

# Current perspectives and the future of domestication studies

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**It is difficult to overstate the cultural and biological impacts that the domestication of plants and animals has had on our species. Fundamental questions regarding where, when, and how many times domestication took place have been of primary interest within a wide range of academic disciplines. Within the last two decades, the advent of new archaeological and genetic techniques has revolutionized our understanding of the pattern and process of domestication and agricultural origins that led to our modern way of life. In the spring of 2011, 25 scholars with a central interest in domestication representing the fields of genetics, archaeobotany, zooarchaeology, geoaerchaeology, and archaeology met at the National Evolutionary Synthesis Center to discuss recent domestication research progress and identify challenges for the future. In this introduction to the resulting Special Feature, we present the state of the art in the field by discussing what is known about the spatial and temporal patterns of domestication, and controversies surrounding the speed, intentionality, and evolutionary aspects of the domestication process. We then highlight three key challenges for future research. We conclude by arguing that although recent progress has been impressive, the next decade will yield even more substantial insights not only into how domestication took place, but also when and where it did, and where and why it did not.**

evolution | selection | agriculture | human ecology | human history

The domestication of plants and animals was one of the most significant cultural and evolutionary transitions in the ~200,000-y history of our species. Investigating when, where, and how domestication took place is therefore crucial for understanding the roots of complex societies. Domestication research is equally important to scholars from a wide range of disciplines, from evolutionary biology to sustainability science (1, 2). Research into both the process and spatiotemporal origins of domestication has accelerated significantly over the past decade through archaeological research, advances in DNA/RNA sequencing technology, and methods used to recover and formally identify changes

in interactions among plants and animals leading to domestication (2–4). In the spring of 2011, 25 scholars with a central interest in domestication and representing the fields of genetics, archaeobotany, zooarchaeology, geoaerchaeology, and archaeology met at the National Evolutionary Synthesis Center to discuss recent progress in domestication research and identify challenges for the future. Our goal was to begin reconsidering plant and animal domestication within an integrated evolutionary and cultural framework that takes into account not just new genetic and archaeological data, but also ideas related to epigenetics, plasticity, gene-by-environment interactions, gene-culture co-

evolution, and niche construction. Each of these concepts is relevant to understanding phenotypic change, heritability, and selection, and they are all fundamental components of the New Biology (5) and Expanded Modern Evolutionary Synthesis (6).

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This PNAS Special Feature presents a collection of papers emanating from that meeting. Some evaluate past evidence and views on fundamental aspects of plant and animal domestication and offer a consensus perspective through the lens of more recent empirical findings and ideas. Others explore how best to investigate challenging research questions. All of the papers provide examples of how domestication research has illuminated, and will continue to enrich, our understanding of evolutionary and cultural change. In this introduction to the Special Feature, we present an outline of what is currently known about the pattern and process of domestication and we discuss foundational issues in domestication research, both in general and in light of the collected contributions. We conclude with a summary of outstanding questions and challenges.

### Spatial and Temporal Patterns of Domestication

The beginnings of plant and animal domestication related to food production began globally 12,000–11,000 y ago at the end of the most recent ice age and during the transition to the Present Interglacial Period (7) (Figs. 1 and 2). Although often characterized as rapid and the result of explicit human intention (8, 9), domestication is a complex process along a continuum of human, plant, and animal relationships that often took place over a long time period and was driven by a mix of ecological, biological, and human cultural factors (2, 3). The process

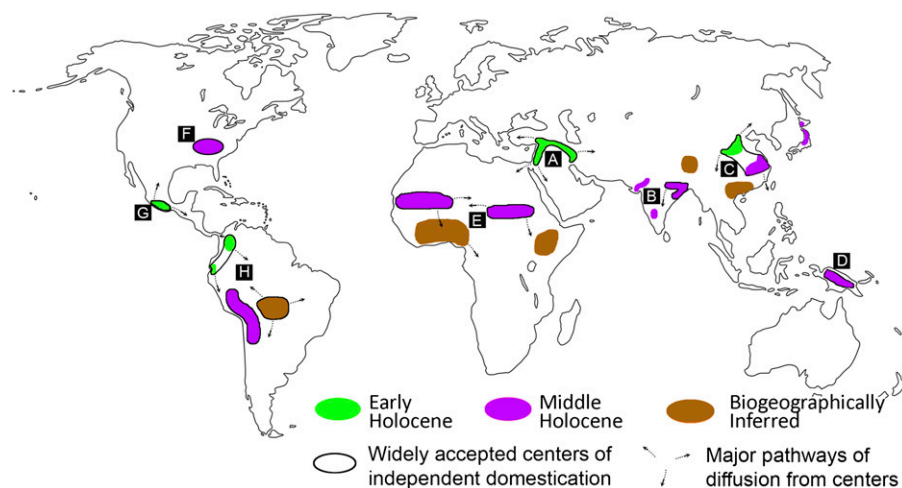
encompassed a wide range of relationships, from commensalism/mutualism to low-level management, and directed control over reproduction (10, 11), although these stages did not necessarily progress in a ratchet-like fashion from wild to domestic.

The addition of a human selective component on top of a natural selection regime has enhanced the power of domestication to reveal insights into long-standing evolutionary issues, including those highlighted below. Although we eschew one-size-fits-all definitions for either plants or animals, domestication can be generally considered a selection process for adaptation to human agro-ecological niches and, at some point in the process, human preferences. Importantly, the wild progenitor species of domesticated taxa must have possessed the potential to live in the context of human ecologies, and to express traits that were favorable for human use, harvesting, and edibility. Finally, the presence of gene flow between populations of domestic and wild plants and animals [and members of the same or closely related but geographically and genetically differentiated domesticated species (12)] often results in modern populations that appear as if they arose outside the regions where the initial domestication process took place (13). As a result, it is crucial that researchers carefully evaluate whether multiple domestications of a single species occurred (13, 14), making sure to reserve the term “domestication” solely for the initial independent process, and to avoid

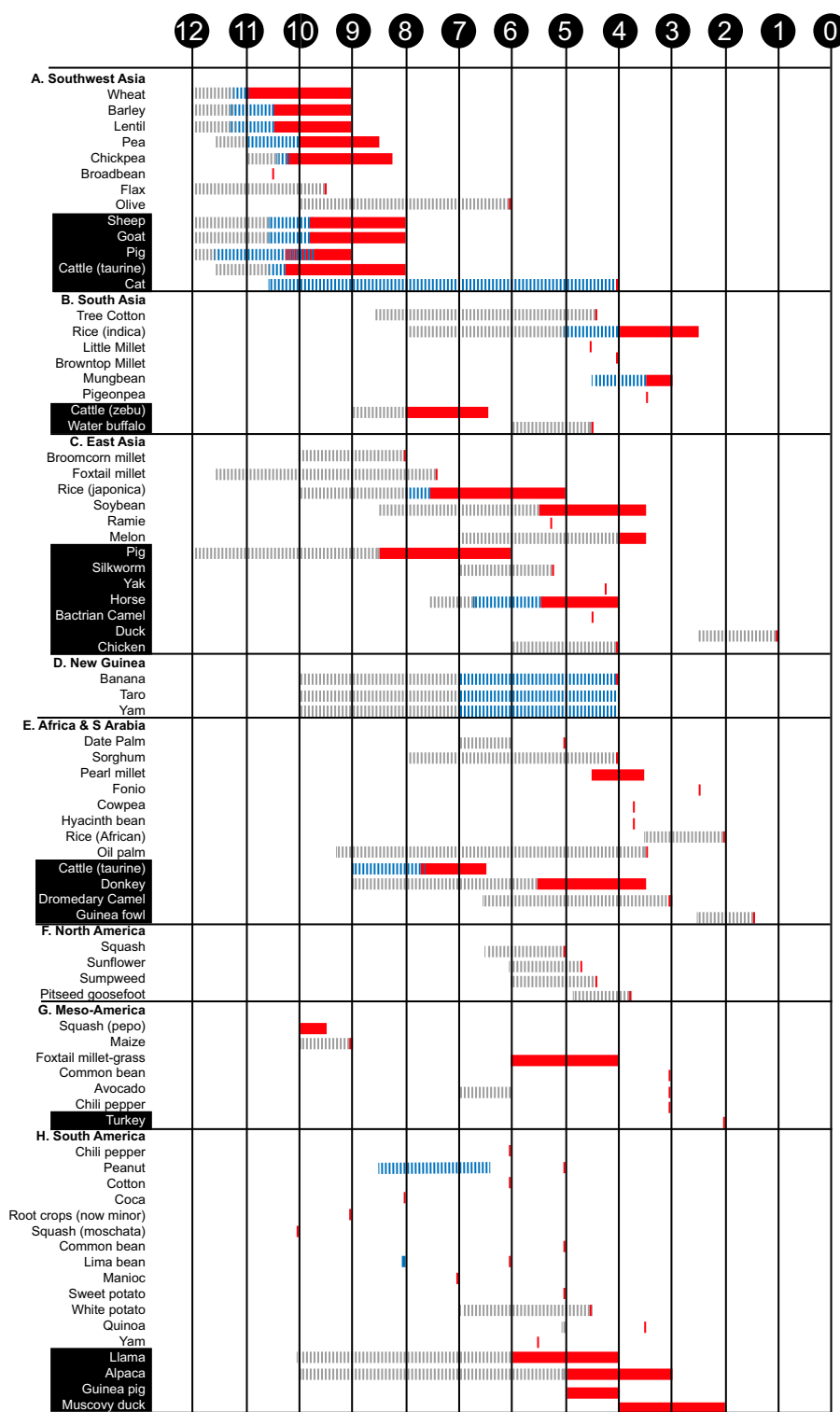
using the term to refer to subsequent admixture that often incorporated genetic and morphological characteristics of wild populations that were never independently domesticated (12, 13).

An increasingly rich and diverse corpus of data from molecular and archaeological research generated over the past 15 y now makes it clear that agriculture began independently over a much larger area of the globe than was once thought, and included a diverse range of plant and animal taxa (Figs. 1 and 2). At least 11 regions of the Old and New World were involved as independent centers of origin, encompassing geographically isolated regions on most continents, but several more have been suggested (Fig. 1) (3, 7, 11, 15, 16). Some of these regions were the sources of major domesticates that spread to adjacent regions, whereas others involved more regionally important species often regarded as “minor” crops today (7, 17). The combined data also clearly show that two major chronological periods are of greatest interest: the transition to the Holocene from about 12,000–9,000 B.P. (all ages are calendar years before CE 1950), and the middle Holocene between 7,000 and 4,000 B.P. (Fig. 1). Dogs were a significant exception and were certainly domesticated in the late Pleistocene before the establishment of agriculture, although both the geographical origins of dog domestication and claims for domestic dogs in ~30,000-y-old contexts remain contentious (18). In the New World, crop domestication occurred thousands of years before animal domestication, whereas the opposite was true in areas such as Africa, Arabia, and India. Some of the asynchronous patterns in individual plant and animal species from different regions may be the result of patchy evidence, as well as the lack of a clear distinction between “primary” (truly independent) vs. “secondary” (e.g., inspired by diffusional processes) domestication.

Hunting and gathering was the primary subsistence strategy for more than 95% of the time since the origin of *Homo sapiens* 200,000 y ago (19). Theories and explanations for why human cultures abandoned this long-term and apparently successful subsistence strategy and turned to food production continue to attract discussion and intense debate. Traditionally, the transition to agriculture was viewed as the result of a few single agents or “prime movers” that operated at the onset of the Holocene. Climate change, human population pressure, and culturally driven alternatives, such as “competitive feasting,” are among numerous additional agents proposed by generations of archaeologists (20–24). Simple unidirectional



**Fig. 1.** A map depicting likely centers where the domestication of at least one plant or animal took place. Black outlines surround the most widely accepted independent centers of domestication, and sources of major diffusions of domesticates are indicated by arrows. Green and purple regions, respectively, are those where the domestication process took place during the late Pleistocene to early Holocene transition (12,000–8,200 B.P.), and in the middle Holocene (8,200–4,200 B.P.). Brown regions represent areas where, at present, the evidence for domestication is interpreted based upon the presence of domestic forms indigenous to these regions found outside of their native distributions. Letters A–H correspond to those listed in Fig. 2. Additional detail and references associated with each region are found in the *SI Text*.



**Fig. 2.** A chronological chart listing the regions where, and the time frames over which, key plants and animals were domesticated. The numbers in the black circles represent thousands of years before present. Gray dashed lines represent documented exploitation before domestication or posited as necessary lead-time to domestication. Blue dashed lines represent either the management of plants or animals (including translocation) or predomestication cultivation of plants, neither of which were associated with morphological indications of domestication. Red bars frame the period over which morphological changes associated with domestication are first documented and a short, solid red bar represents the latest time by which domestication occurred. Although early Holocene plant domestication took place independently in both the Old and New Worlds, early Holocene animal domestication was restricted to the Near East. In addition, the majority of plants and animals on this list were domesticated in the middle Holocene. Additional details and references associated with each taxon are found in Table S1. Letters A–H correspond to those found in Fig. 1.

explanations, however, have proved unsatisfying for a number of researchers, and significant tensions remain between camps advocating different explanatory blueprints. The issue poses an important remaining challenge in domestication research (25) (see below).

### Early Domestication Stages

The initial stages of the multispecies networks involved in domestication were critical because humans acted as: (i) dispersal agents (managing the reproduction of cultivated plants and controlling the mobility, range and density of domestic livestock); (ii) agents of (conscious or unconscious) selection, favoring the reproductive success of particular behavioral and phenotypic variants); and (iii) ecosystem modifiers, who (along with natural environmental changes) alter the developmental conditions and hence the characteristics of associated organisms.

So what is a domesticated plant or animal and how does it differ from its wild ancestor? From a present-day perspective, it is possible to recognize suites of common traits that make up the so-called “domestication syndrome” (26–28), and presumably many of these were key to early selection along the wild-to-domesticated trajectory. In plants, the syndrome is defined by a wide variety of traits that, depending on the species, may include: a reduced ability to disperse seeds without human intervention, reduction in physical and chemical defenses, reduction in unproductive side-shoots, reduction in seed dormancy, bigger seeds, more predictable and synchronous germination, and in some seed-propagated species, bigger and more inflorescences. In animals, these traits include: endocrine changes, increased docility, altered reproduction pattern and output, altered coat color, floppy ears, facial neotony, usually a reduction in size, and other changes in body proportions (26). Recent genetic and archaeological research, however, has demonstrated that not all of these traits arose at the same time in either plants or animals. In addition, it has been helpful to separate genes that controlled the traits that were under early selection (domestication genes) from those that were selected later to produce diversified and improved crops and animals (improvement genes) (4).

The strength of selection for “domestication syndrome” gene variants and their speed of fixation remains controversial. Although strong selection with rapid evolution of domestication traits within as little as 100–200 y has been suggested (8, 9, 29), recent archaeological studies have questioned these conclusions, at least for cereal domestication.



In wheat, barley, and rice, it took ~2,000–4,000 y to fix the nonshattering spikelet phenotype, a key indicator of cereal domestication (7). There are other indications in the Near East of long periods of cultivation without morphological evidence of domestication, including specific field weed flora associated with morphologically wild cereals and legumes, and large stores, suggesting reliance on cultivated production of morphologically wild species (30, 31). Doust et al. (32) show that factors previously underappreciated, such as G×E (gene-by-environment) and epistasis (gene-by-gene) interactions may have been important in slowing domestication rates. A comparison of rates of phenotypic evolution between wild and domesticated species also indicates that, contrary to expectations, evolutionary rates in domesticated species are not generally faster than those observed in wild species (7). Indeed, selection strengths for some traits are at the same level as the strength of natural selection acting on wild species, or even slightly lower (33).

The evidence for a slow pace of domestication implies a cultural period in agricultural origins called “predomestication cultivation” (PDC) (34). These periods lasted for many centuries before fully domesticated cereals appeared, as has been inferred from evidence in the Near East and China (7, 31, 35). Instances of PDC have also recently been documented in northwestern South America (36). Increasing evidence for PDC goes hand-in-hand with increasing indications of a nonsimultaneous development of the suite of traits that make up the domestication syndrome, in turn raising questions about when exactly to call archaeological remains “domesticated” and how and in what order the domestication syndrome was assembled.

These factors also make it more likely that crops were independently brought under cultivation more than once, even within a given “nuclear region,” then hybridized with cultivated or domesticated plants from other regions to become the domesticated versions we study today (37, 38). Neither genetic nor archaeobotanical studies can easily sort out these different activities, which has led to increased skepticism of the traditional models that purport rapid events taking place in a single location to explain transitions from wild to domesticated species (39, 40). In addition, the recent reevaluation of the speed of cereal domestication has led to a renewed discussion of unconscious vs. conscious selection. Charles Darwin was the first to explicitly articulate the difference between conscious selection during domestication, in which humans directly select for

desirable traits (called by Darwin “methodical” selection) (1), versus unconscious selection, where traits evolve as a by-product of growth and natural selection in field environments, or from selection on other traits. In rice, for example, glutinous grains most likely arose from conscious selection by certain Asian cultures for this cuisine-prized trait (41). In contrast, seed nonshattering in cereals is thought to have arisen as a by-product of stalk-harvesting by sickles or harvest knives, which select for seeds that do not readily fall off the stalk, rather than a result of a conscious strategy associated with beating seed heads into baskets (29). Other domestication traits in grasses are generally thought to result from unconscious selection, including seed size, seed dormancy, synchronous seed ripening, and apical dominance (27).

Most domesticated plants are not cereals, and other crops with different domestication syndromes may have had faster rates of domestication once humans targeted them for cultivation, and been more prone to have traits selected by conscious selection. The great cultural geographer Carl Sauer (42) insightfully noted that squashes, beans, and various root crops (along with maize, the premier cereal crop of the Americas) were not mass-harvested and mass-planted, nor likely mass-selected, as the Old World cereals were. Individual harvesting and selection by early farmers, who would be expected to choose and deliberately propagate the crop attributes most useful to them when they could distinguish the useful phenotypes, could foster conscious selection and result in faster fixation of crucial and preferred domestication traits, such as the loss of toxicity and increased size of starch storage organs in tubers and roots. Fruit nonbitterness in squashes and melons, major early domesticates in all regions of the Americas and parts of Asia and Africa may also have been rapidly and consciously selected. For example, botanical remains from human teeth indicate that the loss of fruit bitterness in the squash species *Cucurbita moschata* took place by at least 9200 B.P., only 800 y later than the first evidence for its domestication. In fact, the loss may have taken place even earlier because the seed traits used to document domestication do not inform fruit-flesh characteristics (36, 43). Arguments for relatively fast, conscious selection have also been made for the important seed dormancy trait in Old World lentils and peas (44).

What about conscious vs. unconscious selection in animals? Marshall et al. (12) make a compelling case that intentional breeding of females was largely absent during the early stages of domestication for a wide range

of species. This theory, along with what probably was considerable gene flow between wild and early managed animals (13), poses challenges to a number of commonly held assumptions about early domestication in some species relating to interpretations of genetic bottlenecks and molecular sequences more generally, the number of times a species was domesticated, and how various domestication traits emerged and were maintained in the long term. Clearly, many questions persist about the roles of directed vs. undirected selection across the spectrum of domesticated plants and animals.

Research over the past few decades has made it clear that prehistoric humans around the world significantly modified their environments, sometimes before and during the process of plant and animal domestication, and the role of humans in the enduring modification of environments is no longer underestimated (45–49). A uniquely important aspect of human environmental modification is the additional role cultural transmission plays in maintaining patterns of enduring local ecologies, resulting in a strongly enculturated ecological inheritance. Because they can often be traced archaeologically, cultural transmission processes have received increasing interest and mathematical modeling in the social sciences (50–52) and are embedded both in practice and in material settings (e.g., terraces, canals, mounding, soil management, lassos, penning, somatic modifications such as castration, food-processing tools). Although the process of cultural inheritance differs from that of genetics, it plays a crucial role in maintaining both cultural practices over generations and environments in which domestication and husbandry occurred and were maintained. Human intentionality and knowledge systems must have been key components among the interacting mechanisms within these bio/eco-cultural environments, and cultural transmission provided a basis for the maintenance of cumulative innovation. Traditional ecological knowledge over the longer term has maintained crop landrace diversity, and remains important for biodiversity distribution and ecosystem services more generally (53).

### Genetic and Evolutionary Insights from Domestication

The study of domesticated species has led to increased interest in several important issues in genetics and evolutionary biology, including the underlying genetic architecture of adaptations and parallel evolution. Genetic research is increasingly identifying

domestication genes, especially in plants (4). By contrast, many fewer domestication genes have been identified in animals (13). With the exception of coat-color genes, genetic variants that can be unambiguously assigned to early stages in domestication in animals have not yet been revealed. There are several possible reasons for this. First, discovering the molecular basis of domestication traits is relatively easy and inexpensive in plants compared with animal populations because early animal selection likely focused on behavioral and other characteristics (such as tameness and altered reproduction), with complex genetic foundations that are more difficult to study than classic morphological traits (54). Second, there may simply be few domestication loci with major effects in animals. Early animal domestication may have happened by shifting the allele frequencies at many loci, each with small individual effects, thereby altering the phenotype. This scenario would be consistent with the observation that many domestic animals (e.g., pigs) can readily establish feral populations that in many aspects mimic the phenotype of their wild ancestors (55).

Thus, an important question for both plants and animals is whether the striking phenotypic changes seen during domestication are under the control of single or multiple genes. Thus far, separate studies have identified both single (or few) genes and combinations of numerous genes of small effect, depending on the approach and species in question (4). To some extent, different inferences concerning the genetic architecture of domestication can be because of different methodological approaches. Forward genetic approaches, such as quantitative trait loci (QTL) mapping and genome-wide association studies have the capability of finding multiple loci controlling phenotypic traits, and thus to interpret a domestication trait as under the control of multiple genes (4). Reverse genetic approaches concentrate on particular genes and cannot, by themselves, discover multiple loci for a particular phenotype. Genes in reverse genetic approaches are often chosen because their mutant phenotypes in model systems, such as chicken, mouse, *Arabidopsis*, maize, and rice, are analogous to phenotypic differences between wild and domesticated species. It is then possible to ask whether sequence changes in the locus explain phenotypic differences. An example of this approach involves a mutation of the transcription factor *ramosa1* (*ra1*) locus in maize that results in loss of floral branches (56). Differences in the *ra1* locus were later found to be correlated

with differences in floral branching in maize and other grasses (57). However, it is not the only gene involved, as shown by QTL studies that indicated up to five significant QTL regions controlling these traits (58). Finally, a recent study (59) demonstrated that the action of *sh4* in rice is not always sufficient to produce nonshattering phenotypes.

An additional question is whether the same genes underlie similar phenotypic shifts in numerous domesticated plants and animals. In other words, is there parallelism from the same underlying genetic and developmental pathways or convergent evolution of unrelated taxa using unrelated gene networks (60)? In grasses, such forms are particularly striking, and similar awned and awnless spikelets, hulled and free-threshing grain, black-, red-, and straw-colored seed coats are found in multiple domesticated cereals. The geneticist Vavilov termed this phenomenon the Law of Homologous Series (61), and the first phase of comparative mapping in the grasses, using restriction fragment-length polymorphism markers, inferred QTL for shattering in rice, sorghum, and maize to be at the same location (62). Further work has proved equivocal, since most genes for shattering in grasses are unique to each domesticated lineage (63), though a recent study has shown that the major locus for shattering in sorghum corresponds to minor loci in rice and maize (64). Nevertheless, some mutations in domesticates are in fact parallel mutations. For example, variants of the *MC1R* locus are responsible for independently derived pig coloration patterns (65). Moreover, mutations at this gene appear to be associated with difference in color patterns in numerous domestic animals (66). A similar example of parallel evolution is associated with the rise of sticky cereals in northeast Asia, where glutinous rice, millets, and barley, among others (41, 67), are the result of alternative mutations at the *Waxy* gene (68–70).

Whether mutations selected during domestication were novel or were present as standing genetic variation in ancestral wild populations is a question of increasing interest. It has traditionally been assumed that phenotypic change and new adaptations arise from new mutations, but recent research increasingly shows that standing genetic variation plays important roles in a variety of species (71). For example, traits present as variants in wild progenitors today include the gene for tomato fruit size (*fw2.2*) (72), maize plant architecture (e.g., *teosinte branched1*) (73), seasonality controls (74, 75), and seed size [usually polygenic (76)]. Fast morphological evolution in cultivated plant popula-

tions may have ensued as favorable phenotypes, including those initially exposed by genetic or external environmental perturbations in response to the new field conditions, may have been preferentially selected by farmers who were not constrained by mutation rates (77, 78). Having said that, several traits in domesticated plants, including those associated with the reduction of seed-shattering in legumes and grasses, are deleterious in the wild, and if present, are rarely expressed phenotypically. In animals, analyses of modern dog genomes have revealed a handful of mutations (not found in extant wolves) with large effects on morphological variation, although given the predominance of selection for novel and unusual characteristics in dogs, this pattern is likely the exception (79). In many other domestic animals, humans likely selected for trait variants that were already present in ancestral populations, thereby altering the frequencies of the standing genetic variation.

As success in isolating domestication-related genes proceeds, it should become easier to distinguish between standing and new genetic variation, as well as to recognize parallelism in *de novo* mutations among domesticated species. Additionally, as the availability of genome-wide sequence data for domesticated species increases, it is becoming increasingly feasible to use selective sweep mapping to identify genomic regions that have been targets of selection during domestication without a priori information on candidate domestication genes (e.g., ref. 80). Challenges associated with this approach include the fact that the trait or traits affected by the selected genes may not be known, that selection that favors a *de novo* mutation during the domestication process will generate a more conspicuous signature of a selective sweep than selection for mutations that were already segregating in populations of the wild progenitor, and that some demographic processes can mimic the effects of selection on patterns of genetic variation. Understanding the different genetic architecture of domestication across crop types and in animals remains a major challenge for genetic research.

One new promising direction is the study of ancient DNA. Our increasing ability to identify selected mutations for domestication-associated traits in archaeological plant and animal remains is providing a unique temporal trajectory of the evolution of domesticated species, and the selection strengths that acted upon selected genes. One such example tested claims that two different genes (*TSHR* and *BCDO2*) were involved in

early chicken domestication by typing the mutations in ancient European chickens. Because the wild-type alleles of both genes were segregating at a high frequency as recently as 500 y ago, the ancient DNA evidence demonstrated that the modern ubiquity of a mutation, even one that differentiates domestic and wild populations, cannot automatically be conflated with an ancient origin linked to early domestication (81).

### Key Challenges for the Future

The enormous amount of empirical data compiled on domestication and associated human- and naturally driven circumstances during the past decades has naturally led to the generation of a number of questions, some of which pose key future challenges.

### Filling in Gaps on Maps

One of the fundamental challenges of domestication research is filling the gaps that remain in both geographical and genomic maps. Genetic research provides a growing toolkit for elucidating the relationships between domesticates and their wild ancestors, and between the traits that make domesticates suited to anthropogenic environments and their underlying genetic architecture. The successes of genetics, touched upon above, at identifying domestication genes have been numerous and mostly recent. Expanding this repertoire remains a priority, but it is increasingly evident that we also need more evidence from ancient DNA, so that patterns found in modern populations can be compared with those of the past, and geographies and phylogeographic and adaptive hypotheses can be tested over the evolutionary time period of domestication.

In addition, archaeological research has many gaps on the chronology and regional sequences of domestication of plants and animals, and the contexts of agricultural origins. Recent research has shown that increased sampling and methodological developments have made it possible to clearly document cereal domestication [e.g., rice (82)], push back the earliest evidence for both the domestication of maize in southern Mexico (83) and the arrival of crops in northern Peru (36), and to recognize the likely independent processes of agricultural origins and domestication in New Guinea (45), parts of India (84), and Africa (85). These research successes within the past decade imply that more new information on more species from more regions and earlier periods can be expected and should be actively sought.

Related to this are important continuing challenges in determining why so few of the animal and plant species that were hunted

and gathered by ancestral human populations were ever domesticated (86), and whether most species were domesticated once or multiple times. We recognize that distinguishing these options is complicated, and it is increasingly clear that incomplete archaeological evidence and genetic data are open to conflicting interpretation. This aspect highlights the importance of explicit modeling and simulation of a range of hypotheses concerning the starting conditions and processes of domestication (14, 87). Factors potentially leading to confusion include the fact that multiple domestication episodes may be hidden from genetic view today as a result of both bottlenecks (in some cases leading to extinction) and introgression. Archaeobotany, for example, has increasingly recognized extinct morphotypes of domesticated wheat (88, 89), and ancient DNA can help to identify lost genetic lineages of crops. Introduced domesticates may introgress with local wild populations, thus capturing genetic and phenotypic variation that can later be misinterpreted as the independent domestication of distinct wild animal (13) and plant (e.g., rice) (90–92) populations. Resolving these issues requires more targeted ancient DNA research and more realistic and sophisticated modeling.

### Environmental and Ecological Contexts of Agricultural Origins

Although climate change remains the prime landscape and ecological modifier at the origins of agriculture, human behavior and the activities of diverse cultural traditions must be better understood. Beyond simply collecting more archaeological and paleoecological evidence, there is a need to broaden the study of past landscapes and their related ecosystems for both naturally derived features and the legacies of past human action. For example, more research should systematically map local and regional distributions of enriched soils, created through human activities, which are well known from Amazonia and Europe but much less well documented elsewhere (e.g., refs. 93, 94). Vegetation formations studied by plant ecologists and environmental historians may also be anthropogenic legacies, as has been suggested for a number of regions including South Asia and throughout the Americas (45, 53, 95, 94).

New or underdeveloped fields, such as ecological developmental biology (eco-devo) (96) and epigenetics (97)—together with mechanisms, such as developmental plasticity (98, 99)—are assuming increasing importance in the study of diversification, the origin of novelties, and evolutionary change. These fields should be extended to the realm

of domestication research, in part because phenotypic and genetic responses to natural- and human-created environmental variability are among the most neglected issues in domestication studies. As recent work with teosinte has shown, field- and laboratory controlled experiments are needed to better understand them (99). Another example is that although it has been inferred that large seed size was selected by soil disturbance and depth of burial (e.g., ref. 100), as presumably seeds with the largest mass were better able to emerge from deeper burial depths associated with cultivation practices, others have suggested that seed size increase may be a plastic phenotypic response to enriched soils of early cultivation (101). New experimental research (102) on different legume crops indicate seed mass was important for emergence in some species, including those predicted to conform to the burial hypothesis (60), but not in others, suggesting a common single mechanism for seed size increase was not at work. In another vein, Blumler's analysis (103), suggesting that the Near East was unusually well endowed with large seeded grasses pre-adapted to domestication, might explain the early and diverse domestication of plants in that region. In addition, Marshall et al. (12) make the point that epigenetic mechanisms should also be investigated in animal genetic responses during the domestication process.

A few scholars have discussed the potential role of climate shifts and atmospheric gas concentrations on biota at the transition between the late Pleistocene and early Holocene. More specifically, the authors have suggested that agriculture was a more favorable strategy in the Holocene as a result of these environmental shifts (e.g., refs. 99, and 104–107). Lower CO<sub>2</sub> and temperature reduced plant productivity, in part by reducing photosynthetic efficiency, thus exacerbating drought stress: effects that were more marked on C3 plants but also present to a surprising degree in C4 plants. Did the rapid increase of CO<sub>2</sub> and temperature at the onset of the Holocene make plants more attractive as a readily intensifiable resource and make cultivation more efficient? As plant productivity increased, why would some cultural traditions delay the shift in cultivation until the middle Holocene, and how can we connect the adoption of animal herding to changes in plant productivity? Although important global processes have doubtless impacted foragers and early cultivators, a great deal more research is necessary to unravel the causes, constraints, and exceptions to the early or middle Holocene transitions to farming.

Further experimental data on the impact of late-glacial and early Holocene temperatures



and CO<sub>2</sub> levels on the biological characteristics of wild progenitors of crops are needed to also understand how they may have influenced other phenotypic attributes of crop and animal progenitors on the eve of and during agricultural beginnings (99). Just as genetic studies of domestication have shown that conclusions drawn only from modern populations provide an incomplete and sometimes biased picture of the past (81, 108, 109), we need to better understand the interplay between past ecology, climate, plant phenotypic responses, and human activities.

### Why Hunters and Gatherers Turned to Cultivation and Herding

Explaining the origins of agriculture is still one of the most contentious issues for social scientists. Few dispute that the interplay of climate, human demography, and social systems through time and space played a significant role (110). Although some consider the primary driving factors to be patterns of climatic and ecological change, others argue for the primacy of social imperatives and changes within social systems (23, 24, 111). More generally, some scholars have claimed that no explanations are likely to be universally applicable (112), whereas others have adopted an explicitly comparative approach, identifying parallel processes and exploring common underlying patterns (7, 15, 25). Further progress on this issue should focus not only on the acquisition of more data, but also on marshaling and discussing existing evidence, which may suggest which factors driving agricultural origins were of greater importance. In a number of nuclear centers there are now fewer disagreements about the cultural history of early agriculture (including the chronology and the organisms involved), which should make explanatory endeavors less complicated. As known instances of agricultural origins are further clarified, we will have more parallel histories of domestication from which to derive commonalities or process and patterns of causation.

### Conclusions

The collection of papers presented in this Special Feature attempts to rise to the challenges outlined above. The articles illustrate a range of approaches to the study of domestication, including genetics, archaeological science, and anthropology, and raise new questions and hypotheses that are ripe for further testing. Even so, the new evidence and ideas presented here highlight a minority of the many species that were domesticated and subsequently improved by prehistoric cultures. Domest-

ication remains a vibrant research area in biology and archaeology 145 y after Darwin's seminal work (1), and the coming decade will no doubt generate satisfying and perhaps definitive answers to a wide range of outstanding questions.

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# Supporting Information

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## SI Text

**Information Related to Fig. 1.** Each of the eight macroregions listed below correspond with the named regions in Fig. 2. The regions are then subdivided into the subregions represented on the map in Fig. 1. The references following each region name represent key recent studies and good starting points and are not meant to be comprehensive. In addition to these references, we are indebted to a large volume of older, prominent, and foundational literature on early agriculture around the world (1–22). For each region, a list of key domesticates is given, followed by selected references in which more extensive literature sources can be found. Importantly, not all of the crops listed in each region were taken under cultivation and domesticated simultaneously.

**North America.** 1. Eastern North America (middle Holocene): squash (*Cucurbita pepo* ssp. *ovifera* var. *ovifera*), sunflower (*Helianthus annuus*), pitseed goosefoot (*Chenopodium berlandieri*), marshelder (*Iva annua*). Few of these crops become global crops. Larger scale agriculture developed later with the diffusion of maize (from Mesoamerica, below) (23, 24).

**Mesoamerica.** 2. Mesoamerica, lowlands and highlands (early Holocene): maize (*Zea mays*), common bean (*Phaseolus vulgaris*), sieva lima bean (*Phaseolus lunatus*), squashes (*Cucurbita pepo* ssp. *pepo*, *C. argyrosperma*), avocado (*Persea americana*), chili pepper (*Capsicum annuum*), Guaje tree bean (*Leucaena esculenta*), hogplum (*Spondias mombin*), jicama (*Pachyrhizus erosus*), chayote (*Sechium edule*) (25–31).

**South America.** 3. Northern Lowland South America (early Holocene): squash (*Cucurbita moschata*), leren (*Calathea allouia*), achira (*Canna edulis*), cocoyam (*Xanthosoma sagittifolium*), sweet potato (*Ipomoea batatas*). The extent of early cultural connections or differences with Northwestern Lowland South America (Northwestern Lowland South America, below) deserves further investigation, but independent origins of cultivation in one or both of these areas in the early Holocene is widely accepted (28, 32, 33).

4. Northwestern Lowland South America (early Holocene): squash (*Cucurbita ecuadorensis*), sea island cotton (*Gossypium barbadense*), jackbean (*Canavalia ensiformis*), cocoa (*Theobroma cacao*). The extent of early cultural connections or differences with Northern Lowland South America (above) deserves further investigation, but independent origins of cultivation in one or both of these areas in the early Holocene is widely accepted (28, 32, 34–36).

5. Central/Southern Andes (middle Holocene on current evidence): potato (*Solanum tuberosum*), quinoa (*Chenopodium quinoa*), Andean grain amaranth (*Amaranthus caudatus*), oca (*Oxalis tuberosa*), Ulluco (*Ullucus tuberosus*), common bean (*Phaseolus vulgaris*), lima bean (*Phaseolus lunatus*) (probably northern Andes), squash (*Cucurbita ficifolia*), guinea pig (*Cavia porcellus*), llama (*Lama glama*), alpaca (*Vicugna pacos*) (11, 37–39).

6. Southwestern Amazonia: manioc (*Manihot esculenta*), peanut (*Arachis hypogaea*), peach palm (*Bactris gasipaes*), chilis (*Capsicum baccatum*, *Capsicum chinense*), squash (*Cucurbita maxima*). Although the domestication processes in this region have not yet been documented archaeobotanically, some crops that originated here diffused to other regions in the early Holocene, suggesting that early Holocene evidence should be sought in this region (28, 32, 40–42).

**Africa.** 7. West African Savannah/Sahel (middle Holocene): pearl millet (*Pennisetum glaucum*), fonio (*Digitaria exilis*), black fonio (*Brachiaria deflexa*), African rice (*Oryza glaberrima*), cowpea (*Vigna unguiculata*), bambara groundnut (*Vigna subterranea*), baobab tree (*Adansonia digitata*), kenaf (*Hibiscus cannabinus*). Pastoralism based on cattle, sheep, and goat may have arrived before plant cultivation in this region, but there is no evidence for introduced crop cultivars (43–45).

8. West African tropical forest: oil palm (*Elaeis guineensis*), African yam (*Dioscorea cayenensis*), hausa potato (*Plectranthus rotundifolius*), dazo (*Plectranthus esculentus*), kola nut (*Cola nitida*, *Cola acuminata*). Historical linguistic evidence points to tree crops and tubers being important before the introduction of savannah cereals, like millet, although processes of diffusion of pearl millet from the north (from West African Savannah) are clear from archaeology (43, 45–48).

9. Sudanic Savannah (probably middle Holocene): sorghum (*Sorghum bicolor*), hyacinth bean (*Lablab purpureus*), roselle (*Hibiscus sabdariffa*), donkey (*Equus asinus*), African cattle (*Bos africanus*). African cattle likely result from introgression from a native African *Bos* into West Asian *Bos taurus*. Plant domestication processes are poorly documented in this zone (43, 45, 49).

10. Ethiopian plateau (probably middle Holocene): tef (*Eragrostis tef*), finger millet (*Eleusine coracana*), Ethiopian oat (*Avena abyssinica*), enset (*Ensete ventricosum*), yam (*Dioscorea cayenensis*), Ethiopian pea (*Pisum abyssinicum*), achote (*Coccinia abyssinica*), noog (*Guizotia abyssinica*), coffee (*Coffea arabica*). Historical linguistic evidence points to enset and tubers being important in the southwest of Ethiopia before the introduction of northern plateau cereals, like tef or finger millet. It is plausible that pastoralism and sorghum cultivation was first introduced from the Sudanic savannahs (above). Archaeobotanical and archaeozoological evidence are largely lacking in this zone (45, 50–52).

**Southwest Asia.** 11. Fertile Crescent (early Holocene): wheats (*Triticum* spp.), barley (*Hordeum vulgare*), lentil (*Lens culinaris*), pea (*Pisum sativum*), chickpea (*Cicer arietinum*), broadbean (*Vicia faba*), flax (*Linum usitatissimum*), sheep (*Ovis aries*), goat (*Capra hircus*), taurine cattle (*Bos taurus*), pig (*Sus scrofa*), cat (*Felis domesticus*) (53–57).

**South Asia.** 12. Savannahs of Western India (middle Holocene): water buffalo (*Bubalus bubalis*), chicken (*Gallus gallus*), little millet (*Panicum sumatrense*), sesame (*Sesamum indicum*), urd bean (*Vigna mungo*), horsegram (*Macrotyloma uniflorum*) and mungbean (*Vigna radiata*), melon (*Cucumis melo*). These domestications may postdate the arrival of domesticated animals, wheat and barley in the Indus region to the west, and thereby derive inspiration from West Asia (Fertile Crescent, above) (58–60).

13. South India (middle Holocene): browntop millet (*Brachiaria ramosa*), mungbean (*Vigna radiata*), horsegram (*Macrotyloma uniflorum*). The crop domestications may occur after the arrival of sheep/goat, cattle, but appear to precede introduced crops.

14. Ganges and eastern Indian plains: rice (*Oryza sativa* ssp.), sawa millet, pigeonpea (*Cajanus cajan*), cucumber (*Cucumis sativus*), and numerous cucurbits (*Luffa* spp., *Momordica charantia*, *Praecitrullus fistulosus*, *Trichosanthes cucumerina*, *Coccinia grandis*) (58, 59).

**East Asia.** 15. Chinese loess plateau (early Holocene): broomcorn millet (*Panicum miliaceum*), foxtail millet (*Setaria italica*), soybean (*Glycine max*), hemp (*Cannabis sativus*), peach (*Amygdalus*

*persicus*), apricot (*Armeniaca vulgaris*), pig (*Sus scrofa*). Some authors regard these regions as incorporating multiple independent centers of millet domestication (61–66).

16. Western Yunnan/Eastern Tibet: buckwheats (*Fagopyrum esculentum* and *Fagopyrum tartaricum*), yak (*Bos grunniens*), inferred from wild progenitor ranges. Possibly secondary domestications under influence of millets from Chinese loess plateau (above) (63, 67–70).

17. Lower-Middle Yangtze (middle Holocene): rice (*Oryza sativa* spp. *japonica*), ramie (*Boehmeria nivea*), silkworm (*Bombyx mori*), melon (*Cucumis melo*), pig (*Sus scrofa*). Some authors have argued for early cultural connections between early millet cultivators in Chinese loess plateau and the early rice cultivators in Lower-Middle Yangtze (62, 63, 66, 71).

18. Lingnan (tropical south China): yams (*Dioscorea* spp.), taro (*Colocasia esculenta*), sago palms (*Metroxylon sagu*), ducks (*Anas platyrhynchos*), Asian geese (*Anser anser*). Evidence for vegetational crops has been found from the middle Holocene before the arrival of rice, although evidence for cultivation is ambiguous

and could be regarded as inspired by earlier rice cultivation to the north (66, 72–74).

19. Japanese islands (middle Holocene): barnyard millet (*Echinochloa utilis*), azuki bean (*Vigna angularis*), soybean (*Glycine max*), Perilla (*Perilla frutescens*), burdock (*Arctium lappa*). Few of these crops became global crops, and soybean was separately domesticated in China. Larger scale agriculture developed later with the diffusion of rice and millets from China (from Chinese loess plateau and Lower-Middle Yangtze, above) (75–77).

**New Guinea.** 20. New Guinea (middle Holocene): banana (*Musa acuminata*), taro (*Colocasia esculenta*), giant taro (*Alocasia macrorrhiza*), breadfruit (*Artocarpus altilis*), yams (*Dioscorea* spp.), sago (*Metroxylon sagu*), sugarcane (*Saccharum officinarum*). Exploitation of some of these species is documented back to the early Holocene, although unambiguous evidence for cultivation systems is present only in the middle Holocene from the highlands. Archaeologically documenting morphological changes associated with domestication in many of these species has proven difficult (78–80).

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**Table S1. Additional details and references to support the table shown in Fig. 2**

Region/taxa	Exploitation before domestication		Management and predomestication cultivation		Domestication change		Sources
	Start	Finish	Start	Finish	Start	Finish	
<b>Southwest Asia</b>							
Wheat	12,000	11,250	11,250	11,000	11,000	9,000	(1–3)
Barley	12,000	11,250	11,250	10,500	10,500	9,000	(1–3)
Lentil	12,000	11,000	11,000	10,500	10,500	9,000	(1, 3)
Pea	11,500	11,000	11,000	10,000	10,000	8,500	(1, 3)
Chickpea	11,000	10,500	10,500	10,250	10,250	8,250	(1, 3, 4)
Broadbean	x	x	x	x	10,500		(1, 4)
Flax	12,000	9,500	x	x	9,500		(1, 5)
Olive	10,000	6,000	x	x	6,000		(6)
Sheep	12,000	10,500	10,500	9,750	9,750	8,000	(7–12)
Goat	12,000	10,500	10,500	9,750	9,750	8,000	(7–13)
Pig	12,000	11,500	11,500	9,750	10,250	9,000	(9, 10, 12, 14)
Cattle, taurine	11,500	10,500	10,500	10,250	10,250	8,000	(9, 10, 12, 14–16)
Cat	x	x	10,500	4,000	4,000		(17–19)
<b>South Asia</b>							
Tree cotton	8,500	4,500	x	x	4,500		(20, 21)
Rice ( <i>indica</i> )	8,000	5,000	5,000	4,000	4,000	2,500	(3, 22, 23)
Little millet	x	x	x	x	4,500		(23)
Browntop millet	x	x	x	x	4,000		(23)
Mungbean	x	x	4,500	3,500	3,500	3,000	(3, 23)
Pigeonpea	x	x	x	x	3,500		(23)
Zebu cattle	9,000	8,000	x	x	8,000	6,500	(24)
Water buffalo	6,000	4,500	x	x	4,500		(25)
<b>East Asia</b>							
Broomcorn millet	10,000	8,000	x	x	8,000		(26–28)
Foxtail millet	11,500	7,500	x	x	7,500		(28, 29)
Rice, <i>japonica</i>	10,000	8,000	8,000	7,500	7,500	5,000	(3, 22, 30)
Soybean	8,500	5,500	x	x	5,500	3,500	(3, 31)
Ramie	x	x	x	x	5,250		(32, 33)
Melon	7,000	4,000	x	x	4,000	3,500	(3, 34)
Pig	12,000	8,500			8,500	6,000	(35, 36)
Silkworm	7,000	5,250	x	x	5,250		(32, 37, 38)
Yak	x	x	x	x	4,250		(39)
Horse	7,500	6,750	6,750	5,500	5,500	4,000	(40–43)
Bactrian camel	x	x	x	x	4,500		(44–46)
Duck	2,500	1,000	x	x	1,000		(47, 48)
Chicken	6,000	4,000	x	x	4,000		(49–51)
<b>New Guinea</b>							
Banana	10,000	7,000	7,000	4,000	4,000		(3, 52–54)
Taro	10,000	7,000	7,000	4,000	x	x	(3, 52, 53)
Yam	10,000	7,000	7,000	4,000	x	x	(3, 52, 53)
<b>Africa and Arabia</b>							
Date palm	7,000	6,000	x	x	5,000		(55, 56)
Sorghum	8,000	4,000	x	x	4,000		(56, 57)
Pearl millet	x	x	x	x	4,500	3,500	(3, 58)
Fonio	x	x	x	x	2,500		(57)
Cowpea	x	x	x	x	3,750		(59)
Hyacinth bean	x	x	x	x	3,750		(56, 57)
Rice, African	3,500	2,000	x	x	2,000		(57, 60)
Oil palm	9,250	3,500	x	x	3,500		(57, 59)
Cattle, African	x	x	9,000	7,750	7,750	6,500	(61–70)
Donkey	9,000	5,500	x	x	5,500	3,500	(71–76)
Dromedary camel	6,500	3,000	x	x	3,000		(56, 77–82)
Guinea fowl			2,500	1,500	1,500		(83–85)
<b>North America</b>							
Squash	6,500	5,000	x	x	5,000		(3, 86, 87)
Sunflower	6,000	4,750	x	x	4,000		(3, 86, 87)
Sumpweed	6,000	4,500	x	x	4,000		(3, 86, 87)
Pitseed goosefoot	4,750	3,750	x	x	3,750		(3, 86, 87)

Table S1. Cont.

Region/taxa	Exploitation before domestication		Management and predomestication cultivation		Domestication change		Sources
	Start	Finish	Start	Finish	Start	Finish	
<b>Meso-America</b>							
Squash (pepo)	x	x	x	x	10,000	9,500	(3, 86, 88)
Maize	10,000	9,000	x	x	9,000		(89, 90)
Foxtail millet-grass	x	x	x	x	6,000	4,000	(91)
Common bean	x	x	x	x	3,000		(92)
Avocado	x	x	x	x	3,000		(93)
Chile pepper	x	x	x	x	3,000		(93, 94)
Turkey	x	x	x	x	2,000	x	(95)
<b>South America</b>							
Chili pepper	x	x	x	x	6,000		(96)
Peanut	x	x	8,500	6,500	5,000		(97)
Cotton	x	x	x	x	6,000		(97)
Coca	x	x	x	x	8,000		(98)
Now-minor root crops (arrowroot, leren)	x	x	x	x	9,000		(99, 100)
Squash (moschata)	x	x	x	x	10,000		(97)
Common bean	x	x	x	x	5,000		(92)
Lima bean	x	x	8,250	x	6,000		(92, 101)
Manioc	x	x	x	x	7,000		(3, 102, 103)
Sweet potato	x	x	x	x	5,000		(104)
White potato	7,000	4,500	x	x	4,500		(105)
Quinoa	5,000	x	x	x	3,500		(106)
Yam	x	x	x	x	5,500		(107)
Llama	10,000	6,000	x	x	6,000	4,000	(108, 109)
Alpaca	10,000	5,000	x	x	5,000	3,000	(108, 109)
Guinea pig	x	x	x	x	5,000	4,000	(110, 111)
Muscovy duck	x	x	x	x	4,000	2,000	(112, 113)

Dates (in calibrated years before present) listed in each of the three categories: exploitation before domestication, management and predomestic cultivation, and phenotypic change associated with domestication have been gleaned from the literature and rounded to the nearest 250 y. Cells with an "x" indicate there is no evidence as yet available for that specific category of management or change. Where there is a date for the start time for domestication change but the finish time has been left blank, this means that the date in the start time column represents a conservative time by which the organism had been domesticated, although there is yet no evidence for size or other morphological change following domestication. In addition, the missing end dates for quinoa and lima bean reflect gaps in the archaeobotanical records of these species. Because the domestication process operates over a continuum, defining categories and break points during the process is never clear-cut. The precision of numbers provided here should therefore be interpreted as estimates based upon the best available information, and many may shift as additional archaeological and genetic evidence is collected. Finally, there remain significant uncertainties and debates regarding whether many of the plants and animals (e.g., African cattle) listed here were domesticated independently in more than one region (114). In these cases, the listed dates represent those for the earliest domestication episodes in each region, although the processes may not have been truly independent.

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