Core questions in domestication research

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The domestication of plants and animals is a key transition in human history, and its profound and continuing impacts are the focus of a broad range of transdisciplinary research spanning the physical, biological, and social sciences. Three central aspects of domestication that cut across and unify this diverse array of research perspectives are addressed here. Domestication is defined as a distinctive coevolutionary, mutualistic relationship between domesticator and domesticate and distinguished from related but ultimately different processes of resource management and agriculture. The relative utility of genetic, phenotypic, plastic, and contextual markers of evolving domesticatory relationships is discussed. Causal factors are considered, and two leading explanatory frameworks for initial domestication of plants and animals, one grounded in optimal foraging theory and the other in niche-construction theory, are compared.

domestication | mutualism | genetic impacts | ecophenotypic impacts | niche-construction theory

The domestication of plants and animals marks a major evolutionary transition in human history—one with profound and lasting global impacts. The origins of domestication—when and where, how, and why our ancestors targeted plant and animal species for domestication—is an enduring and increasingly active area of scientific inquiry for researchers from many different disciplines. Enhancing present-day productivity of longstanding and recently domesticated species and exploring social and biological issues surrounding their role in feeding rapidly expanding global populations are topics of pressing concern. The volume and breadth of domestication research is underscored by a keyword search on the term "domestication" for the year 2013 which yielded a total of 811 papers in more than 350 different journals (Table S1), including 42 articles published in *PNAS* (Table S2).

Given the large and growing number of studies on domestication across a wide array of disciplines, it is worthwhile to address three central questions. (*i*) Is there a definition of domestication applicable to both plants and animals from the distant past to present day that distinguishes domestication from related processes of resource management and agriculture? (*ii*) How does domestication change both the domesticate and domesticator, and how can we track these changes through time? (*iii*) Why did humans domesticate plants and animals, and are there common causal factors that underlie the process of domestication wherever it takes place?

Defining Domestication and Distinguishing Domestication from Management and Agriculture

There is a surprising lack of consensus on how to define domestication. Beyond agreeing that it involves a relationship between a domesticator and a domesticate, there is little agreement on what this relationship entails or how and when it results in the creation of a domesticated plant or animal. Domestication is frequently defined from the perspective of the domesticator, emphasizing the role of humans in separating a target domesticate from free-living populations and assuming mastery over all aspects of its life cycle (1). Domestication has also been

viewed as a mutualistic, symbiotic relationship that benefits both domesticator and domesticate (2), with domesticates sometimes considered as having benefited more than their human partners (3). Some researchers see genetically driven change in a domesticate's phenotype as the central defining characteristic of domestication (4). Others maintain that such an emphasis misdirects attention to a narrow aspect of domestication that may vary from case to case, or seem not to occur at all (5). Instead of focusing on the effects of domestication, some argue that domestication should be defined in terms of the relationship between humans and target species that causes genetic and other responses. This shift in focus sometimes results in a broadening of the definition of domestication to cover a much wider array of human interactions with plants and animals (6), including declaring a species domesticated "whenever another species knows how to harvest it" (5), or proposals for replacing the term domestication with less prejudicial ones such as "cultural control" (7).

Against this confusing backdrop of conflicting approaches to conceptualizing domestication, the following definition is offered: Domestication is a sustained multigenerational, mutualistic relationship in which one organism assumes a significant degree of influence over the reproduction and care of another organism in order to secure a more predictable supply of a resource of interest, and through which the partner organism gains advantage over individuals that remain outside this relationship, thereby benefitting and often increasing the fitness of both the domesticator and the target domesticate.

This distinctive kind of mutualism is not restricted to humans and domestic crops and livestock but is well documented in nonhuman species, especially among a number of social insect domesticators and their plant and animal domesticates (8). Domesticatory relationships between organisms such as leaf cutter ants and fungi, however, arise through a gradual

Significance

Domestication of plants and animals marks a major transition in human history that represents a vibrant area of interdisciplinary scientific inquiry. Consideration of three central questions about domestication—what it is, what it does, and why it happened—provide a unifying framework for diverse research on the topic. Domestication is defined in terms of a coevolutionary mutualism between domesticator and domesticate and is distinguished from related but ultimately different processes of management and agriculture. Domestication results in a range of genotypic, phenotypic, plastic, and contextual impacts that can be used as markers of evolving domesticatory relationships. A consideration of causal scenarios finds greater empirical support for explanatory frameworks grounded in niche-construction theory over those derived from optimal foraging theory.

coevolutionary process of selection operating on mutation-induced behavioral, physiological, and morphological changes in both partners that are passed on to offspring through the hit-or-miss process of sexual reproduction. Humans, in contrast, are able to opportunistically invent and modify behaviors that enhance benefits gained from coevolutionary relationships with target species, and, most importantly, humans are able to transmit behaviors that meet perceived goals not only to their offspring but more widely to others outside their immediate kin group through social learning (9). This human ability to choose between genetic variants of partner species, to leave one relationship in favor of another, to consciously manipulate a symbiont's life history to the domesticator's benefit, is the key feature that distinguishes human domesticatory relationships from those between nonhuman species (8). *Contra* researchers who reject the role of deliberate intent or agency in early human domesticatory relationships (3, 10), it is precisely this capacity for goal-oriented behavior that makes human-driven domestication qualitatively different from that between nonhuman partners. Clearly the goal of these behaviors was not to deliberately, in a teleological fashion, domesticate another species or invent agriculture. However, decisions to modify environments, move plants and animals to new environments, and selectively harvest and breed certain species—decisions that initiated and fostered the development of the mutualistic relationships at the core of domestication—were, nonetheless, arrived at consciously with defined goals in mind made possible by the uniquely human ability to spontaneously invent new behaviors and to pass them on to others (11).

The definition offered here does not encompass genetic or plastic responses to domestication in either the domesticator or domesticate. Defining domestication in terms of these changes begs the question of how many genes and how much phenotypic change is needed to distinguish between domestication and other kinds of adaptive responses that might occur as the result of manipulation of a species or its environment. Similarly, defining domestication in terms of the degree to which the plant or animal is incorporated into human socioeconomic organization (12) misdirects attention toward aspects of the relationship that are not universal and away from the relationship that more properly lies at the center of any definition of domestication.

Although the proposed definition focuses on the relationship between partners rather than on the biological or cultural outcomes of the relationship, it also differs in significant ways from definitions that emphasize the domesticator's role in controlling or harvesting the domesticate. Such definitions are actually more relevant to the term "management," which for purposes here can be defined as: the manipulation of the conditions of growth of an organism, or the environment that sustains it, in order to increase its relative abundance and predictability and to reduce the time and energy required to harvest it.

This basic "niche-constructing" behavior is widely practiced by humans and nonhuman species and is argued to be a major driver of evolution in both the niche-constructing species and other species living within the constructed niche (13). Some form of management is an essential prerequisite of domestication, but it is not sufficient for the development of a domesticatory relationship. Management that does not substantially alter the selective pressures on the managed resource from those experienced in a free-living state or that does not persist over several generations of the managed population (i.e., that relies on continuous restocking from free-living populations without breeding or cloning managed individuals) will likely not lead to domestication. In order for management to result in domestication, a sustained multigenerational relationship must develop between the manager and the managed from which both reap mutual, although not necessarily symmetrical, benefits. Sustaining the relationship over the long term requires that both partners undergo modifications (genetically driven or facultative) that enhance the benefits each accrues. In an evolving human/plant domesticatory

relationships, for example, the development of artificial irrigation benefits the human partner by increasing the yield of the plant, while also increasing the irrigated plant's reproductive success over populations situated outside the irrigation system. Adaptations that might make a plant a more attractive partner include alterations in physiological functions controlling ripening synchrony that benefit humans by making harvest schedules more predictable, while increasing the probability that individuals ripening at the same time dominate seed stock reserved for next year's planting. Such modifications not only increase mutual benefits to both partners, they may also make one or both more dependent on the other, limiting opportunities to leave the partnership.

Another feature that distinguishes domestication from resource management is the capacity of each partner to make modifications that help sustain the relationship. For humans this might involve assessing whether the returns of a managed resource justify continuing investment, especially in light of the returns from other available resources whose exploitation carry different or perhaps conflicting requirements. Traits that make a plant or animal responsive to management are key prerequisites in a successful domesticate. The ability to colonize open, disturbed anthropogenic habitats is one such trait in plants (14); in animals these traits include a hierarchical social structure and, especially, lower reactivity to humans (15). Another adaptive feature in a successful domesticate is the capacity for rapid response to selective pressures under domestication (genetically driven or plastic) in ways that enhance the benefits they and their partners derive from the relationship.

The pathways that humans and target species follow from initial management into domestication are shaped by a number of contingencies affecting both partners and can be broadly classified into three types: (*i*) a commensal pathway in which the plant or animal first moves into an anthropogenic habitat and later develops a two-way partnership with humans, (*ii*) a prey or harvest pathway initiated by a human interest in enhancing the yield or predictability of a resource provided by target species, and (*iii*) a directed pathway in which humans deliberately set out to domesticate a species (15). Species following the first two pathways tend to possess more traits that make them suitable candidates for domestication. Species on directed pathways, in contrast, likely possess barriers to domestication that require more knowledge on the part of humans to overcome. This is the pathway taken in all of the more recent domestication efforts where domestication may involve more advanced technologies (e.g., artificial insemination or genetic manipulation).

Some species, moreover, possess behavioral or morphological characteristics that pose insurmountable barriers to domestication, despite human efforts at manipulation that in other species led to domestication. Although there is some evidence of tentative steps toward management of gazelle in the early Neolithic of the southern Levant (16), for example, the animal's well-developed flight reflex and resistance to captive breeding precluded the relationship between humans and gazelle from moving beyond the initial audition phase (15). On the human side of the equation, potential domesticates might be abandoned in favor of other equally attractive candidate species that subsequently move on become to full-fledged domesticates. Wild oats, barley, and emmer wheat, for example, were each intensively used and likely managed in some way in the Levant, but oats lagged far behind barley and emmer in developing into a domesticate (17). There are also examples of multiple independent domestications of a single species following very different pathways in different regions (18, 19).

Just as some level of management is an essential precursor to domestication, the presence of domesticates is a prerequisite for agriculture. Human utilization of one or more domesticates, however, does not constitute agriculture. Instead, agriculture is distinguished by the degree of dependence on domesticates (20) and is

defined here as: a provisioning system based primarily on the production and consumption of domesticated resources.

Not only are the terms "domestication" and "agriculture" not interchangeable, as often implied (10), agriculture is not an automatic outcome of domestication. In virtually every instance of agricultural emergence there is a long delay of up to a thousand years or more between initial domestication and the development of fully formed agricultural systems (20, 21). Low-level food-producing economies that include a mix of domesticates and an array of loosely managed or entirely free-living resources, moreover, have existed for millennia without ever developing into agricultural economies (20). There are also examples of societies that abandoned a fully agricultural way of life in favor of broad-spectrum foraging strategies practiced hundreds of years earlier (22).

There is, then, a continuum between resource management, domestication, and agriculture. Although the existence of each precursor component of the continuum is essential for the development of the next, the development of any one of these different phenomena does not necessarily result in the development of the next. It is also difficult, along this continuum of closely related phenomena, to draw clear and sharply defined thresholds that separate one stage from the next. How much investment in tending a plant or animal or how much genetic or plastic response on the part of the plant or animal is needed before it can be said to have crossed the boundary between managed and domesticated? What percentage of overall caloric intake and labor investment in domesticates is needed before an economy can be identified as having transitioned from low-level food production to agriculture? Focusing on precise demarcation of such thresholds and establishing when, exactly, they have been crossed is a largely unproductive exercise that creates the erroneous impression of dichotomous states between wild and domestic, foraging and farming, and distracts attention from the often opaque, but far more interesting, middle-ground areas that lie between them. Rather than trying to define such thresholds, it is more productive to concentrate on the contexts and processes that shape behaviors involved in management, domestication, and agriculture and the evolutionary progression between them.

Thus, although management, domestication, and agriculture have overlapping elements, they are nonetheless distinct phenomena. The definitions proposed here focus on core aspects of each in a way that allows useful distinctions to be drawn between them. Management, as defined here, centers on the actions of the manager in attempting to enhance the returns of a resource of interest. The definition of domestication emphasizes the coevolving mutualism between the manager and the managed resource and the responses each make to promote this relationship. Agriculture is defined as a provisioning system in which the production and consumption of domesticates plays a dominant role. Defining these closely related terms in this way spotlights different key features of each, making it clear that each is the product of different circumstances influenced by different causal factors and best monitored using different types of markers.

Impacts and Markers

Although domestication should not be defined in terms of its impacts, identifying these impacts and understanding how they relate to the process of domestication is essential. Current research on domestication is, in fact, largely focused on identifying the impacts of domestication and using them as markers of the timing and nature this evolutionary transition in the distant past, as well as to monitor ongoing efforts at improving existing domesticates and creating new ones. Domestication produces a wide array of changes that vary in how directly they can be causally linked to the relationship between domesticator and domesticate. Establishing the existence and relative strength of such cause-and-effect linkages is important in determining the utility or value of different markers used to trace the initial development and subsequent evolution of domestication partnerships.

Genetic Impacts. Genetic responses that maintain and enhance the domesticatory relationship are the most proximate result of domestication and, if clearly linked to this relationship, are its most compelling indicators. Genetic change can occur in both partners, especially when nonhuman species are the domesticators. When humans are involved, genetic change is almost always confined to the plant or animal partner species, with genetic impacts of domestication in humans only occasionally identified (23).

Genetic responses to domestication are the result of a number of different selective pressures. The two most important of these in early domesticates were most likely the relaxation of selective pressures experienced in a free-living state and the introduction of new selective factors arising from closer association with humans (15, 24). Once humans began to isolate managed resources from free-living populations, especially when they were moved outside of the natural range of their progenitors, both genetic drift and founder effects came into play. Directed or artificial selection through deliberate breeding to encourage specific traits is thought to be a relatively late development in most domesticates responsible for the appearance of "improvement traits" that follow initial domestication (25). It is, however, often hard to isolate any specific individual causal factors that result in particular genetic responses, with multiple selective pressures likely involved.

In both plants and animals there are constellations of traits that may not be the proximate result any of the selective pressures associated with the domestication process, but are instead linked to some other directly selected trait. In mammals this "domestication syndrome" includes lop ears, mottled coats, decreases in brain size, and changes in developmental rates—all traits that may all be linked to strong selection for lowered reactivity to external stimuli (15, 26). The appearance of this pleiotropic cascade of genetically driven traits may result from mutations in single genes responsible for the orchestration of gene expression during development (27). As a result only a small number of mutations in regulatory genes may be needed to account for many of the evolutionary changes that separate wild from domesticated plants and animals.

Full genome sequencing has vastly enhanced our ability to identify genes responsible for phenotypic changes that distinguish domesticates from their wild progenitors, with the greatest advances involving the identification of domestication genes in crop plants (28). Discovering key genes responsible for behavioral shifts in domestic animals has proven more difficult, although there have been some promising advances in this direction (29). Perhaps the most exciting work in documenting genetic change associated with early domestication involves ancient DNA extracted from archaeobiological remains and the resultant identification of the timing and sequence of the appearance of key domestication genes in both crops (30) and livestock (31).

The majority of genetic research on domestication has focused on neutral noncoding genes used to trace the phylogeny of domesticates. Early work concentrated on the chloroplast genome in plants and mitochondrial genome in animals (32). Studies of a single genome only tell one side of the story, however, and more recent nuclear genome sequencing technology has provided a much more complete picture of the heritage of domesticates. Nuclear genome research, for example, has demonstrated that what seemed to be multiple independent domestication events in various livestock species are more likely attributable to introgression between introduced domesticates and indigenous wild populations (25). Once again the most significant insights into the phylogenies of domesticates are gained through the analysis of ancient DNA, which promises a picture of the early divergence of domesticates from wild progenitors unclouded by the millennia of subsequent introgression and directed breeding (25, 33).

Phenotypic Impacts. Genetically driven phenotypic changes in morphology, physiology, or behavior of emergent domesticates are one step removed from the selective factors operating on the

genomes of domesticates. As a result there is a somewhat higher burden of proof in determining whether specific phenotypic traits in domestic crops and livestock are, in fact, the product of the domesticatory relationship and, if so, how and when they arose. The challenges in using these traits to trace domestication pathways are compounded by the fact that only a small portion of the phenotypic impacts of domestication are visible in the archaeological record.

In annual plants impacts of domestication are seen primarily in traits related to germination and dispersal—changes in dormancy rates, seed size, and testa thickness, as well as in the timing and morphology of dispersal mechanisms (14, 34). It had been thought that that the most archaeologically visible impacts of domestication in some annual plants (i.e., seed size increases and the loss of indehiscent structures for seed dispersal) would appear quite quickly with sustained human sowing and harvesting (35). Recent work, however, has shown that these responses may appear substantially later than other phenotypic changes. The appearance of nonshattering rachises in Near Eastern cereals, for example, is not, as once argued, a marker of the beginning of a domesticatory relationship with humans, but instead an artifact of changes in harvest technology and timing that occurred long after humans were actively engaged in sowing, cultivating, and harvesting cereals (34). Recent evidence also indicates that seed size increase in Near Eastern pulses only appeared after other responses to human cultivation occurred—the lowering of seed dormancy rates and the development of indehiscent seed pods, attributes that in pulses are not generally preserved in archaeobiological assemblages (36).

In contrast to annual plants, it has been argued that deliberate selection for desired traits played a significant early role in the domestication of perennial plants and tree species, especially those clonally propagated through vegetative cuttings (14, 37). Phenotypic responses in root crops and tubers, for example, are argued to include changes in the size, chemical, and starch composition of underground organs that made these plants more palatable and more profitable (38). In the absence of decay-resistant diagnostic parts, especially in the humid tropics where many of these crops were first domesticated, research has focused on the recovery of starches, which seem to display distinctive phenotypic responses to domestication in both morphology and their size (38). Although highly susceptible to postdepositional decay, starches can be recovered from the surface and interstitial cracks in chipped and ground stone and pottery and even in the calculus on human teeth (39).

Phytoliths are another microscopic plant component argued to have undergone genetically driven phenotypic change under domestication. Found in many annual and perennial crop plants, these opal silica bodies provide structural support, protect against predation, and are highly resistant to postdepositional decay under most conditions (40). As with starches, it is argued that there is a direct relationship between selection for larger fruit size and an increase in phytolith size, sometimes accompanied by distinctive changes in morphology—traits used as markers of domestication in a number of crop plants (41–43).

The utility of microbotanical remains such as starches and phytoliths as markers of domestication is tempered by a number of factors. These include a lack of clarity about the linkage between selection forces on plants under domestication and observed differences in the size and morphology of starches and phytoliths (40), as well as difficulty in distinguishing domestication traits from those caused by factors unrelated to domestication (i.e., pathogens, soil substrate, water availability, and food preparation techniques) (44–47). Taphonomic issues surrounding the preservation and stratigraphic integrity of plant microfossils are not well understood (48). Uncertainties about the movement of phytoliths in soils, in particular, raise questions about the reliability of indirect dates of phytoliths recovered from archaeological deposits, and even direct radiocarbon dating of phytoliths may be affected by the sequestration of old carbon

in phytoliths (49). Inconsistencies in the description and quantification of distinguishing criteria, especially uncertainty over inter- and intrataxa variability (48, 50), are cited as serious concerns limiting the utility and reliability of microfossils in documenting domestication that call for more conscientious publication of images of reference collections and archaeological assemblages (48) and freer access to assemblages by researchers seeking to replicate results.

In animals the earliest and most universal genetically driven phenotypic impacts of domestication focus on behavioral attributes, especially on endocrine-controlled behaviors that lower the animal's reactivity to humans and facilitate its adaptation to an anthropogenic environment (15). These selective pressures are argued to result in brain size reduction in domestic animals (51), especially in those areas of the brain controlling endocrine function, that, as discussed above, are linked to pedomorphism in developmental rates and the retention of juvenile morphological characteristics in adult animals (15). The neotonization of domestic pig and dog cranial morphology attributed to this process is argued to have caused a decrease in prognathism that, in turn, is responsible for reduction in the size of teeth, crowding, and variations in tooth number—traits used as markers of initial domestication in these species (52, 53). It may be difficult, however, to tell whether these traits arose during an initial commensal phase as these animals moved into anthropogenic niches, rather than as responses to a later phase of active domestication.

Once thought a marker of initial domestication in sheep and goat, changes in horn morphology—linked to a relaxation of the selective advantage of large horns in mate competition, active selection against large horns no longer useful in securing mates, and perhaps deliberate directed selection by humans against aggressive large-horned males—are now known to have appeared after domesticates were moved out of the natural habitat of their wild progenitors, a millennia or more after clear signs that these animals were managed in ways consistent with domestic herds (54). The utility of body size reduction, once considered an essentially instantaneous product of domestication (55), has also been called into question. Apparent decreases in ovi-caprid body size at about 10,000 y ago are now known to be the result of demographic shifts in the archaeological assemblages of managed animals (dominated by smaller females) compared with assemblages composed of hunted animals (dominated by large prime-age males) (56).

Geometric morphometrics (GMM) is a relatively new and widely heralded technique for distinguishing between the teeth of wild and domestic pigs (31, 57–59). Rather than the result of specific selective pressures, it is argued that subtle changes in tooth shape measured by GMM are proxies for the neutral genetic shifts used to trace the phylogenetic histories of domestic animals (18). Demonstration is still lacking, however, of how and why these changes in tooth shape track the genetic differentiation between wild and domestic taxa (60). If shape can to be shown to be a marker of phylogeny, the next challenge will be to determine how phylogenetic differentiation caused by domestication can be distinguished from other processes, (i.e., geographic barriers or habitat shifts) that also result in reproductive isolation and subsequent genetic differentiation. As with plant microfossils, issues of interanalyst comparability, quantification, and standardization need to be addressed before the potential of GMM in documenting domestication can be fully realized.

Plastic Impacts. Domestication also results in plastic responses unrelated to genetic responses to the new selective pressures experienced under domestication, or their phenotypic expression. Nonetheless, plastic responses to domestication may be both numerous and dramatic and, as a result, can provide significant information regarding the domestication process. In humans, these "ecophenotypic" responses include: contraction of zoonotic diseases carried by domestic animals; changes in stature or growth rates; increased prevalence of dental caries owing to

greater reliance on carbohydrate-rich crop plants; changes in bone chemistry reflecting dietary shifts; and biomechanical stresses on human skeletons from tending domesticates (61). In animals proposed domestication-induced plastic responses include: dental irregularities (hypoplasias) caused by nutritional and other stresses experienced under human management; diseases that cause large fetal and neonatal mortality; bone chemistry changes owing to provision of forage or changes in the mobility; and pathologies arising from tethering, use as draft animals, riding, or carrying heavy loads (62–65). Plastic responses in plants that arise as a consequence of human cultivation are fewer and include possible responses to artificial watering that increase the plumpness of cereal grains or affect the size and aggregation of phytoliths, as well as chemical responses to field conditions (66–68).

The linkage of plastic responses to domestication, however, is more difficult to differentiate from other causal factors unrelated to domestication. It is also difficult to identify at what point these responses become manifest, with many arising after domesticates become the underpinnings of agricultural economies.

Impacts on Natural and Cultural Contexts. Impacts of domestication are also seen in the natural and cultural settings in which the evolving relationship takes place. Human niche-constructing activities directed at enhancing the yield or predictability of resources of economic interest that are prerequisites for domestication may have profound impacts on natural environments. These activities include: modifying vegetative communities through burning to increase abundance of herbaceous plants and animals of economic importance; modifying landscapes to enhance water delivery or expand habitat zones of plants and sessile animals; broadcast sowing of wild annuals near water sources; transplanting perennial fruit-bearing species nearer to settlements; and selectively culling competing vegetation to encourage the growth of fruit- and nut-bearing trees (69, 70). Increases in the abundance of an animal species in the archaeological record may result from efforts that promote population growth (i.e., burning), or through the construction of structures that facilitate capture (i.e., fish weirs or kites) (69, 71). Efforts at enhancing access to economically important animals also find expression in harvest strategies designed to increase prey availability that may lead to active management of animal populations and domestication (54, 56).

Evolving relationships between humans and target plant and animal species also have enduring impacts on the cultural setting in which these relationships developed. Tending plants and animals and storing resources they produce may find expression in the built environment (appearance of corrals, storage pits, or silos, the presence of manure and its use as a fuel or building material) that may be used to trace the increasingly close relationships between humans and managed resources (72, 73). Greater investment in resource management may strengthen notions of ownership over resources and the catchment areas in which they are grown and harvested, resulting in more tightly defined and defended territories (74). Alterations in labor relations, in access to resources within communities, in mechanisms for maintaining community cohesion, and even in beliefs about the relationship between humans and the natural world have all accompanied increasing human investment in emergent domesticates in ways that have found expression in the archaeological record (75).

Impacts on natural and cultural settings, however, may be especially hard to link to domestication. The effects of resource management on natural settings are difficult to detect and, if detected, difficult to distinguish from natural forces (70). Arguments for human involvement in the movement of domesticates beyond the geographical range of their wild progenitors based on modern distributions may not reliably reflect ancient distributions (54, 76). Cultural responses to increasing engagement in managing plants and animals may vary and may arise in the absence of domesticates. Whereas many of the archaeological markers resulting from these impacts can be used to detect

resource management, they are not necessarily indicative of the development of a domesticatory relationship between humans and managed species. This requires demonstrating the existence of a sustained coevolving mutualism between humans and target species.

This is not to say that evidence of genetic or resulting phenotypic change necessarily takes priority over other markers. The detection of "domestication" genes controlling coat color among pigs recovered from forager settlements in northern Europe, for example, does not indicate that these hunter-gatherers "possessed" domestic pigs or that these were "the earliest domestic animals" in this region (57, 77). Rather, it indicates that these pigs had some degree of domestic ancestry, likely acquired through introgression between escaped domestic pigs from nearby farming communities and indigenous wild boar (60, 78). In addition to genetic markers, establishing the domestic status of these animals would require some evidence that foragers were engaged in an ongoing domesticatory relationship with the pigs in question, based on, for example, harvest profiles, evidence of penning, or nutritional changes indicative of active human management.

No one marker—genetic, phenotypic, plastic, or contextual—is sufficient to definitively document domestication. Because domestication is a multifaceted relationship involving both biological and cultural processes, documenting it requires looking across a wide range of markers and tracking how and when they are manifested. Fortunately, methods for tracing multiple markers of domestication up through time have been developing at a rapid pace and, as a result, there are now relatively high-resolution records of the origins and evolution of plant and animal domestication in a number of world areas. These increasingly detailed regional-scale developmental sequences are making it possible for researchers to better address the most difficult of the core questions of domestication research: why these relationships arose in the first place.

Causal Factors

Early causal explanations for domestication conflated domestication and agriculture, and focused on identifying single factors that were thought to account for both phenomena (79). These "prime-mover" explanations can be grouped into "push" and "pull" scenarios. Push scenarios set developments in the context of external stresses that forced people to domesticate and adopt agricultural practices—factors such as climate change or population increase. Pull scenarios were usually set in more benign, even bountiful, contexts, emphasizing internal factors that encouraged humans to adopt these practices—an interest in social promotion or cognitive changes in how people view their relationship to the natural world (75).

Such single-factor scenarios were easier to advance when the outlines of domestication and agricultural origins in various world areas were poorly documented. The high-resolution regional-scale records that are now becoming available, however, indicate that these developments were shaped by a number of complex and locally contingent factors that cannot be accounted for by single-factor explanatory frameworks (79). As a result, attention has shifted toward identifying broader contextual frames of reference within which different regional trajectories of domestication and agriculture have unfolded. The long delay between initial domestication and the development of agriculture in different independent regions (20, 76) also makes it clear that a single explanatory framework cannot account for both the origins of domestication and the subsequent emergence of agriculture. Although the descriptive gloss "origins of agriculture" or "OA" is sometimes still used (10), almost all current research is focused not on agricultural origins but on initial domestication (76). Two alternative explanatory frameworks for initial domestication have recently drawn considerable attention. Although both are characterized as grounded in evolutionary biology, they draw on very different paradigms and offer oppositional explanatory accounts.

For over a decade researchers endorsing optimal foraging theory (OFT) have argued that goals of optimizing energetic returns were primary shaping factors in domestication (80–83). Characterized as derived from neo-Darwinian evolutionary theory, OFT is based on the premise that optimizing behaviors confer a selective advantage to individuals who practice them. Of the various OFT models that have been developed, only the diet breadth model (DBM) has been used in efforts to explain initial domestication (10). DBM predicts that foragers will always choose resources with higher net energy returns, after search and processing costs, over lower return resources. Items are added to the diet in descending rank order, with items falling below a certain level of return always ignored, regardless of their abundance, as long as there is a reasonable expectation of the availability of higher-ranked resources. The model further predicts that when high-ranking resources are abundant, diet breadth will narrow and foraging efficiency will increase. Conversely, when availability of high-ranked resources decreases, diet breadth will broaden because a wider range of lower-ranked resources will be added to the diet to compensate for reduced access to higher-ranked resources, resulting in an overall lowering of foraging efficiency. Moreover, under DBM rules foragers will only opt for resources with delayed returns (resources that require tending over a growth cycle) when resources that provide immediate returns are no longer as plentiful.

Because domestication frequently focuses on resources OFT proponents identify as low-ranking—plants and small to medium-size mammals (10)—the addition of progenitors of future domesticates to forager diets is automatically cast as a response to lowered availability of higher-ranking resources (i.e., larger game animals). Moreover, because management of these resources entails a system of delayed returns, the impetus for increasing engagement in management is also, by definition, a response to continued resource pressure that precludes a return to the immediate-return strategies focused on high-ranked resources. Such DBM-derived explanations for initial domestication represent a recent incarnation of stress-based or "push" prime-mover models, providing a framework in which resource depression, environmentally or demographically induced, accounts for the addition of domesticate progenitors into the diet and their subsequent domestication.

In direct opposition to DBM-based explanatory frameworks, a cultural niche construction (CNC) explanatory framework for initial domestication is directly derived from macroevolutionary theory (69, 74, 76, 84–86). In contrast to a neo-Darwinian focus on selection-driven allele frequency changes in individual organisms, macroevolutionary theory considers organisms as integrated wholes that do not simply adapt to changes in their environment but that may, through more hierarchical and interactive processes, actually shape their environments (23). This is accomplished through niche construction or ecosystem engineering, with organisms acting "as co-directors of their own and other species evolution" (87). Although many organisms engage in niche-constructing activities, humans, with their ability to spontaneously invent and modify new goal-directed behaviors and pass them on through cultural transmission, are considered the "ultimate niche constructors" (84, 88). These are the behaviors that CNC explanatory frameworks hold central to the domestication of plants and animals.

Whereas OFT explanatory frameworks cast efforts at modifying environments leading to domestication as adaptive responses to resource depression (81, 83), CNC explanatory frameworks see niche construction as an important driver of evolutionary change that does not require resource depression to be set into motion. In fact, a CNC approach argues that long-term commitments to niche-constructing activities required for domestication are more likely to occur in stable or resource-rich environments (76, 86). So, whereas OFT scenarios place domestication in the context of imbalances between population and a region's carrying capacity (10), CNC explanatory frameworks argue that stable to resource rich environments made it possible for human groups to abandon more mobile strategies and establish relatively permanent communities that served as the nexus for the increase and dissemination of information about the environment, each other, and the broader world (86). Environments with abundant, diverse resources predictably found within well-defined resource catchment territories provided particularly productive platforms for the development of broad-based subsistence economies capable of supporting larger and more permanent communities. Stable, resource-rich environments also provided opportunities for experimentation with different productivity-enhancing exploitation techniques (74, 86). At the same time other species took advantage of newly created anthropogenic niches, fostering new relationships with humans. Long-term investment in these environments served as an added incentive for human groups to defend resource catchment territories and continue to enhance the growing store of ecological knowledge that allowed communities to continue to reap the rewards of previous generations' investment in modifying and shaping these environments (74).

CNC explanatory frameworks are similar in some respects to earlier pull scenarios in that, in contrast to DBM explanations, they include an important social element—although in this case forces enhancing social cohesion are emphasized over those that promote differential access to resources. However, unlike earlier pull explanations that tend to cast social and ideological factors as sole drivers of the process at the expense of environmental or economic considerations, a CNC approach demonstrates how, in the context of resource-rich environments, goals of preserving community cohesion and longevity combine with complementary goals of creating a secure and predictable resource base, producing natural and cultural contexts in which niche-constructing activities lead to the development of domesticatory relationships between humans and target plant and animal species.

OFT-derived explanatory frameworks for domestication have recently been characterized as superior to other explanatory approaches based on their supposed purer scientific pedigree and the shortcomings of alternatives, including those derived from niche-construction theory, which are described as a "hodgepodge" of inductively derived particularistic just-so stories that represent a "retreat from theory" (10). Explanations derived from DBM are characterized as providing compelling accounts for "agricultural origins" (initial domestication) that are well supported by empirical data in two of the world's independent centers of domestication, the Neotropics and southwest Asia. A third center where DBM is acknowledged as failing to explain domestication, eastern North America, is argued nonetheless to be in accordance with other models based on core OFT optimizing principles. Closer scrutiny, however, shows that DBM/OFT explanatory frameworks lack empirical support in all three of these centers of domestication (76, 79, 86).

In the Neotropics, for example, climate-induced resource depression in the form of late Pleistocene megafaunal extinction is identified as forcing human foragers to adapt by expanding their diet to include lower-ranking root crops, which were then domesticated (83). Recent research, however, indicates that megafauna disappeared from northern South America a full 3,000 y before initial human occupation of the region, and 5,000 y before the earliest evidence for domesticates (76, 89). In addition, a proposed northern South America center of domestication of more than a dozen root crops is situated not in the savanna/dry shrub environment of Pleistocene megafauna, but rather in the seasonal dry forests of inter-Andean river valleys—environments that did not witness any apparent decline in resource availability leading up to initial domestication (76, 90).

Similarly, DBM-based explanations for the increase in dietary diversity and resource intensification leading up to initial domestication in the Levantine region of southwest Asia are based on troubling tautologies that interpret the loss of mobility as evidence for the causal role of population packing in the loss of mobility, and the diversification in the dietary resources as an

indication of the role of resource depression in causing resource diversification (81, 91). In the eastern areas of the Fertile Crescent where three major livestock species and a number of crop plants were initially domesticated (21), even OFT proponents admit that there is no evidence for either population packing or resource depression (92).

Finally, claims that OFT practitioners have engaged in a rigorous "hypothetical-deductive" program of "theoretically driven hypothesis testing" in eastern North America, where DPM predications are not supported by empirical data (10, 82), are instead examples of post hoc theorizing in which one OFT-derived model is replaced with another without further testing or consideration of other models that lie outside OFT optimizing precepts (76).

However, there is abundant evidence that would support alternative CNC-informed explanatory frameworks for initial domestication in all three regions (76, 79, 86). Initial domestication in each takes place in the context of foraging communities situated in river valley catchments with easy access to multiple ecozones supporting an array of abundant and predictably available resources. There is also ample evidence for a protracted period of human enhancement of environments that preceded initial domestication in each region—evidence of anthropogenic fires resulting in shifts in forest composition, as well as increased availability of high-value plant and animal species that moved into newly created anthropogenic environments (76, 82, 90, 93–95).

The relative value of these two very different explanatory approaches to initial domestication can now be determined through side-by-side comparison in an expanding number of world areas where enhanced methods for tracking the impacts of evolving domesticatory relationships are producing detailed empirical records of these evolutionary transitions (76, 86). Advancing our understanding of the causal context of domestication, however, will be based on conscientious comparison of alternative explanatory frameworks with empirical reality, rather than the polemics and posturing that often accompany the defense of favored paradigms.

Relevance

A final question to be addressed is whether defining domestication, identifying its impacts, and exploring the reasons why humans and certain plant and animal species first entered into domesticatory relationships has any relevance to current pressing issues concerning domesticates and their role in feeding the world's growing populations. The answer is, quite simply, yes. Understanding how plant and animal species respond to varying levels of human manipulation is directly relevant to ongoing efforts at improving existing crops and livestock and bringing new and ever more challenging species with greater innate barriers to domestication under human control. Tracing the pathway that humans took to become primary drivers of earth systems, ushering in the Anthropocene, begins with human efforts at ecosystem engineering that led to initial domestication of plants and animals more than 10,000 y ago and created the platform for the agricultural economies that have transformed Earth's biota, landforms, and atmosphere and the trajectory of human cultural evolution (96). A look backward at the ways in which humans and their domesticate partners created anthropogenic landscapes that both sustained and enhanced ecosystems around the world and, at times, rendered them uninhabitable for organisms living outside human ecoengineered systems, has direct relevance for understanding present-day issues of sustainability and biodiversity loss. Finally, exploring core concepts of domestication provides an unparalleled opportunity to examine the interface between humans and the natural world and how processes that shape human cultural evolution interact with those governing biological evolution.

Achieving the full potential of domestication research requires a broadly transdisciplinary approach that brings together genetics, evolutionary biology, ecology, and anthropology in ways that promise exciting new insights regarding the coevolution of coupled human and natural systems. Asking the fundamental questions about domestication addressed here—what it is, what is does, and why it happens—provides a unifying framework that grounds diverse and far-ranging research reaching from the initial steps human and plant and animal partners followed into domesticatory relationships up to the present day and beyond.

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