

## SPECIAL FEATURE: INTRODUCTION

# 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, geoarchaeology, 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, geoarchaeology, 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

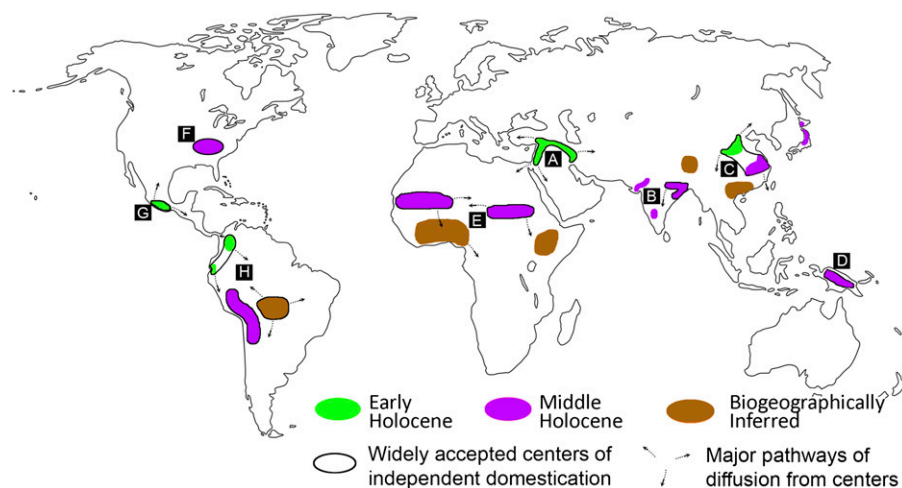
encompassed a wide range of relationships, from commensalism/mutualism to low-level management, and directed control over reproduction (10, 11), although these stages did not necessarily progress in a ratchet-like fashion from wild to domestic.

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

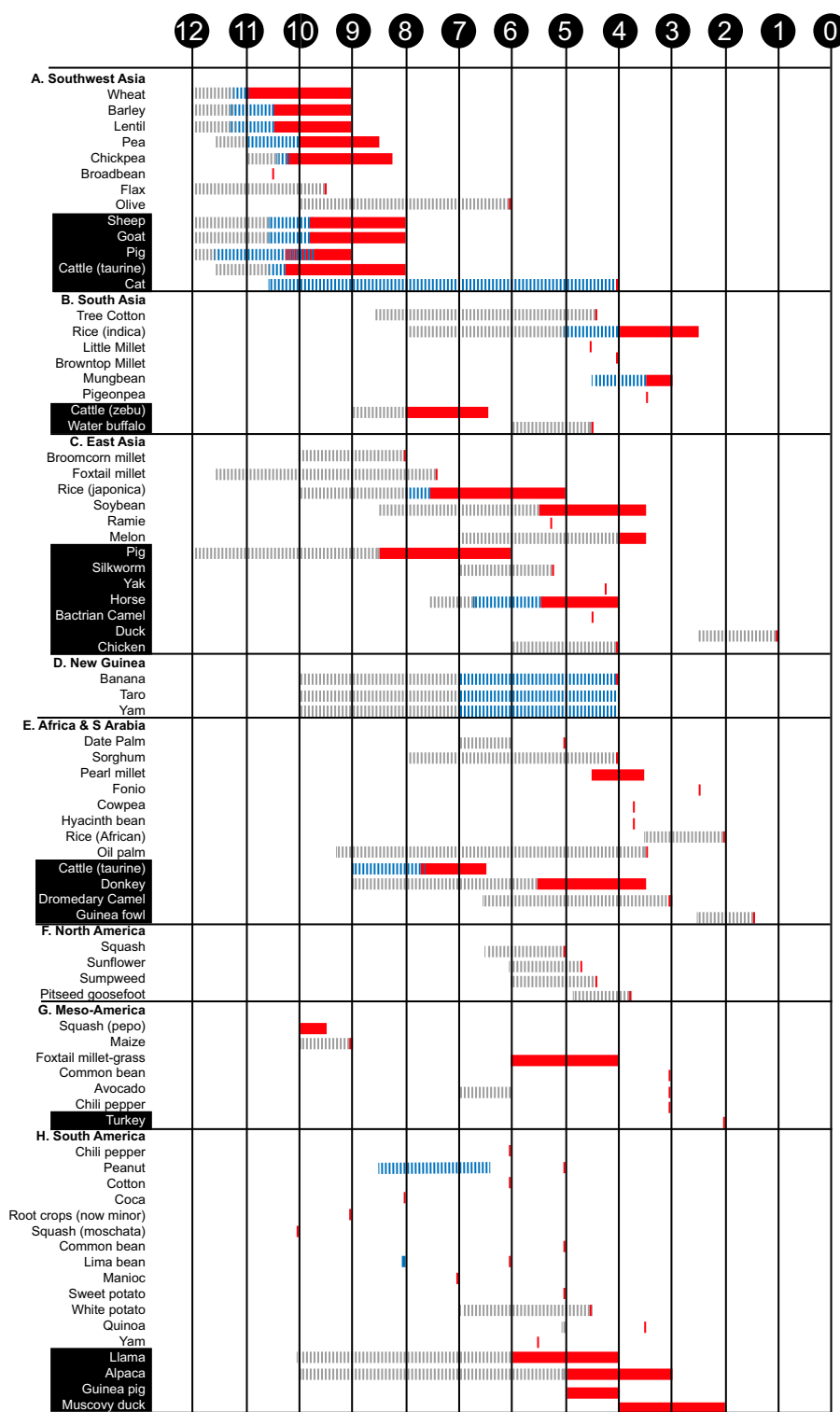
using the term to refer to subsequent admixture that often incorporated genetic and morphological characteristics of wild populations that were never independently domesticated (12, 13).

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 preadapted 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-

tication 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.

- 1 Darwin C (1868) *The Variation of Animals and Plants under Domestication* (John Murray, London).
- 2 Gepts P, et al., eds (2012) *Biodiversity in Agriculture: Domestication, Evolution, and Sustainability* (Cambridge Univ Press, Cambridge).
- 3 Price D, Bar-Yosef O eds (2011) *The Beginnings of Agriculture: New Data, New Ideas. Curr Anthropol 52* (Supp 4. Wenner-Gren Symposium Series; Univ of Chicago Press, Chicago).
- 4 Olsen KM, Wendel JF (2013) A bountiful harvest: Genomic insights into crop domestication phenotypes. *Annu Rev Plant Biol* 64:47–70.
- 5 Council MotNR (2009) *A New Biology for the 21st century. Committee on a New Biology for the 21st Century: Ensuring the United States Leads the Coming Biology Revolution* (National Academies, Washington, DC).
- 6 Wake M (2010) Development in the real world. Review of *Ecological Developmental Biology: Integrating Epigenetics, Medicine, and Evolution* by Gilbert, S.F., Epel, D. *Am Sci* 98(1): 75–78.
- 7 Fuller DQ, et al. (2014) Convergent evolution and parallelism in plant domestication revealed by an expanding archaeological record. *Proc Natl Acad Sci USA* 111:6147–6152.
- 8 Abbo S, Lev-Yadun S, Gopher A (2010) Agricultural origins: Centers and noncenters; a Near Eastern reappraisal. *Crit Rev Plant Sci* 29(5):317–328.
- 9 Innan H, Kim Y (2004) Pattern of polymorphism after strong artificial selection in a domestication event. *Proc Natl Acad Sci USA* 101(29):10667–10672.
- 10 Zeder MA (2012) Pathways to animal domestication. *Biodiversity in Agriculture: Domestication, Evolution and Sustainability*, eds Gepts P, et al. (Cambridge Univ Press, Cambridge).
- 11 Piperno DR (2011) The origins of plant cultivation and domestication in the New World tropics. *Curr Anthropol* 52(S4): S453–S470.
- 12 Marshall FB, Dobney K, Denham T, Capriles JM (2014) Evaluating the roles of directed breeding and gene flow in animal domestication. *Proc Natl Acad Sci USA* 111:6153–6158.
- 13 Larson G, Burger J (2013) A population genetics view of animal domestication. *Trends Genet* 29(4):197–205.
- 14 Gerbault P, et al. (2014) Storytelling and story testing in domestication. *Proc Natl Acad Sci USA* 111:6159–6164.
- 15 Barker G (2006) *The Agricultural Revolution in Prehistory: Why did Foragers Become Farmers?* (Oxford Univ Press, Oxford).
- 16 Fuller DQ (2010) An emerging paradigm shift in the origins of agriculture. *General Anthropology* 17(2):1–12.
- 17 Kraft KH, et al. (2014) Multiple lines of evidence for the origin of domesticated chili pepper, *Capsicum annuum*, in Mexico. *Proc Natl Acad Sci USA* 111:6165–6170.
- 18 Larson G, et al. (2012) Rethinking dog domestication by integrating genetics, archeology, and biogeography. *Proc Natl Acad Sci USA* 109(23):8878–8883.
- 19 McDougall I, Brown FH, Fleagle JG (2005) Stratigraphic placement and age of modern humans from Kibish, Ethiopia. *Nature* 433(7027):733–736.
- 20 Binford LR (1968) *Post-Pleistocene Adaptations*, eds Binford SR, Binford LR (Aldine, Chicago), pp 313–342.
- 21 Moore A, Hillman GC (1992) The Pleistocene to Holocene transition and human economy in Southwest Asia: The impact of the Younger Dryas. *Am Antiq* 57:482–494.
- 22 Cohen MN (2009) Introduction: Rethinking the origins of agriculture. *Curr Anthropol* 50(5):591–595.
- 23 Hayden B (2009) The proof is in the pudding: Feasting and the origins of domestication. *Curr Anthropol* 50(5):597–601.
- 24 Bowles S, Choi J-K (2013) Coevolution of farming and private property during the early Holocene. *Proc Natl Acad Sci USA* 110(22): 8830–8835.
- 25 Gremillion KJ, Barton L, Piperno DR (2014) Particularism and the retreat from theory in the archaeology of agricultural origins. *Proc Natl Acad Sci USA* 111:6171–6177.
- 26 Hammer K (1984) Das domestikationssyndrom. *Kulturpflanze* 32(1):11–34.
- 27 Harlan JR (1992) *Crops and Man* (American Society of Agronomy, Madison, WI), 2nd Ed.
- 28 Darwin C (1859) *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life* (John Murray, London).
- 29 Hillman GC, Davies MS (1992) Domestication rates in wild wheats and barley under primitive cultivation. *Préhistoire de l'Agriculture: Nouvelles Approches Expérimentales et Ethnographiques, Monographie du CRA*, ed Anderson PC (Centre de Recherches Archéologiques, CNRS, Paris), pp 113–158.
- 30 Weiss E, Kislev ME, Hartmann A (2006) Anthropology. Autonomous cultivation before domestication. *Science* 312(5780): 1608–1610.
- 31 Willcox G, Stordeur D (2012) Large-scale cereal processing before domestication during the tenth millennium cal BC in northern Syria. *Antiquity* 86(331):99–114.
- 32 Doust AN, et al. (2014) Beyond the single gene: How epistasis and gene-by-environment effects influence crop domestication. *Proc Natl Acad Sci USA* 111:6178–6183.
- 33 Purugganan MD, Fuller DQ (2011) Archaeological data reveal slow rates of evolution during plant domestication. *Evolution* 65(1): 171–183.
- 34 Harris DR, Hillman GC (1989) *Foraging and Farming: The Evolution of Plant Exploitation* (Unwin Hyman, London).
- 35 Yang X, et al. (2012) Early millet use in northern China. *Proc Natl Acad Sci USA* 109(10):3726–3730.
- 36 Piperno DR, Dillehay TD (2008) Starch grains on human teeth reveal early broad crop diet in northern Peru. *Proc Natl Acad Sci USA* 105(50):19622–19627.
- 37 Allaby RG, Fuller DQ, Brown TA (2008) The genetic expectations of a protracted model for the origins of domesticated crops. *Proc Natl Acad Sci USA* 105(37):13982–13986.
- 38 Bettinger R, Barton L, Morgan C (2010) The origins of food production in North China: A different kind of agricultural revolution. *Evol Anthropol* 19:9–21.
- 39 Brown TA, Jones MK, Powell W, Allaby RG (2009) The complex origins of domesticated crops in the Fertile Crescent. *Trends Ecol Evol* 24(2):103–109.
- 40 Fuller DQ, Willcox G, Allaby RG (2011) Cultivation and domestication had multiple origins: Arguments against the core area hypothesis for the origins of agriculture in the Near East. *World Archaeol* 43(4):628–652.
- 41 Fuller D, Rowlands M (2011) Ingestion and food technologies: Maintaining differences over the long-term in West, South and East Asia. *Interweaving Worlds: Systematic Interactions in Eurasia, 7th to 1st millennia BC. Essays from a Conference in Memory of Professor Andrew Sherratt*, eds Bennet J, Sherratt S, Wilkinson TC, (Oxbow Books, Oxford).
- 42 Sauer CE (1965) American agricultural origins: a consideration of nature and culture. *Land and Life. A Selection of the Writing of Carl Ortwin Sauer*, ed Leighly J (Univ of California Press, Berkeley).
- 43 Dillehay TD, Rossen J, Andres TC, Williams DE (2007) Pre-ceramic adoption of peanut, squash, and cotton in northern Peru. *Science* 316(5833):1890–1893.
- 44 Abbo S, et al. (2011) Experimental growing of wild pea in Israel and its bearing on Near Eastern plant domestication. *Ann Bot (Lond)* 107(8):1399–1404.
- 45 Denham TP, et al. (2003) Origins of agriculture at Kuk Swamp in the highlands of New Guinea. *Science* 301(5630):189–193.
- 46 Piperno DR (2006) Quaternary environmental history and agricultural impact on vegetation in Central America. *Ann Mo Bot Gard* 93(2):274–296.
- 47 Lentz DL, ed (2000) *Imperfect Balance: Landscape Transformations in the Pre-Columbian Americas* (Columbia Univ Press, New York).
- 48 Ellis EC, et al. (2013) Used planet: A global history. *Proc Natl Acad Sci USA* 110(20):7978–7985.
- 49 Arroyo-Kalin M (2012) Slash-burn-and-churn: Landscape history and crop cultivation in pre-Columbian Amazonia. *Quat Int* 249:4–18.
- 50 Richerson PJ, Boyd R (2005) *Not By Genes Alone* (Univ of Chicago Press, Chicago).
- 51 Shennan SJ (2002) *Genes, Memes and Human History: Darwinian Archaeology and Cultural Evolution* (Thames and Hudson, London).

- 52 Powell A, Shennan S, Thomas MG (2009) Late Pleistocene demography and the appearance of modern human behavior. *Science* 324(5932):1298–1301.
- 53 Ford A, Nigh R (2009) Origins of the Maya forest gardens. *J Ethnobiol* 29:213–236.
- 54 Albert FW, et al. (2009) Genetic architecture of tameness in a rat model of animal domestication. *Genetics* 182(2):541–554.
- 55 Albarella U, Dobney K, Rowley-Conwy P (2006) The domestication of the pig (*Sus scrofa*): New challenges and approaches. *Documenting Domestication: New Genetic and Archaeological Paradigms*, eds Zeder MA, Bradley DG, Emshwiller E, Smith BD (Univ of California Press, Berkeley), pp 209–227.
- 56 Vollbrecht E, Springer PS, Goh L, Buckler ES, 4th, Martienssen R (2005) Architecture of floral branch systems in maize and related grasses. *Nature* 436(7054):1119–1126.
- 57 Sigmon B, Vollbrecht E (2010) Evidence of selection at the *ramosa1* locus during maize domestication. *Mol Ecol* 19(7):1296–1311.
- 58 Upadhyayula N, da Silva HS, Bohn MO, Rocheford TR (2006) Genetic and QTL analysis of maize tassel and ear inflorescence architecture. *Theor Appl Genet* 112(4):592–606.
- 59 Ishikawa R, et al. (2010) Allelic interaction at seed-shattering loci in the genetic backgrounds of wild and cultivated rice species. *Genes Genet Syst* 85(4):265–271.
- 60 Fuller DQ, Allaby RG (2009) Seed dispersal and crop domestication: Shattering, germination and seasonality in evolution under cultivation. *Fruit Development and Seed Dispersal, Annual Plant Reviews*, ed Ostergaard L (Wiley-Blackwell, Oxford), Vol 38, pp 238–295.
- 61 Vavilov NI (1951) Phytogeographic basis of plant breeding. The origin, variation, immunity and breeding of cultivated plants. *Chron Bot* 13:1–366.
- 62 Paterson AH, et al. (1995) Convergent domestication of cereal crops by independent mutations at corresponding genetic loci. *Science* 269(5231):1714–1718.
- 63 Li W, Gill BS (2006) Multiple genetic pathways for seed shattering in the grasses. *Funct Integr Genomics* 6(4):300–309.
- 64 Lin ZW, et al. (2012) Parallel domestication of the Shattering1 genes in cereals. *Nat Genet* 44(6):720–U154.
- 65 Fang M, Larson G, Ribeiro HS, Li N, Andersson L (2009) Contrasting mode of evolution at a coat color locus in wild and domestic pigs. *PLoS Genet* 5(1):e1000341.
- 66 Linderholm A, Larson G (2013) The role of humans in facilitating and sustaining coat colour variation in domestic animals. *Semin Cell Dev Biol* 24(6–7):587–593.
- 67 Eriksson G (1969) The waxy character. *Hereditas* 63(1–2):180–204.
- 68 Ma J, et al. (2010) Molecular characterization and comparative analysis of two waxy alleles in barley. *Genes & Genomics* 32(6):513–520.
- 69 Araki M, Numaoka A, Kawase M, Fukunaga K (2012) Origin of waxy common millet, *Panicum miliaceum* L. in Japan. *Genet Resour Crop Evol* 59(7):1303–1308.
- 70 Olsen KM, Purugganan MD (2002) Molecular evidence on the origin and evolution of glutinous rice. *Genetics* 162(2):941–950.
- 71 Barrett RD, Schluter D (2008) Adaptation from standing genetic variation. *Trends Ecol Evol* 23(1):38–44.
- 72 Nesbitt TC, Tanksley SD (2002) Comparative sequencing in the genus *Lycopersicon*. Implications for the evolution of fruit size in the domestication of cultivated tomatoes. *Genetics* 162(1):365–379.
- 73 Studer A, Zhao Q, Ross-Ibarra J, Doebley J (2011) Identification of a functional transposon insertion in the maize domestication gene *tb1*. *Nat Genet* 43(11):1160–1163.
- 74 Jones H, et al. (2008) Population-based resequencing reveals that the flowering time adaptation of cultivated barley originated east of the Fertile Crescent. *Mol Biol Evol* 25(10):2211–2219.
- 75 Cloutault J, et al. (2012) Evolutionary history of pearl millet (*Pennisetum glaucum* [L.] R. Br.) and selection on flowering genes since its domestication. *Mol Biol Evol* 29(4):1199–1212.
- 76 Gupta PK, Rustgi S, Kumar N (2006) Genetic and molecular basis of grain size and grain number and its relevance to grain productivity in higher plants. *Genome* 49(6):565–571.
- 77 Pickersgill B (2007) Domestication of plants in the Americas: Insights from Mendelian and molecular genetics. *Ann Bot (Lond)* 100(5):925–940.
- 78 Gremillion KJ, Piperno DR (2009) Human behavioral ecology, phenotypic (developmental) plasticity, and agricultural origins. *Curr Anthropol* 50(5):615–619.
- 79 Boyko AR, et al. (2010) A simple genetic architecture underlies morphological variation in dogs. *PLoS Biol* 8(8):e1000451.
- 80 Rubin C-J, et al. (2010) Whole-genome resequencing reveals loci under selection during chicken domestication. *Nature* 464(7288):587–591.
- 81 Flink LG, et al. (2014) Establishing the validity of domestication genes using DNA from ancient chickens. *Proc Natl Acad Sci USA* 111:6184–6189.
- 82 Fuller DQ, et al. (2009) The domestication process and domestication rate in rice: Spikelet bases from the Lower Yangtze. *Science* 323(5921):1607–1610.
- 83 Piperno DR, Ranere AJ, Holst I, Iriarte J, Dickau R (2009) Starch grain and phytolith evidence for early ninth millennium B.P. maize from the Central Balsas River Valley, Mexico. *Proc Natl Acad Sci USA* 106(13):5019–5024.
- 84 Fuller DQ (2011) Finding plant domestication in the Indian subcontinent. *Curr Anthropol* 52(5):S347–S362.
- 85 Fuller DQ, Hildebrand L (2013) *Domesticating Plants in Africa. The Oxford Handbook of African Archaeology*, eds Mitchell P, Lane P (Oxford Univ Press, Oxford), pp 507–525.
- 86 Diamond J (2002) Evolution, consequences and future of plant and animal domestication. *Nature* 418(6898):700–707.
- 87 Allaby R (2010) Integrating the processes in the evolutionary system of domestication. *J Exp Bot* 61(4):935–944.
- 88 Jones G, Valamoti S, Charles M (2000) Early crop diversity: A “new” glume wheat from northern Greece. *Vegetation History and Archaeobotany* 9(3):133–146.
- 89 Fuller DQ, Willcox G, Allaby RG (2012) Early agricultural pathways: Moving outside the “core area” hypothesis in Southwest Asia. *J Exp Bot* 63(2):617–633.
- 90 Fuller DQ (2011) Pathways to Asian civilizations: Tracing the origins and spread of rice and rice cultures. *Rice* 4:78–92.
- 91 Molina J, et al. (2011) Molecular evidence for a single evolutionary origin of domesticated rice. *Proc Natl Acad Sci USA* 108(20):8351–8356.
- 92 Gross BL, Zhao Z (2014) Archaeological and genetic insights into the origins of domesticated rice. *Proc Natl Acad Sci USA* 111:6190–6197.
- 93 Baade J (2012) Irragic anthrosols—Artifacts of human adaptation to arid conditions: Examples from the high Himalaya and the coastal desert of Peru. *Climates, Landscapes, and Civilizations Geophysical Monograph Series* 198:203–208.
- 94 Fairhead J, Leach M (2009) *Amazonian Dark Earths in Africa? Amazonian Dark Earths: Wim Sombroek’s Vision* (Springer, New York), pp 265–278.
- 95 Woods WI, et al. (2009) *Amazonian Dark Earths: Wim Sombroek’s Vision* (Springer, New York).
- 96 Gilbert SF, Epel D (2009) *Ecological Developmental Biology: Integrating Epigenetics, Medicine and Evolution* (Sinauer Associates, Inc., Sunderland, MA).
- 97 Jablonka E, Raz G (2009) Transgenerational epigenetic inheritance: Prevalence, mechanisms, and implications for the study of heredity and evolution. *Q Rev Biol* 84(2):131–176.
- 98 West-Eberhard MJ (2003) *Developmental Plasticity and Evolution* (Oxford Univ Press, New York).
- 99 Piperno DR, Holst I, Winter K, McMillan O (2014) Teosinte before domestication: Experimental study of growth and phenotypic variability in late Pleistocene and early Holocene environments. *Quat Int*, 10.1016/j.quaint.2013.12.049.
- 100 Fuller DQ, Harvey E, Qin L (2007) Presumed domestication? Evidence for wild rice cultivation and domestication in the fifth millennium BC of the Lower Yangtze region. *Antiquity* 81(312):316–331.
- 101 Willcox G (2004) Measuring grain size and identifying Near Eastern cereal domestication: Evidence from the Euphrates valley. *J Archaeol Sci* 31(2):145–150.
- 102 Klyver TA, Charles M, Jones G, Rees M, Osborne CP (2013) Did greater burial depth increase the seed size of domesticated legumes? *J Exp Bot* 64(13):4101–4108.
- 103 Blumler MA (1998) *Evolution of Caryopsis Gigantism and Agricultural Origins* (Binghamton Univ, New York).
- 104 Piperno DR, Pearsall DM (1998) *The Origins of Agriculture in the Lowland Neotropics* (Academic, San Diego, CA).
- 105 Richerson PJ, Boyd R, Bettinger RL (2001) Was agriculture impossible during the Pleistocene but mandatory during the Holocene? A climate change hypothesis. *Am Antiq* 66(3):387–411.
- 106 Cunniff J, Charles M, Jones G, Osborne CP (2010) Was low atmospheric CO<sub>2</sub> a limiting factor in the origin of agriculture? *Environmental Archaeology* 15(2):113–123.
- 107 Sage RF (1995) Was low atmospheric CO<sub>2</sub> during the Pleistocene a limiting factor for the origin of agriculture? *Glob Change Biol* 1(2):93–106.
- 108 Asplund L, Hagenblad J, Leino MW (2010) Re-evaluating the history of the wheat domestication gene NAM-B1 using historical plant material. *J Archaeol Sci* 37(9):2303–2307.
- 109 Roullier C, Benoit L, McKey DB, Lebot V (2013) Historical collections reveal patterns of diffusion of sweet potato in Oceania obscured by modern plant movements and recombination. *Proc Natl Acad Sci USA* 110(6):2205–2210.
- 110 Belfer-Cohen A, Goring-Morris AN (2011) Becoming farmers. *Curr Anthropol* 52(5):S209–S220.
- 111 Hayden B, Canuel N, Shanse J (2013) What was brewing in the Natufian? An archaeological assessment of brewing technology in the Epipaleolithic. *J Archaeol Method Theory* 20(1):102–150.
- 112 Zeder MA, Smith BD (2009) A conversation on agricultural origins. *Curr Anthropol* 50(5):681–690.



# Supporting Information

Larson et al. 10.1073/pnas.1323964111

## 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 reach 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).

- Anderson E (1954) *Plants, Man and Life* (Melrose, London).
- Ford RI (1978) *The Nature and Status of Ethnobotany* (Museum of Anthropology, Univ of Michigan, Ann Arbor, MI).
- Watson PJ, Kennedy MC (1991) The development of horticulture in the Eastern Woodlands of North America: Women's role. *Engendering Archaeology: Women and Prehistory*, eds Gero J, Conkey M (Basil Blackwell, Oxford), pp 255–275.
- Cohen MN (1977) *The Food Crisis in Prehistory. Overpopulation and the Origins of Agriculture* (Yale Univ Press, New Haven).
- Watson PJ (1991) Origins of food production in Western Asia and Eastern North America. *Quaternary Landscapes*, eds Shane L, Cushing E (Univ of Minnesota Press, Minneapolis), pp 1–37.
- Harlan JR, Wet JMJ (1976) *Origins of African Plant Domestication*, ed Stemler A (Walter de Gruyter, The Hague).
- MacNeish RS (1967–1972) *The Prehistory of the Tehuacan Valley, vols. 1–5* (Univ of Texas Press, Austin, TX).
- Flannery KV (1973) The origins of agriculture. *Annu Rev Anthropol* 2:271–310.
- Flannery KV, ed (1986) *Guila Naquitz: Archaic Foraging and Early Agriculture in Oaxaca, Mexico* (Academic, New York).
- Harlan JR (1971) Agricultural origins: Centers and noncenters. *Science* 174(4008):468–474.
- Kaplan L, Lynch TF (1999) *Phaseolus* (fabaceae) in archaeology: AMS radiocarbon dates and their significance for pre-Columbian agriculture. *Econ Bot* 53(3):261–272.
- Rindos D (1984) *The Origins of Agriculture: An Evolutionary Perspective* (Academic, Orlando, FL).
- Sauer CO (1952) *Agricultural Origins and Dispersals* (American Geographical Society, New York).
- Sauer CO (1950) Cultivated plants of South and central America. *Handbook of South American Indians*, ed Steward J (Bureau of American Ethnology, Bulletin 143, US Government Printing Office, Washington, DC), Vol 6, pp 487–543.
- Mangelsdorf P (1953) Review of agricultural origins and dispersals. *Am Antiq* 19:87–90.
- Stothert K (1985) The preceramic Las Vegas culture of coastal Ecuador. *Am Antiq* 50:613–637.
- Harris DR (1972) The origins of agriculture in the tropics. *Am Sci* 60:180–193.
- Harris DR, Hillman GC (1989) *Foraging and Farming: The Evolution of Plant Exploitation* (Unwin Hyman, London).
- Pearsall DM (1978) Phytolith analysis of archeological soils: Evidence for maize cultivation in formative Ecuador. *Science* 199(4325):177–178.
- Ucko PJ (1969) *The Domestication and Exploitation of Plants and Animals*, ed Dimbleby GW (Gerald Duckworth, Chicago).
- Zohary D (1954) Unconscious selection and the evolution of domesticated plants. *Econ Bot* 58(1):5–10.
- Zohary D, Hopf M (1988) *Domestication of Plants in the Old World* (Oxford Univ Press, Oxford).
- Smith BD, Cowan CW, Hoffman MP (2007) *Rivers of Change: Essays on Early Agriculture in Eastern North America* (Univ of Alabama Press, Tuscaloosa, Alabama).
- Smith BD (2006) Eastern North America as an independent center of plant domestication. *Proc Natl Acad Sci USA* 103(33):12223–12228.
- Hughes CE, et al. (2007) Serendipitous backyard hybridization and the origin of crops. *Proc Natl Acad Sci USA* 104(36):14389–14394.
- Kwak M, Kami JA, Gepts P (2009) The putative Mesoamerican domestication center of is located in the Lerma-Santiago Basin of Mexico. *Crop Sci* 49(2):554–563.
- Piperno DR, Ranere AJ, Holst I, Iriarte J, Dickau R (2009) Starch grain and phytolith evidence for early ninth millennium B.P. maize from the Central Balsas River Valley, Mexico. *Proc Natl Acad Sci USA* 106(13):5019–5024.
- Piperno DR (2011) The origins of plant cultivation and domestication in the New World tropics. *Curr Anthropol* 52(54):S453–S470.
- Smith BD (1997) The initial domestication of *Cucurbita pepo* in the Americas 10,000 years ago. *Science* 276(5314):932–934.
- van Heerwaarden J, et al. (2011) Genetic signals of origin, spread, and introgression in a large sample of maize landraces. *Proc Natl Acad Sci USA* 108(3):1088–1092.
- Zizumbo-Villarreal D, Colunga-GarcíaMarín P (2010) Origin of agriculture and plant domestication in West Mesoamerica. *Genet Resour Crop Evol* 57(6):813–825.
- Clement CR, de Cristo-Araújo M, Coppens D'Eeckenbrugge G, Alves Pereira A, Picanço-Rodrigues D (2010) Origin and domestication of native Amazonian crops. *Diversity* 2(1):72–106.
- Roullier C, et al. (2013) Disentangling the origins of cultivated sweet potato (*Ipomoea batatas* (L.) Lam.). *PLoS ONE* 8(5):e62707.
- Dillehay TD, et al. (2010) Early Holocene coca chewing in northern Peru. *Antiquity* 84(326):939–953.
- Thomas E, et al. (2012) Present spatial diversity patterns of *Theobroma cacao* L. in the neotropics reflect genetic differentiation in pleistocene refugia followed by human-influenced dispersal. *PLoS ONE* 7(10):e47676.
- Westengen OT, Huamán Z, Heun M (2005) Genetic diversity and geographic pattern in early South American cotton domestication. *Theor Appl Genet* 110(2):392–402.
- Kwak M, Gepts P (2009) Structure of genetic diversity in the two major gene pools of common bean (*Phaseolus vulgaris* L., Fabaceae). *Theor Appl Genet* 118(5):979–992.
- Mengoni Goñalons GL, Yacobaccio H (2006) The domestication of South American camelids: A view from the South-Central Andes. *Documenting Domestication: New Genetic and Archaeological Paradigms*, eds Zeder M, Bradley D, Emshwiller E, Smith B (Univ of California Press, Berkeley, CA), pp 228–244.
- Pearsall DM (2008) Plant domestication and the shift to agriculture in the Andes. *The Handbook of South American Archaeology*, eds Silverman H, Isbell WH (Springer, New York), pp 105–120.
- da Cunha FB, et al. (2008) Genetic relationships among *Arachis hypogaea* L. (AABB) and diploid *Arachis* species with AA and BB genomes. *Genet Resour Crop Evol* 55(1):15–20.
- Olsen KM, Schaala BA (1999) Evidence on the origin of cassava: Phylogeography of *Manihot esculenta*. *Proc Natl Acad Sci USA* 96(10):5586–5591.
- Perry L, et al. (2007) Starch fossils and the domestication and dispersal of chili peppers (*Capsicum* spp. L.) in the Americas. *Science* 315(5814):986–988.
- Harlan JR (1992) Indigenous African agriculture. *The Origins of Agriculture*, eds Cowan CW, Watson PJ (Smithsonian Institution, Washington), pp 59–70.
- Manning K, Pelling R, Higham T, Schwenniger J-L, Fuller DQ (2011) 4500-Year old domesticated pearl millet *Pennisetum glaucum* from the Tilemsi Valley, Mali: New insights into an alternative cereal domestication pathway. *J Archaeol Sci* 38(2):312–322.
- Fuller DQ, Hildebrand L (2013) Domesticating Plants in Africa. *The Oxford Handbook of African Archaeology*, eds Mitchell P, Lane P (Oxford Univ Press, Oxford), pp 507–525.
- D'Andrea AC, Logan AL, Watson DJ (2006) Oil palm and prehistoric subsistence in tropical West Africa. *J African Archaeol* 4(2):195–222.
- Neumann K, et al. (2012) First farmers in the Central African rainforest: A view from southern Cameroon. *Quat Int* 249:53–62.
- Williamson K (1993) Linguistic evidence for the use of tree and tuber food plants. *The Archeology of Africa: Food, Metals and Towns*, eds Shaw T, Sinclair P, Andah B, Okpoko A (Routledge, London), pp 139–153.
- Marshall F, Weissbrod L (2011) Domestication processes and morphological change. *Curr Anthropol* 52(54):S397–S413.
- D'Andrea AC (2008) T'ef (*Eragrostis tef*) in ancient agricultural systems of highland Ethiopia. *Econ Bot* 62(4):547–566.
- Ehret C (2011) A linguistic history of cultivation and herding in northeastern Africa. *Windows on the African Past: Current Approaches to African Archaeobotany*, eds Fahmy AG, Kahlheber S, D'Andrea AC (Africa Magna, Frankfurt am Main), pp 185–208.



**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.

- Asouti E, Fuller DQ (2013) A contextual approach to the emergence of agriculture in Southwest Asia. *Curr Anthropol* 54(3):299–345.
- Tanno K-I, Willcox G (2012) Distinguishing wild and domestic wheat and barley spikelets from early Holocene sites in the Near East. *Vegetation History and Archaeobotany* 21(2):107–115.
- Fuller DQ, et al. (2014) Convergent evolution and parallelism in plant domestication revealed by an expanding archaeological record. *Proc Natl Acad Sci USA*, 10.1073/pnas.1308937110.
- Tanno K-I, Willcox G (2006) The origins of cultivation of *Cicer arietinum* L. and *Vicia faba* L.: Early finds from Tell el-Kerkh, north-west Syria, late 10th millennium BP. *Vegetation History and Archaeobotany* 15(3):197–204.
- Karg S (2011) New research on the cultural history of the useful plant *Linum usitatissimum* L. (flax), a resource for food and textiles for 8,000 years. *Vegetation History and Archaeobotany* 20(6):507–508.
- Kaniewski D, et al. (2012) Primary domestication and early uses of the emblematic olive tree: Palaeobotanical, historical and molecular evidence from the Middle East. *Biol Rev Camb Philos Soc* 87(4):885–899.
- Legge AJ (1996) The beginning of caprine domestication in Southwest Asia. *The Origins and Spread of Agriculture and Pastoralism in Eurasia*, ed Harris DR (UCL Press, London), pp 238–262.
- Arbuckle BS, Öztan A, Gülçür S (2009) The evolution of sheep and goat husbandry in central Anatolia. *Anthropozoologica* 44(1):129–157.
- Conolly J, et al. (2011) Meta-analysis of zooarchaeological data from SW Asia and SE Europe provides insight into the origins and spread of animal husbandry. *J Archaeol Sci* 38(3):538–545.
- Helmer D, Gourichon L (2008) Premières données sur les modalités de subsistance à Tell Aswad (Syrie, PPNB moyen et récent, néolithique céramique ancien) - Fouilles 2001-2005. *Archaeozoology of the Near East VIII: Actes des Huitièmes Rencontres Internationales d'Archéozoologie de l'Asie du Sud-Ouest et des Régions Adjacentes*, eds Vila E, Gourichon L, Choyke AM, Buitenhuis H (Travaux de la Maison de l'Orient et de la Méditerranée, Lyon, France), pp 119–151.
- Hongo H, Meadow RH, Oksuz B, Ilgezdi G (2005) Sheep and goat remains from Cayonu Tepesi, Southeastern Anatolia. *Archaeozoology of the Near East VI: Proceedings of the Sixth International Symposium on the Archaeozoology of Southwestern Asia and Adjacent Areas*, eds Buitenhuis H, Choyke A, Martin L, Bartosiewicz L, Mashkour M (ARC, Groningen), pp 113–124.
- Vigne JD, Carrère I, Briois F, Guilaine J (2011) The early process of mammal domestication in the Near East. *Curr Anthropol* 52(54):255–271.
- Zeder MA (2005) New perspectives on livestock domestication in the Fertile Crescent as viewed from the Zagros Mountains. *The First Steps of Animal Domestication: New Archaeological Approaches*, eds Vigne J-D, Peters J, Helmer D (Oxbow Books, Oxford).
- Arbuckle BS (2013) The late adoption of cattle and pig husbandry in Neolithic Central Turkey. *J Archaeol Sci* 40(4):1805–1815.
- Helmer DL, Gourichon L, Monchot H, Peters J, Segui MS (2005) Identifying early domestic cattle from Pre-Pottery Neolithic sites on the Middle Euphrates using sexual dimorphism. *The First Steps of Animal Domestication*, eds Vigne J-D, Peters J, Helmer D (Oxbow Books, Oxford), pp 86–95.

16. Hongo H, Pearson J, Öksük B, Ilgezdi G (2009) The process of ungulate domestication at Çayönü, Southeastern Turkey: A multidisciplinary approach focusing on *Bos* sp. and *Cervus elaphus*. *Anthropozoologica* 44:63–73.
17. Vigne J-D, Guilaine J, Debue K, Haye L, Gérard P (2004) Early taming of the cat in Cyprus. *Science* 304(5668):259.
18. Linseele V, Van Neer W, Hendrickx S (2007) Evidence for early cat taming in Egypt. *J Archaeol Sci* 34(12):2081–2090.
19. Vigne J-D, et al. (2012) First wave of cultivators spread to Cyprus at least 10,600 years ago. *Proc Natl Acad Sci USA* 109(22):8445–8449.
20. Fuller DQ (2008) The spread of textile production and textile crops in India beyond the Harappan zone: An aspect of the emergence of craft specialization and systematic trade. *Linguistics, Archaeology and the Human Past Occasional Paper 3*, eds Osada T, Uesugi A (Indus Project, Research Institute for Humanity and Nature, Kyoto), pp 1–26.
21. Pokharia AK, et al. (2011) Archaeobotany and archaeology at Kanmer, a Harappan site in Kachchh, Gujarat: Evidence for adaptation in response to climatic variability. *Current Science (Bangalore)* 100(12):1833–1846.
22. Fuller DQ, et al. (2010) Consilience of genetics and archaeobotany in the entangled history of rice. *Archaeol Anthropol Sci* 2(2):115–131.
23. Fuller DQ (2011) Finding plant domestication in the Indian subcontinent. *Curr Anthropol* 52(54):S347–S362.
24. Meadow R (1993) Animal domestication in the Middle East: A revised view from the eastern Margin. *Harappan Civilization: A Recent Perspective*, ed Possehl GL (Oxford and IBH, New Delhi), pp 295–320.
25. Patel AK, Meadow R (1998) The exploitation of wild and domestic water buffalo in prehistoric northwestern South Asia. *Archaeozoology of the Near East III*, eds Buitenhuis H, Bartosiewicz L, Choyke AM (Centre for Archaeological Research and Consultancy, Rijksuniversiteit Groningen, Groningen), pp 180–199.
26. Lu H, et al. (2009) Earliest domestication of common millet (*Panicum miliaceum*) in East Asia extended to 10,000 years ago. *Proc Natl Acad Sci USA* 106(18):7367–7372.
27. Bettinger RL, Barton L, Morgan C (2010) The origins of food production in north China: A different kind of agricultural revolution. *Evolutionary Anthropology: Issues, News, and Reviews (Melb)* 19(1):9–21.
28. Zhao Z (2011) New archaeobotanic data for the study of the origins of agriculture in China. *Curr Anthropol* 52(54):S295–S306.
29. Yang X, et al. (2012) Early millet use in northern China. *Proc Natl Acad Sci USA* 109(10):3726–3730.
30. Fuller DQ (2011) Pathways to Asian civilizations: Tracing the origins and spread of rice and rice cultures. *Rice* 4:78–92.
31. Lee G-A, Crawford GW, Liu L, Sasaki Y, Chen X (2011) Archaeological soybean (*Glycine max*) in East Asia: Does size matter? *PLoS ONE* 6(11):e26720.
32. Fuller DQ, Qin L (2010) Declining oaks, increasing artistry, and cultivating rice: The environmental and social context of the emergence of farming in the Lower Yangtze Region. *Environ Archaeol* 15(2):139–159.
33. Saraswat KS, Sharma NK, Saini DC (1994) Plant economy by ancient Narhan (ca. 1,300 B.C.– 300/400 A.D.). *Excavations at Narhan (1984–1989)*, ed Singh P (Banaras Hindu Univ, Varanasi), pp 255–346.
34. Fuller DQ (2012) New archaeobotanical information on plant domestication from macro-remains: Tracking the evolution of domestication syndrome traits. *Biodiversity in Agriculture. Domestication, Evolution, and Sustainability*, eds Gepts P, et al. (Cambridge Univ Press, Cambridge), pp 110–135.
35. Cucchi T, Hulme-Beaman A, Yuan J, Dobney K (2011) Early Neolithic pig domestication at Jiahu, Henan Province, China: Clues from molar shape analyses using geometric morphometric approaches. *J Archaeol Sci* 38(1):11–22.
36. Flad RK, Yuan J, Li S (2007) Zooarchaeological evidence for animal domestication in Northwest China. *Late Quaternary Climate Change and Human Adaptation in Arid China, Developments in Quaternary Science, Vol. 9* eds Madsen DB, Chen F, Gao X, (Elsevier, Amsterdam), pp 163–199.
37. Zhang S, Gao H (1999) Study and observation on unearthed fabrics of the relics in the Qingtai village of Yingyang city. *Zhongyuan Wenwu* 1999(3):10–16. Chinese.
38. Good I (2011) Strands of connectivity: Assessing the evidence for long distance exchange of silk in later prehistoric Eurasia. *Interweaving Worlds. Systematic Interactions in Eurasia, 7th to the 1st Millennia BC*, eds Wilkinson TC, Sherratt S, Bennet J (Oxbow Books, Oxford), pp 218–230.
39. Meyer MC, et al. (2009) Holocene glacier fluctuations and migration of Neolithic yak pastoralists into the high valleys of northwest Bhutan. *Quat Sci Rev* 28(13):1217–1237.
40. Benecke N, von den Driesch A (2003) Horse exploitation in the Kazakl Steppes during the Eneolithic and Bronze Age. *Prehistoric Steppe Adaptation and the Horse*, eds Levine MA, Renfrew C, Boyle KV (McDonald Institute Monographs, Univ of Cambridge, Cambridge), pp 69–82.
41. Ludwig A, et al. (2009) Coat color variation at the beginning of horse domestication. *Science* 324(5926):485.
42. Outram AK, et al. (2009) The earliest horse harnessing and milking. *Science* 323(5919):1332–1335.
43. Anthony DW (2009) *The Horse, the Wheel, and Language: How Bronze-Age Riders from the Eurasian Steppes Shaped the Modern World* (Princeton Univ Press, Princeton).
44. Olsen SJ (1988) The camel in ancient China and an osteology of the camel. *Proc Acad Nat Sci Philadelphia* 140(11):22–23.
45. Kohl PL (2007) *The Making of Bronze Age Eurasia* (Cambridge Univ Press, Cambridge).
46. Meadow R, Patel AK (2001) From Mehrgarh to Harappa and Dholavira: Prehistoric pastoralism in North-Western South Asia through the Harappan Period. *Indian Archaeology in Retrospect*, eds Settar S, Korisettar R (Manohar, New Delhi), Vol Protohistory, pp 391–408.
47. Luff R (2000) Ducks. *Cambridge World History of Food*, eds Kiple KF, Ornelas KC (Cambridge University Press, Cambridge), pp 517–524.
48. Museum ZC (1979) The excavation of the Mound Tomb at Guoyuan of Fushan, Jurong county, Jiangsu province. *Kaogu [Archaeology]* 1979(2):113.
49. Fuller DQ (2006) Agricultural origins and frontiers in South Asia: A working synthesis. *J World Prehist* 20(1):1–86.
50. Deng H, Yuan J, Song GD, Wang CS, Masaki E (2013) The re-examination of the domestic chicken in Ancient China. *Kaogu* 2013(6):83–96.
51. Peters J (1998) *Römische Tierhaltung und Tierzucht: Eine Synthese aus Archäozoologischer Untersuchung und Schriftlich-Bildlicher Überlieferung [Roman Animal Keeping and Breeding: A Synthesis Based on Zooarchaeological Analysis and the Written and Pictorial Record]*. German (Passauer Universitäts-schriften zur Archäologie, Rahden, Germany).
52. Denham TP, et al. (2003) Origins of agriculture at Kuk Swamp in the highlands of New Guinea. *Science* 301(5630):189–193.
53. Haberle SG, Lentfer C, O'Donnell S, Denham T (2012) The palaeoenvironments of Kuk Swamp from the beginnings of agriculture in the highlands of Papua New Guinea. *Quat Int* 249:129–139.
54. Perrier X, et al. (2011) Multidisciplinary perspectives on banana (*Musa* spp.) domestication. *Proc Natl Acad Sci USA* 108(28):11311–11318.
55. Terral JF, et al. (2012) Insights into the historical biogeography of the date palm (*Phoenix dactylifera* L.) using geometric morphometry of modern and ancient seeds. *J Biogeogr* 39(5): 929–941.
56. Boivin N, Fuller DQ (2009) Shell middens, ships and seeds: Exploring coastal subsistence, maritime trade and the dispersal of domesticates in and around the ancient Arabian Peninsula. *J World Prehist* 22(2):113–180.
57. Fuller DQ, Hildebrand L (2013) Domesticating plants in Africa. *The Oxford Handbook of African Archaeology*, eds Mitchell P, Lane P (Oxford Univ Press, Oxford), pp 507–525.
58. Manning K, Pelling R, Higham T, Schwenniger J-L, Fuller DQ (2011) 4500-Year old domesticated pearl millet (*Pennisetum glaucum*) from the Tilemsi Valley, Mali: New insights into an alternative cereal domestication pathway. *J Archaeol Sci* 38(2):312–322.
59. D'Andrea AC, Kahlheber S, Logan AL, Watson DJ (2007) Early domesticated cowpea (*Vigna unguiculata*) from Central Ghana. *Antiquity* 81(313):686–698.
60. Murray S (2007) Identifying African rice domestication in the middle Niger Delta (Mali). *Fields of Change: Progress in African Archaeobotany*, ed Cappers R (Barkhuis, Groningen), pp 53–62.
61. Gautier A (2001) The Early to Late Neolithic archaeofaunas from Nabta and Bir Kiseiba. *Holocene Settlement of the Egyptian Sahara. Playa*, eds Wendorf F, Schild R (Kluwer/Plenum, New York), *The Archaeology of Nabta*, pp 609–635.
62. Schild R, Wendorf F (2001) Geoarchaeology of the Holocene climatic optimum at Nabta playa, Southwestern desert, Egypt. *Geoarchaeology* 16(1):7–28.
63. Boessneck J, von den Driesch A, Ziegler R (1989) Die Tierreste von Maadi und Wadi Digla. *Maadi III*, eds Rizkana I, Seeher J (von Zabern, Mainz), pp 87–128.
64. Gautier A (1984) Archaeozoology of the Bir Kiseiba region, Eastern Sahara. *Cattle-Keepers of the Eastern Sahara: The Neolithic of Bir Kiseiba*, ed Close AE (SMU Dallas, Department of Anthropology, Dallas, TX), pp 49–72.
65. Chenal-Vélarde I (1998) Les premières traces de boeuf domestique en Afrique du Nord: Etat de la recherche centré sur les données archéozoologiques. *Archaeozoologia* 9(1–2):11–40.
66. Gautier A (1987) Prehistoric men and cattle in North Africa: A dearth of data and a surfeit of models. *Prehistory of Arid North Africa. Essays in Honor of Fred Wendorf*, ed Close AE (SMU Press, Dallas), pp 163–187.
67. Gautier A (2002) The evidence for the earliest livestock in North Africa: Or adventures with large bovids, ovicaprids, dogs and pigs. *Droughts, Food and Culture: Ecological Change and Food Security in Africa's Later Prehistory*, ed Hassan FA (Kluwer Academic/Plenum, New York), pp 195–207.
68. Linseele V (2013) Early stock keeping in northeastern Africa: Near Eastern influences and local developments. *Neolithisation of Northeastern Africa. Studies in Early Near Eastern Production, Subsistence, and Environment*, ed Shirai N (Ex oriente, Berlin), pp 97–108.
69. MacDonald KC (2000) The origins of African livestock: Indigenous or imported. *The Origins and Development of African Livestock: Archaeology, Genetics, Linguistics and Ethnography*, eds Blench RM, MacDonald KC (UCL Press, London), pp 2–17.
70. Peters J (1986) A revision of the faunal remains from two Central Sudanese sites: Khartoum Hospital and Esh Shaheinab. *Mélanges Publiés à l'Occasion du 5e Congrès International d'Archéozoologie, Août 1986*, (La Pensée Sauvage Editions, Grenoble, France), pp 11–33.
71. Cattani M, Bokonyi S (2002) Ash-Shumah: An early Holocene settlement of desert hunters and mangrove foragers in the Yemeni Tihamah. *Essays on the Late Prehistory of the Arabian Peninsula*, eds Cleuziou S, Tosi M, Zarins J (Istituto Italiano per l'Africa e l'Oriente, Rome), pp 31–53.
72. Rosell S, et al. (2008) Domestication of the donkey: Timing, processes, and indicators. *Proc Natl Acad Sci USA* 105(10):3715–3720.

73. Marshall F, Weissbrod L (2011) Domestication processes and morphological change. *Curr Anthropol* 52(54):S397–S413.
74. Kimura B, et al. (2011) Ancient DNA from Nubian and Somali wild ass provides insights into donkey ancestry and domestication. *Proc Biol Sci* 278(1702):50–57.
75. Marshall F, Asa C (2013) A study of African wild ass behavior provides insights into conservation issues, domestication processes and archaeological interpretation. *J Archaeol Method Theory* 20(3):479–494.
76. Shackelford L, Marshall F, Peters J (2013) Identifying donkey domestication through changes in cross-sectional geometry of long bones. *J Archaeol Sci* 40(12):4170–4179.
77. Uerpmann HP (2008) Animal Domestication. *Encyclopedia of Archaeology*, ed Pearsall DM (Elsevier, Amsterdam), pp 434–445.
78. Beech M, Mashkour M, Huelms M, Zazzo A (2009) Prehistoric camels in south-eastern Arabia: The discovery of a new site in Abu Dhabi's Western Region, United Arab Emirates. *Proceedings of the Seminar for Arabian Studies*, (JSTOR) 39(2009):17–30.
79. Driesch A, Obermaier H (2007) The hunt for wild dromedaries during the 3rd and 2nd millennia cal BC on the United Arab Emirates coast. Camel bone finds from the excavation at Al Sufouh 2, Dubai, UAE. *Skeletal Series and Their Socio-Economic Context*, eds Grupe G, Peters J (Rahden/Westf, Leidorf), Vol Documenta Archaeobiologiae, pp 133–167.
80. Kinne J, Wani NA, Wernery U, Peters J, Knosp C (2010) Is there a two-humped stage in the embryonic development of the dromedary? *Anat Histol Embryol* 39(5):479–480.
81. Peters J (1997) [The dromedary: Ancestry, history of domestication and medical treatment in early historic times]. *Tierarztl Prax Ausg G Grosstiere Nutztiere* 25(6):559–565. German.
82. Uerpmann H, Uerpmann M (2002) The appearance of the domestic camel in south-east Arabia. *Journal of Oman Studies* 12:235–260.
83. MacDonald KC (1992) The domestic chicken (*Gallus gallus*) in Sub-Saharan Africa: A background to its introduction and its osteological differentiation from indigenous fowls (*Nunudinae* and *Fracolinus* sp.). *J Archaeol Sci* 19:303–318.
84. MacDonald KC, MacDonald RH (2000) The origins of domesticated animals in arid West Africa. *The Origins and Development of Livestock in Africa*, eds Blench RM, MacDonald KC (UCL Press, London), pp 127–162.
85. Töröl L (1987) The historical background: Meroe, North and South. *Meroitistische Forschungen 1980*, ed Hintze F (Akademie, Berlin), pp 139–229.
86. Smith BD (2006) Eastern North America as an independent center of plant domestication. *Proc Natl Acad Sci USA* 103(33):12223–12228.
87. Smith BD, Yarnell RA (2009) Initial formation of an indigenous crop complex in eastern North America at 3800 B.P. *Proc Natl Acad Sci USA* 106(16):6561–6566.
88. Smith BD (1997) The initial domestication of *Cucurbita pepo* in the Americas 10,000 years ago. *Science* 276(5314):932–934.
89. Piperno DR, Ranere AJ, Holst I, Iriarte J, Dickau R (2009) Starch grain and phytolith evidence for early ninth millennium B.P. maize from the Central Balsas River Valley, Mexico. *Proc Natl Acad Sci USA* 106(13):5019–5024.
90. Ranere AJ, Piperno DR, Holst I, Dickau R, Iriarte J (2009) The cultural and chronological context of early Holocene maize and squash domestication in the Central Balsas River Valley, Mexico. *Proc Natl Acad Sci USA* 106(13):5014–5018.
91. Callen EO (1967) The first new world cereal. *Am Antiq* 32(4):535–538.
92. Kaplan L, Lynch TF (1999) Phaseolus (Fabaceae) in archaeology: AMS. *Econ Bot* 53(3):261–272.
93. Smith CE (1967) Plant remains. *The Prehistory of the Tehuacan Valley*, ed Byers DS (Univ of Texas Press, Austin), Vol 1, Environment and Subsistence, pp 220–255.
94. Kraft KH, et al. (2014) Multiple lines of evidence for the origin of domesticated chili pepper, *Capsicum annum*, in Mexico. *Proc Natl Acad Sci USA*, 10.1073/pnas.1308933111.
95. Thornton EK, et al. (2012) Earliest Mexican Turkeys (*Meleagris gallopavo*) in the Maya Region: Implications for pre-Hispanic animal trade and the timing of turkey domestication. *PLoS ONE* 7(8):e42630.
96. Perry L, et al. (2007) Starch fossils and the domestication and dispersal of chili peppers (*Capsicum* spp. L.) in the Americas. *Science* 315(5814):986–988.
97. Dillehay TD, Rossen J, Andres TC, Williams DE (2007) Pre-ceramic adoption of peanut, squash, and cotton in northern Peru. *Science* 316(5833):1890–1893.
98. Dillehay TD, et al. (2010) Early Holocene coca chewing in northern Peru. *Antiquity* 84(326):939–953.
99. Piperno DR, Stothert KE (2003) Phytolith evidence for early Holocene *Cucurbita* domestication in southwest Ecuador. *Science* 299(5609):1054–1057.
100. Ezell KC, Pearsall DM, Zeidler JA (2006) Root and tuber phytoliths and starch grains document manioc (*Manihot esculenta*) arrowroot (*Maranta arundinacea*) and Ilerén (*Calathea* sp.) at the real alto site Ecuador. *Econ Bot* 60(2):103–120.
101. Piperno DR, Dillehay TD (2008) Starch grains on human teeth reveal early broad crop diet in northern Peru. *Proc Natl Acad Sci USA* 105(50):19622–19627.
102. Piperno DR, Ranere AJ, Holst I, Hansell P (2000) Starch grains reveal early root crop horticulture in the Panamanian tropical forest. *Nature* 407(6806):894–897.
103. Dickau R, Ranere AJ, Cooke RG (2007) Starch grain evidence for the pre-ceramic dispersals of maize and root crops into tropical dry and humid forests of Panama. *Proc Natl Acad Sci USA* 104(9):3651–3656.
104. Solis RS, Haas J, Creamer W (2001) Dating Caral, a pre-ceramic site in the Supe Valley on the central coast of Peru. *Science* 292(5517):723–726.
105. Hawkes JG (1990) *The Potato: Evolution, Biodiversity and Genetic Resources* (John Wiley and Sons, New York).
106. Bruno MC, Whitehead WT (2003) *Chenopodium Cultivation and Formative Period Agriculture at Chiripa* (Latin American Antiquity, Bolivia), pp 339–355.
107. Piperno DR (2011) The origins of plant cultivation and domestication in the New World tropics. *Curr Anthropol* 52(54):S453–S470.
108. Mengoni-Góñalons GL, Yacobaccio HD (2006) The domestication of South American camelids. A view from the South-Central Andes. *Documenting Domestication: New Genetic and Archaeological Paradigms*, eds Zeder M, Bradley DG, Emshwiller E, Smith BD (Univ of California Press, Berkeley), pp 228–244.
109. Mengoni-Góñalons GL (2008) Camelids in ancient Andean societies: A review of the zooarchaeological evidence. *Quat Int* 185(1):59–68.
110. Stahl PW (2008) Animal Domestication in South America. *Handbook of South American Archaeology*, eds Silverman H, Isbell WH (Springer, New York), pp 121–130.
111. Dunnum JL, Salazar-Bravo J (2010) Molecular systematics, taxonomy and biogeography of the genus *Cavia* (Rodentia: Caviidae). *J Zoological Syst Evol Res* 48(4):376–388.
112. Stahl PW (2005) An exploratory osteological study of the muscovy duck (*Cairina moschata*) (Aves: Anatidae) with implications for neotropical archaeology. *J Archaeol Sci* 32(6):915–929.
113. Stahl PW, Muse MC, Delgado-Espinoza F (2006) New evidence for pre-Columbian Muscovy Duck *Cairina moschata* from Ecuador. *Ibis* 148(4):657–663.
114. Larson G, Burger J (2013) A population genetics view of animal domestication. *Trends Genet* 29(4):197–205.