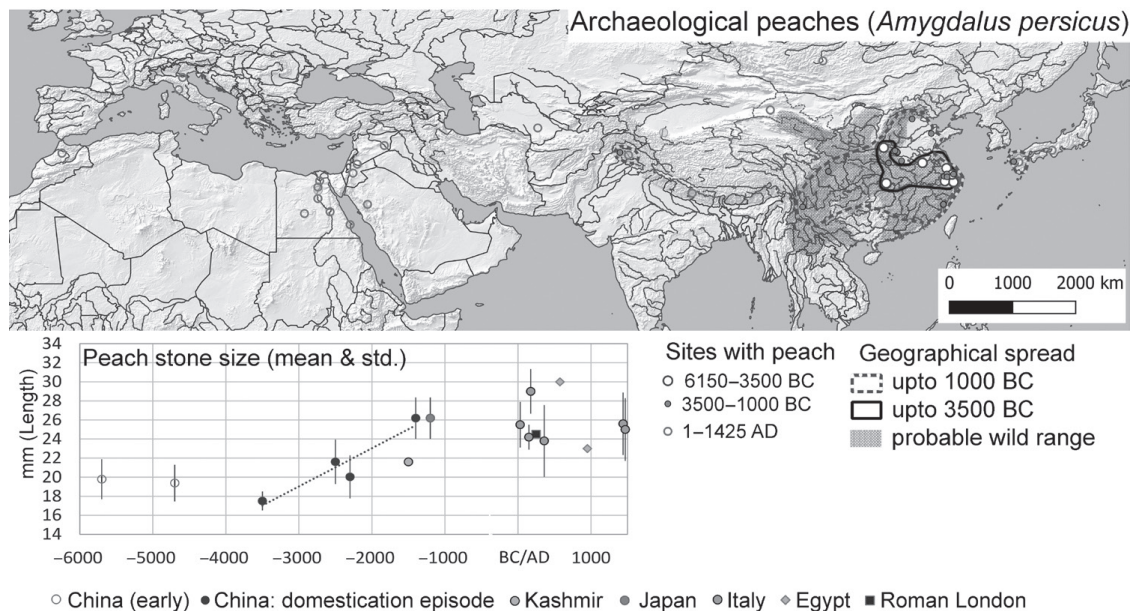


Figure 10.9

Peach (*Amygdalus persicus*) as an example of perennial tree fruit domestication. The map above shows the distribution of archaeological evidence of peaches, illustrating the gradual geographical expansion. Graph at lower left illustrates average and standard deviations of measured stone length plotted against median age estimate, highlighting a domestication episode of morphological change (after Fuller 2018; Fuller and Stevens 2019b).

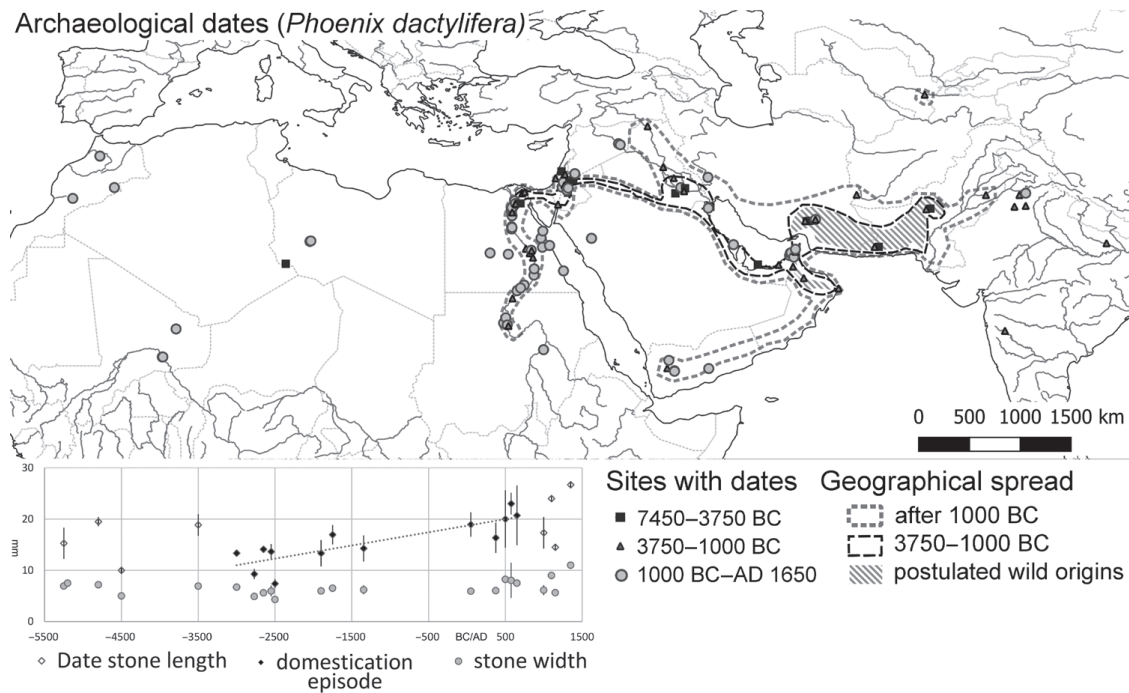


Figure 10.10

Date palm (*Phoenix dactylifera*) as an example of perennial tree fruit domestication. The map above shows the distribution of archaeological evidence of dates, illustrating the gradual geographical expansion. Graph at lower left illustrates average and standard deviations of measured stone length plotted against median age estimate, highlighting a domestication episode of morphological change (after Fuller 2018; Flowers et al. 2019, dataset S1; Fuller and Stevens 2019b).

were already based on seed crops, the addition of tree fruits expanded agriculture not just in diversity but in the nature of temporal cycles, regional flows in foodstuffs, and specialization in production (Renfrew 1972; Sherratt 1999; McCorrison 2009). Unlike annual cereals, these tree-fruits required many years of labor investment before providing returns. This implies changes in temporality—namely, longer time horizons in cycles of planting and return—as well as in social systems—namely, establishment of land tenure over longer periods (of decades or generations). Taken together these have been characterized as moving from earlier “sustainability agriculture” of the Neolithic toward an “investment agriculture” of the Metal Ages (Fuller and Stevens 2019b). With large scale production, surpluses of tree fruit production contributed to increasing trade, because they became commodities of dried fruits, nuts, wine, or olive oils, and as such played key roles in expanding the geographical range over which agricultural producers and consumers were interlinked.

Discussion: Temporalities of Practice and Transmission

If domestication is defined as the management of captive plants and animals, regardless of whether those plants and animals are modified due to domestication by humans, then the earliest detectable changes in the archaeological record provide only minimum dates of origin. In other words, the historical origin of a particular human-domesticated symbiosis is necessarily older than the earliest detectable morphological markers detected in the archaeological record. (Schultz et al. 2005, 164)

Archaeology enables reconstruction of several different pathways of plant domestication, including for cereals, secondary cereals (derived from weeds), vegetatively propagated root crops, and fruit trees. Other possible domestication pathways include ecosystem engineering—sometimes referred to as “landscape domestication” (Yen 1989; Terrell et al. 2003)—and fiber crops, selected for their raw material use, such as cotton (Viot 2019), jute, and several others. Similarly, multiple pathways to domestication have been proposed for domestic animals, principally commensal, directed, and prey pathways (Zeder 2012; Larson and Fuller 2014).

Despite inherent limitations, archaeology has enabled the domestication of several plant species, especially several cereals and legumes, to be reconstructed fairly accurately in terms of the relative timings for the emergence and fixation of domestication traits such as nonshattering and larger grain sizes (Fuller et al. 2014, 2018). For most other types of plant enmeshed in different domestication pathways, archaeological traces are scant. Instead, archaeological inferences often rely on a combination of archaeological, pedological, and palaeoecological evidence for inferring the character of cultivation systems in the past; these provide often indirect evidence for inferring plant domestication drawing on botanical, ecological, and genetic information about present-day domesticates and their wild progenitors, but without the direct evidence of preserved morphological change. There are, though, several key aspects of human-plant domesticatory relationship that emerge.

Foremost, early forms of plant exploitation, movement, and cultivation were designed to favor specific phenotypes, which gradually and inadvertently led to the accumulation of specific genetic lineages at the expense of others. Plants that were adapted to human environments benefited, whether disturbed environments in and around settlements, within managed landscapes, or within small-scale cultivated plots. Through time, selection for favored phenotypes inadvertently led to the accumulation of domestication traits within managed subpopulations relative to the wild population as a whole. Human suppression of other herbivores may also have shifted selection away from some plant defenses, especially where human harvesting led to increased seed dispersal.

However, a stepped change in selective pressure can be envisaged in which people cultivated increasingly curated propagules, whereby seed and vegetative parts were increasingly derived only from cultivated stock within anthropic landscapes that were increasingly denuded of wild plants. The genetic isolation of cultivated stock due to a reduction or absence of cultivated–wild plant interbreeding—as well as through vegetative propagation and movement beyond the natural range—would have greatly accelerated the genotypic divergence of cultivated plants from the wild progenitor population. In other words, these conditions would have greatly accelerated the emergence of domestication traits.

The period of pre-domestication cultivation, during which domestication traits emerged and rose toward fixation, can be estimated to take anywhere from 1,000 to 4,000 years in studied seed crops. Recent estimates of the strength of selection for domestication traits near the start of these domestication pathways suggest that there was an even earlier lead-in with some very weak symbiotic selection (Allaby et al. 2017). Indeed, it is estimated that human-plant symbioses began anywhere from 4,000 to 10,000 years prior to clear evidence for cultivation. These time spans can be contrasted with the period of ~30 million years between the time when attine ants evolved cultivation behaviors and when higher attines coevolved with obligate domesticated fungi (McGhee 2011, 225; Schultz et al.

2005). Unlike among insect agriculturalists, no speciation took place among the cultivating hominins (chapters 12 and 14, this volume), although cultivation may have played a key role in the social and cultural differentiation of human groups. In addition, many of the same human groups also domesticated livestock during the same periods as plant domestication (Larson et al. 2014), and while this is also paralleled in ant-aphid mutualisms, these involved very divergent Formicidae ants (McGhee 2011, 226; chapter 8, this volume).

Although early forms of seed-based cultivation (for cereals and legumes) and vegetative propagation (root crops, as well as bananas and cane grasses) were deliberate interventions in plant reproduction and growth, the domesticatory consequences of these practices were, at least initially, cumulative and unintentional. However, later forms of secondary cereal domestications, and some fruit tree domestications, were more rapid and undertaken by communities already practicing other forms of cultivation; here, people would have been more aware of the longer-term consequences of their actions in terms of making plants more amenable to exploitation and use. In the case of woody fruiting species, these were initially cultivated sexually with some subsequent clonal propagation and later grafting of preferred fruit varieties onto hardy root stock. Only beginning with these later, diversification domestications (secondary seed crops, fruit trees) does anything approaching *artificial selection* (as opposed to unconscious selection) begin to play a role in human agriculture.

Sauer (1952), among others, speculated that vegetative forms of propagation preceded seed-based cultivation. Currently, there is no robust archaeological evidence to support this claim. Rather, people in different parts of the world engaged in different forms of cultivation, which led to seed-based and vegetative domestication pathways. Currently this appears to relate more to environmental differences between biomes and available plant foods: vegetative cultivation is more associated with wetter, tropical environments or mountain zones, whereas early seed-based cultivation is found in semi-arid open ecosystems—including tropical savannahs and temperate steppes.

Certainly, in parts of the world where vegetative propagation is the dominant mode of cultivation, people incorporate into their plots cuttings from varieties grown in neighboring communities as well as those from wild/feral plants (Denham 2018). Over time, these processes can lead to the wholesale replacement of cultivated lineages, as documented for the sweet potato in Polynesia (Roullier et al. 2013b) and postulated for taro in New Guinea (Denham 2018). Furthermore, flowering, pollination, and seed-set are often deliberately suppressed under vegetative cultivation to increase yield, maintain starch or sugar contents, obtain preferred taste, and so on, as well as to restrict sexual reproduction and retain preferred phenotypes (Denham 2018). These human practices are cognate with many of those undertaken by fungus-growing ants (Mueller et al. 2005; Schultz et al. 2005; chapter 14, this volume). Ants vegetatively propagate fungus and periodically translocate and incorporate wild fungi into cultivated stock within their nests, as well as domesticated fungi from other nests. These practices lead to the wholesale replacement of fungal lineages over time. Also comparably to human practices, ants engage in a range of cultivation and harvesting practices to suppress fruiting and sexual reproduction in fungi in order to maintain preferred fungal production and limit gene flow among cultivated and wild fungal populations.

Early forms of human-plant domesticatory relationship can be conceived as mutualistic: they benefited both species. Over time, as environments of cultivation became increasingly anthropic and wild populations became increasingly sparse, this relationship became one of asymmetrical control with people as proactive partner and plants as reactive partner.

Cultivated plants became increasingly reliant on people for reproduction (i.e., in regard to gathering of nonshattering seed heads, processing, storage, and sowing) and growth (i.e., in specially prepared ground within demarcated plots or fields, often improved in terms of moisture and nutrient availability and protected from pests and competitor species). Only with modern agribusiness and genetically engineered seed stock has the relationship changed further toward enslavement—a characteristic most starkly seen in modern factory farming of animals.

The coevolution of humans and domesticates, however, was achieved through two very different forms of evolutionary transmission. Changes in the plants ultimately occurred in their genomes as they acquired adaptations either fixed through vegetative cloning or through the fixation of recessive alleles for many seed crops. Human adaptation mainly took the form of cultural information, practices, technologies, and traditions—memes in the broad sense, which were both handed down through human generations and had the potential to be transmitted laterally between unrelated human individuals and across cultures (see, e.g., Shennan 2002). As noted by Schultz (chapter 14, this volume), this makes humans facultative farmers, not obligate ones. The lateral transmission process of culture—of farming practices—contributed to regional trends towards increasing diversity of domesticated species tied into the human agricultural systems. A parallel in insects is the widespread evidence of lateral transmission of fungal cultivars across species (Mueller et al. 2005), but a contrast is the fungal monocultures that characterize many ant, termite, and beetle crops. The evolution of farming in insects took millions of years and involved adaptive speciation, whereas human facultative farmers could adapt much more rapidly in part through testing and choosing among a diversity of crops at any one time.

The increasing biodiversity of human agriculture over the long term is evident on local, continental, and global scales. However, a reversal away from agricultural diversity has occurred in many regions, mostly over the past century, as the human-domesticated relationship has shifted towards high-throughput monoculture at the expense of species or varietal diversity (Perfecto, Vandermeer, and Wright 2009). This is paralleled by the move to enslavement that can be taken to characterize many industrial animal farms, and perhaps commercial crop varieties with “genetic use restriction technologies” (Lombardo 2014). It is in this more recent phase, since the twentieth century, that humans have begun to use chemical herbicides to control weeds among their crops. By contrast many ants evolved the use of chemical control of weeds among their farmed fungi as an essential part of their cultivation symbioses (Mueller et al. 2005; chapter 11, this volume). Thus despite remarkable parallels, the various pathways of evolution of human agricultural systems and those of insects have been quite different. In this chapter we have outlined four alternative pathways of crop domestication by people, all of which have shared a tendency to contribute to increasing crop diversity over time and increasing lateral transmission across cultures, although these tendencies may have been reversed in the late industrial era.

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