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ISSUES

Niche Construction and the Behavioral Context of Plant and Animal Domestication

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Many animal species attempt to enhance their environments through niche construction or environmental engineering. Such efforts at environmental modification are proposed to play an important and underappreciated role in shaping biotic communities and evolutionary processes.[1,2] *Homo sapiens* is acknowledged as the ultimate niche constructing species in terms of our rich repertoire of ecosystem engineering skills and the magnitude of their impact. We have been trying to make the world a better place—for ourselves—for tens of thousands of years. I argue here that it is within this general context of niche-construction behavior that our distant ancestors initially domesticated plants and animals and, in the process, first gained the ability to significantly alter the world's environments.

The general concept of niche construction also provides the logical link between current efforts to understand domestication being conducted at two disconnected scales of analysis. At the level of individual plant and animal species, on one hand, there recently have been significant advances in our knowledge of the *what*, *when*, and *where* of domestication of an ever-increasing number of species worldwide.[3] At the same time, large-scale regional or universal developmental models of the transition to food production continue to be formulated. These incorporate a variety of "macro-evolutionary" causal variables that may account for *why* human societies first domesticated plants and animals.[4,5] This essay employs the general concept of niche construction to address the intervening question of *how*, and to connect these two scales of analysis by identifying the general behavioral context within which human societies responded to "macroevolutionary" causal variables and forged new human plant or animal relationships of domestication.

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REGIONAL AND SPECIES-LEVEL APPROACHES TO UNDERSTANDING DOMESTICATION

The initial domestication of plants and animals and the subsequent development of agricultural economies marks a major escalation in the niche-construction potential of human societies. Domesticates provided humans with a significant new means of reshaping biotic communities and natural landscapes more to their liking. Eight to ten centers of domestication are now recognized worldwide.[3–10] These independent centers of domestication exhibit considerable variation in terms of climate, physical environment, biotic community composition, and human developmental history. As a result, they comprise a significant comparative data set of independent, parallel, regional-scale case-study situations with which not only to search for similarities, but to consider alternative explanatory frameworks for domestication. At the same time, different plants and animals were independently domesticated in these world regions, and when taken together, provide an equally diverse set of comparative case-study opportunities with which to consider domestication at the species level.

Efforts to explain and understand domestication carried out at these two different scales of analysis, regional and species-specific, also address different aspects of what is increasingly recognized as a long, complex, and regionally quite variable co-evolutionary process. At the regional level and above, analyses focus on characterization and consideration of the relative importance of a variety of "macroevolutionary" variables, among them climate change, population growth, landscape packing and hardening of between-group boundaries, and intra and intergroup competition for resources and social status. Identified as potentially causal in nature, these variables are cast in roles of varying importance in frameworks of explanation that address the central question of *why* human societies initially established and subsequently sustained relationships of domestication with some species. At the species level of analysis, in contrast, research focuses on documenting a variety of different aspects of *where* and *when* domestication of different species occurred, and specifically *what* genetic and morphological changes distinguish the newly created domesticates from their wild ancestors.

DOCUMENTING THE WHAT, WHEN, AND WHERE OF DOMESTICATION AT THE SPECIES LEVEL

Identification of the likely wild ancestors of domesticated species has been accomplished by comparing the genetic profile of domesticates with that of the modern descendant populations of their suspected progenitors throughout the present-day range of a species, resulting in the identification of the wild populations that provide the closest genetic match.[9–14] The present-day distributions of such "best-match" wild populations often can be employed to infer the specific environmental and spatial contexts in which domestication of the species in question occurred. In a growing number of cases, the earliest directly dated archeological evidence for domestication of different species has been recovered from sites located relatively close to where the modern best-match wild progenitor populations still exist, providing additional evidence of both the spatial and temporal context of initial domestication.[15] Not all domesticates, of course, are developed from single progenitor populations. Efforts to unravel the complex hybridiztion histories for a range of domesticated taxa constitute a rapidly expanding area of inquiry.[16]

The morphological changes that show evidence of domestication in a particular species can also provide insights regarding the specific human behavior patterns that produced them. In seed-bearing plants, for example, a number of distinct morphological markers of domestication, such as seed retention, uniform seed maturation, terminal seed clusters, loss of germination dormancy, and increased seed size, have been identified as automatically resulting from a specific set of human behaviors involved in the intervention in the life cycle of the plant populations in question—the deliberate and sustained human planting of stored seed stock.[17]

Any such morphological changes associated with domestication are, of course, the result of genetic changes in the domesticates. Considerable progress has been made in recent years in gaining a better understanding of such changes at the molecular level. More than half a dozen "domestication genes" have now been identified that control many of the major morphological and other changes associated with domestication in seed-bearing plants. These changes include, for example, seed retention in rice, seed compaction in wheat, loss of branching and germination dormancy in maize, and an increase in fruit size in tomatoes.[10,18] Only a few of these genes that have been linked to specific attributes associated with domestication have so far been studied in archeological specimens.[19,20]

Along with morphological and genetic changes associated with domestication, evidence of the human behavior patterns that comprise a relationship of domestication with a particular species are also sometimes directly observable in the archeological record.

Like the morphological changes I have mentioned, genetic changes associated with domestication in a particular species are in turn the result and evidence of a specific set of human behaviors that comprise the established and sustained relationships of domestication, such as, for seed plants, the sustained planting and harvesting of stored seed stock. Along with morphological and genetic changes associated with domestication, evidence of the human behavior patterns that comprise a relationship of domestication with a particular species are also sometimes directly observable in the archeological record. Shifts in the age and sex composition of faunal assemblages, for example, can provide a clear signature of initial human herd management and domestication.[21] Pollen and phytolith evidence of forest clearing, structural evidence of corrals or water management projects such as canals or check dams, and changes in material culture assemblages have also been proposed as potential markers of the existence of relationships of domestication between human societies and a range of different species.[17]

Paralleling this progress in documenting the details of domestication at the species level, general explanatory approaches focusing on the possible reasons *why* human societies first domesticated plants and animals also continue to be developed at the regional level or higher.

REGIONAL SCALE MACROEVOLUTIONARY CAUSAL EXPLANATIONS FOR WHY HUMAN SOCIETIES DOMESTICATED PLANTS AND ANIMALS

In the seven decades since V. Gordon Childe's[22] pioneering effort to explain the "Neolithic Revolution" within a framework of human response to a changing world, researchers have continued to develop a wide range of different overarching explanatory frameworks for why humans initially brought a variety of different species under domestication.[23] Some of these explanations remain relatively simple and straightforward, and are proposed as being universally applicable. In looking outward beyond the actual human behavior patterns that comprised the newly formed relationships of domestication in search of larger-scale causal understanding, for example, recent studies have outlined a universal explanation for the transition from hunting and gathering to food production in terms of end-Pleistocene climatic shifts. It has been argued that human domestication of plants and animals was not possible before the end of the Pleistocene at about 12,000 B.P. due to several key aspects of Pleistocene climates. Low rainfall over large areas of the globe, as well as low CO_2 levels, it is proposed, restricted plant growth during the late Pleistocene. Climates are characterized as having been turbulent, with high-amplitude fluctuations on time scales of less than a decade to a millennium.[24,25] With the onset of warmer, wetter climates in the Holocene, however, accompanied by an increase in CO_2 levels, and most importantly, the establishment of much more stable and quiescent weather patterns, constraints were lifted on human development of viable, sustainable relationships of domestication and agricultural economies.

Few researchers would argue with the general point that Pleistocene climates may well have constrained the development of relationships of domestication. Considerably less plausible, however, is the corollary argument that early Holocene climates were the central, universal, and immediate cause of plant and animal domestication: that the onset of stable Holocene climates was the "trigger" that made subsequent domestication and agriculture not only possible but compulsory, with no alternatives or other options.[24,25] Improving Holocene climates, it is proposed, produced greater abundance of plant and animal resources and an associated increase in carrying capacity. Human population levels, in turn, steadily increased and the ensuing resource competition between neighboring groups generated a "competitive ratchet" favoring the origin and diffusion of agriculture.[25]

At the opposite end of the spectrum of proposed universal explanations, Brian Hayden's[26] "food fight" theory of domestication assigns a central causal role not to an external environmental variable such as Holocene climatic amelioration, but to an internal social motivating force. According to Hayden, the worldwide domestication of all plant and animal species can be explained in terms of the increasing demand for rare delicacies to enhance competitive feasts hosted by different kin-units within societies in an effort to increase their relative social standing.

In stark contrast to such explanatory frameworks based on "universal inevitability," a rich variety of other far more fine-grained and more empirically based macro-evolutionary approaches have been proposed at a regional scale of consideration. These regional perspectives incorporate a range of different theoretical perspectives, including human behavioral ecology, macroevolutionary theory, and several processual approaches.[4,5,27–30] These regional-scale models are also region-specific; they focus on the interplay of climatic, environmental, and social variables within specific natural and cultural-developmental contexts.

In a landmark study, for example, Flannery[31] offers a detailed and well-supported model of cost-based shifting resource use in the valley of Oaxaca leading up to the first domestication of a crop plant (*Cucurbita pepo*) anywhere in the Americas. Similarly, Piperno[32] addresses the initial domestication of crop plants in the tropical deciduous forests of the Neotropics within an exhaustively documented context of post-Pleistocene environmental change and associated shifts in demography and resource selection, arguing that people began to cultivate some plants as soon as the net return from subsistence strategies involving plant propagation exceeded those resulting from full-time foraging. In a comparable manner, a developmental scenario has been proposed for initial plant domestication in eastern North America that considers the specific attributes of the species in question, as well as their economic roles and habitat preferences in the lead-up to their domestication.[33]

Various other similar explanatory frameworks, each specifically tailored to a particular world region, have been developed in the last decade to address the question of why human societies first domesticated plants and animals, with the Near East drawing the most interest because it provides the most detailed archeological record of the developmental transition from hunting and gathering to food production.[34–37] In a recent comprehensive overview of alternative macro-evolutionary approaches for the Near East, Zeder[5] argues for a nuanced fine-grained framework of explanation incorporating macroevolutionary and processual approaches that also draws on concepts of human agency, historical contingency, and directed variation.

Although these explanatory frameworks for why human societies established and maintained relationships of domestication differ widely in terms of the temporal precedence, causal importance, and interrelatedness assigned to potential causal variables, they all share a common emphasis on a region-specific approach and the integration of relevant information of many different kinds. Rather than assessing the relative strengths of these causal explanations or adding to them, however, I am interested here in considering how they can be better linked to available evidence regarding the specifics of the *what*, *when*, and *where* of domestication.

NICHE CONSTRUCTION: THE GENERAL INTERFACE BETWEEN REGIONAL-SCALE EXPLANATIONS AND SPECIES-LEVEL STUDIES

Regional-scale explanatory frameworks that consider the *why* of domestication continue to be developed and refined for different world areas. Substantial progress continues to be made in documenting the *what*, *when*, and *where* of domestication at the species level. Relatively little attention has been focused, however, on the nature of the interface between these two scales of analysis. *How* do changes in the various regional-scale environmental and cultural variables actually influence societies to domesticate some species? *How* are such larger-scale explanatory frameworks linked, at the species level, to the actual initiation of relationships of domestication by humans? What is the nature of the intersecting general behavioral context within which human societies establish and sustain relationships of domestication? The term "niche construction" provides a recently well-characterized and much-discussed heading for consideration of this larger behavioral domain within which human domestication of plants and animals emerged.

Niche construction is defined as "organism-driven environmental modification" and "the activities of organisms that bring about changes in environment."[1] Not surprisingly, *Homo sapiens* is acknowledged as being the species with the most impressive record of niche construction. Odling-Smee, Laland, and Feldman[1] identify humans as "the ultimate niche constructors." They also provide abundant examples of niche construction by a wide range of other taxa, proposing that niche construction plays an important and almost ubiquitous, if underappreciated, general role in shaping environments and evolutionary processes worldwide. Through niche construction or ecosystem engineering many organisms reshape both their own environments and those of other organisms. By forming complex "engineering webs" of interaction, they modify the natural selection pressures acting on a range of other components of the biotic community.[2] To have any sort of evolutionary effect, however, such niche-construction efforts by humans or other species must persist across generations, either through genes or "ecological inheritance" or, in the case of humans, by cultural transmission. Human dependence on cultural processes, however, does not make human niche construction unique: "niche construction is a general process exhibited by all organisms".[1]

This recognition of the existence of niche construction by other species and across all of the earth's ecosystems and biotic communities provides an important general foundation and broad context for understanding niche construction as carried out by those human populations that initially brought plants and animals under domestication. Much of human niche construction can be included within the general category of ecosystem engineering activities carried out by nonhumans; such activities include tool making, selection and consumption of resources, storage of food and water, farming of food resources, production of detritus, import and export of nutrients, modification of chemical environments, creation of paths, and transport of other organisms.[1] Given that niche construction is not a uniquely human attribute, but widely documented among other species, and that most if not all human niche construction efforts can be grouped under general niche construction categories developed for the animal kingdom, it is reasonable to conclude that the human societies involved in the initial domestication of plants and animals worldwide were actively engineering their ecosystems in a variety of different ways. Other than cultural inheritance, what qualitatively distinguishes humans from other species in terms of niche-construction efforts is, of course, the diversity of the human repertoire of ecosystem engineering and the far greater potential impact of human niche-construction efforts.

HUMAN NICHE CONSTRUCTION AND DOMESTICATION

Against this general backdrop of niche construction as an activity exhibited by all organisms, human efforts to restructure local biotic communities have been documented across a wide range of diverse environmental zones worldwide. Over the years, human efforts at shaping their natural landscapes have been classed under a number of terms, including environmental manipulation,[38] indigenous management,[39] aboriginal agronomy and domestication of environment,[40] domesticated landscapes,[41,42] indigenous resource management,[43] and traditional resource management.[44] In addition, general classification schemes for human ecosystem engineering have been developed.[45,46] All of these roughly synonymous terms and characterizations fall comfortably under the now far more commonly used and more general heading of niche construction.

Both ethnohistorical and present-day descriptions of human niche construction have usually focused on particular types of human resource management influencing wild resources or efforts focused on individual species or species groups of nondomesticates. Often, such descriptions are embedded within the context of general descriptions of overall subsistence economies of both hunting and gathering and food-producing societies.

In contrast to studies that are focused on particular human management activities such as burning, or human intervention in the life cycle of certain wild species, Kat Anderson[44] provides comprehensive documentation of the full spectrum of different land management practices employed by Indian societies in what is now California over the past 10,000 years. She includes, for example, discussions of the following categories of ecosystem engineering that targeted plant populations: burning, coppicing, pruning, sowing, weeding, tilling, selective harvesting, transplanting, irrigating, harrowing, seed scattering, and digging. As Anderson underscores, all of these different activities comprised an integrated and coordinated traditional resource management strategy of direct and sustained manipulation of a broad array of culturally significant populations of plants and animals and their habitats in order to maintain and heighten their abundance, productivity, and diversity.[44] Such broad-spectrum strategies of human niche construction are not unique to California. They were and, in some places, still are an integral aspect of the human condition, involving keen observation, patience, experimentation, and long-term relationships with a broad spectrum of plants and animals, and have been adjusted and refined over many generations of experience and contact with the environment.[43,44] Anderson[44] defines the traditional resource management strategies of Californian Indian populations as a "culturally mediated relationship with the natural world in which humans intervene in the life cycle of native plants and animals to direct their growth and

Figure 1. Agave management in the Southwest. Grid field features near Stafford Arizona have yielded evidence for the management of transplanted Agave.

reproduction." This general definition of human resource management or niche construction, not surprisingly, comfortably encompasses most definitions of domestication and supports the recognition of domestication as a particular form of niche construction.[17]

In contrast to ethnohistorical and present-day research on human resource management activities, "the empirical search for signatures of past human cultural niche construction"[1] remains a difficult challenge.[47] Relatively few archeological indications of human management of nondomesticated plants or animals have been documented to date, and these provide only temporally and geographically scattered clues regarding the time depth and developmental history of integrated systems of human environmental management. Occasionally, however, the archeological evidence of landscape management by human societies can be impressive. In the Phoenix, Tonto, and Tucson Basins of the Southwest United States, for example, more than 550 individual locations where agave plants were transplanted by Hohokam societies at ca. A.D. 600–1350 have been documented.[48–50] Individual agave plants were taken from naturally occurring populations and transplanted to locations near stream or river-valley dwellings and village sites, or into larger fields located on suboptimal bajadas some distance from dwellings (Fig. 1). Water manipulation features, specifically rainfall runoff collection features and rock-pile complexes around individual plants to increase soil moisture, as well as discarded processing tools, roasting pits, and relict agave populations mark the location of these cultivation sites.

In the same general time frame (A.D. 600–1000) human societies in the Owens Valley of eastern California were enriching and expanding water-meadow habitats of various wild bulbous hydrophytic plant species through labor-intensive construction of diversion dams and feeder ditches.[51,52] These archeologically visible niche-construction activities were sustained into the historic period, when they were described in some detail.

The archeological record of eastern North America provides several less compelling but still plausible examples of human management of wild resources. A shift in the relative frequency of gray squirrels versus fox squirrels in Late Archaic period faunal assemblages, for example, has been proposed as evidence of the selective cutting of trees in favor of nut- and mast-bearing species.[53] In addition, evidence of range extension and a notable increase in the relative abundance of three eastern North American seed-bearing plants in Late Archaic and Early Woodland archeobotanical assemblages (ca. 3000–2000 B.P.) has been suggested as indicating that they were cultivated and of considerable economic importance, even though they did not exhibit any unequivocal morphological indications of domestication.[33] These three plants were maygrass, *Phalaris caroliniana*; erect knotweed, *Polygonum erectum*; and little barley, *Hordeum pusillum*.

The Northwest Coast of North America has also witnessed considerable recent interest in documentation of various forms of human niche construction, both present-day and precontact. Studies have included, for example, documentation of human-mediated range extension and transplanting of wild root crops, evidence of "ownership" and weeding or cultivation of wild plant resources, and controlled burning.[43,47]

One of the most frequently encountered archeological signatures of environmental management is the deliberate use of fire in controlled seasonal burning of vegetation. Such controlled burns, while a uniquely human form of niche construction, can also be considered a specific type of conservative, counteractive, stabilizing perturbation as carried out by a wide range of other species, in that it involves reversing or neutralizing a prior change in the environment in order to maintain a preferred ecosystem state.[1] Scheduled burning has been documented historically as an important niche-construction effort employed by human societies in many world areas and has been recognized or suspected in the archeological record of areas as diverse as Australia,[40] eastern North America,[54] the Neotropics,[55] and the west coast of North America.[43,44] Controlled burning of vegetation by human societies appears to extend as far back as the beginning of the Holocene in the Americas, perhaps to 30,000 B.P. in Island Southeast Asia,[9] and to 55,000 B.P. in South Africa.[56]

DOMESTICATES PROVIDE EVIDENCE OF NICHE CONSTRUCTION

Occasionally, human niche-construction efforts in the distant past developed into sustained relationships of domestication with particular species. Various aspects of the archeological record of domestication worldwide in fact provide the best indication of the existence of comprehensive human strategies for the overall management of ancient biotic communities. Significantly, and not surprisingly, when considered within the broader context of proposed ubiquitous human niche-construction activities, the development of such relationships of domestication was not limited to a particular place or a narrow time frame. Each of the eight to ten environmentally and culturally diverse world regions currently identified as likely independent centers of domestication and agricultural origin exhibits a unique multiple-millennia sequence of domestication of different species.[3–10]

Further evidence in support of the proposition that initial domestication occurred within broad strategies of resource management is provided by the diversity of human behavior patterns included under the general heading of "domestication." For each of the hundreds of different species of plants and animals brought under domestication at widely scattered times and places around the world, human societies had to develop a unique, species-specific set of new behaviors. As a result, while taxa with similar attributes (for example, annual grasses versus tree crops versus caprines) could be expected to have responded in similar ways to generally similar forms of human intervention in their life cycle, "domestication" as a general category of human activity encompasses a remarkable spectrum of different causal human behavior patterns. A brief consideration of ten of the earliest domesticates in different world regions can provide a clear demonstration of this diversity.

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The domestic dog (*Canis familiaris*) and bottle gourd (*Lagenaria siceraria*) comprise an unlikely but informative pair in this regard. They are thought to be the first two species brought under domestication, between 12,000 and 15,000 years ago, somewhere in Asia, and to have likely colonized the Americas in the company of Paleoindian populations.[57] Both were primarily of utilitarian value, dogs for hunting and gourds as containers, rather than food sources. The initial formation of a relationship of domestication with the two has often been characterized as not so much involving unilateral intervention on the part of humans as it was dogs and bottle gourds being welcomed to colonize and share the human niche.[58]

Often described as "camp followers" and "dump heap" plants, bottle gourds are active pioneers of disturbed soil situations, and do not require much care or attention once introduced into a disturbed human habitat. The initial phase of domestication of the bottle gourd may have been marked by human harvesting of wild gourds and the subsequent discard of seeds along with other refuse near habitation sites, establishing them as refuse area colonizers and fellow travelers, with subsequent deliberate human selection resulting in thicker rind and larger fruits.

Human refuse may also have played a role in initially attracting dogs to come into closer contact with humans. Movement by canines into the "human niche" can also be associated with their automatic self-selection for reduced aggression, thereby facilitating the development of a relationship of domestication. Reduced aggression in dogs as they occupy the human niche is reflected in linked morphological markers such as snout shortening, as well as crowding and size reduction in teeth.[59,60]

As was the case with the dog and bottle gourd, the initial domestication of the fig (*Ficus carica*) in the Near East by 11,400 years ago also involved a relatively limited level of intervention by human societies in the life cycle of the species in question: the simple cutting and planting of branches from fig trees.[61] This simple human action, however, reflected a sophisticated biological knowledge of their environment, since the fig trees that were selected for such vegetative cloning were parthenocarpic, and while they produced soft sweet fruit, they did not set germinative seeds. As a result, they would have been reproductive dead-ends unless humans intervened by deliberately propagating their shoots.[61–63] As was the case with agave, such replanting of fig branches could also have taken place close to human habitation sites, expanding the niche of the encouraged species while making each year's fig crop easier to monitor and harvest. In addition, since such planted shoots could not be expected to yield fruit for some years, humans had clearly accepted the delayed reward associated with a slow-maturing crop.

Like the fig, the banana *Musa* sp., another relatively long-lived and delayed-yield tree crop, was the subject of early human management as part an overall strategy of landscape modification, but with a substantially greater level of human investment of labor. The archeological site of Kuk Swamp, situated at an elevation of 1,560 meters above sea level in highland New Guinea, has yielded *Musa* phytoliths thought to reflect experimental cultivation of indigenous plants by 10,000 B.P., followed by the construction of increasingly substantial water management canals associated with the cultivation of bananas and other crops after 7,000 B.P.[9] Kuk Swamp, in island Southeast Asia, thus provides very early evidence of the apparent relocation and transplanting of a tree crop outside of its natural range, along with substantial human investment in sustained management paired with a clear awareness of delayed return.

Although the goat (*Capra hircus*) is far different from figs and bananas in most respects, and required quite different efforts on the part of humans in the initial creation of a relationship of domestication, it again reflects both a sophisticated human understanding of its management requirements and the acknowledgment of delayed return linked to a substantial commitment to sustained management. By 10,000 years ago, human societies in the Zagros Mountains of present-day Iran had intervened to a significant extent in the life cycle of goat herds, and had taken control of their reproduction. As is the case with other domesticated livestock species worldwide, humans selectively culled immature males, restructuring breeding populations into the distinctive general age and sex profile that is the hallmark of present-day livestock management for meat production: a substantial majority of adult breeding females are kept along with a few adult males.[21]

In the Americas, two species of squash provide the earliest evidence of domestication of food crops. In Mexico, an increase in seed size marks the initial domestication of *Cucurbita pepo* at ca. 10,000 B.P.,[64,65] while in Ecuador, at about the same time, an increase in the size of rind phytoliths, reflecting an increase in fruit size, indicates the deliberate human cultivation of *Cucurbita ecuadorensis*.[66] As is the case for seed-bearing plants worldwide, among them barley, maize, millets, rice, sorghum sunflower, and wheat, the specific set of human behaviors involved in the initial domestication of these two squashes centered on the sustained planting of stored seed stock in prepared planting areas.

Plants with starch-rich underground organs, such as manioc (*Manihot esculenta*), arrowroot (*Maranta arundinacea*), and leren (*Calathea allouia*), were also domesticated very early in South America, based on the recovery of diagnostic root crop starch grains and phytoliths from 9,000 to 8,000 B.P. contexts.[32,67] As with other species in the general category of root crops, initial human cultivation of manioc, leren, and arrowroot would have involved the replanting of clonal fragments of parent plants in concert with sustained cultivation and deliberate selection for desired attributes such as larger tubers and preferred starch types.

Interestingly, at the same time that recent research in different world regions has documented an increasingly diverse range of human behavior patterns associated with successful early domestication of plants and animals, there has also been substantial recent evidence of early efforts that were not sustained over the long term. Initial efforts to domesticate barley (*Hordeum spontaneum*), oats (*Avena sterilis*), and rye (*Secale cerale*), for example, dating from before 11,000 B.P. (and the end-Pleistocene climatic shift?) have been recognized in the Near East.[68] Each of these early efforts at plant management and manipulation was abandoned, however. Sustained cultivation of the species in question did not occur until several thousand years later in different locales. In the Americas a species of runner bean (*Phaseolus* sp.) has similarly been identified as a possible early, ca. 9,000 B.P., subject of human efforts at cultivation and management that were not sustained.[32] It has also recently been suggested that the sunflower (*Helianthus annuus*) may have been domesticated twice, with the domestication of wild populations in eastern North America at ca 4,400 B.P. being sustained and leading to all documented present-day cultivar varieties; a second, roughly contemporaneous and independent domestication of the sunflower in Mexico was subsequently abandoned.[33] In eastern North America, three indigenous seed plants, maygrass (*Phalaris caroliniana*), erect knotweed (*Polygonum erectum*), and little barley (*Hordeum pusillum*), have also been identified as likely having been cultivated and of considerable economic importance between 3,000 and 2,000 B.P., even though they do not exhibit any unequivocal morphological indications of domestication and subsequently disappeared from cultivation.[33]

This brief consideration of the diverse array of human activities involved in the initial domestication of plants and animals, both sustained and short-lived, when combined with other lines of evidence discussed, provides considerable support for the proposition that plants and animals were initially domesticated within a broad behavioral context of human niche construction. What then, does placing human domestication within such a broad behavioral context add to our overall understanding of this major transition in human history?

DISCUSSION

Often described under a range of different terms, including environmental manipulation, indigenous management, domestication of the environment, and traditional resource management, niche construction is the broad strategy employed by humans to shape, enhance, and sustain their "natural" world while also expanding their developmental horizons. More than 40 years ago, James Downs[27] noted the substantial variation that existed among different small kin groups of Great Basin hunter-gatherers in the details of how they managed and manipulated their environment. He identified two factors, variation and manipulation, as central to the general evolutionary potential of human societies. More recently, Odling-Smee, Laland, and Feldman[1] have argued that environmental engineering or niche construction is a major, if widely underappreciated general factor in the overall shaping of biotic communities and evolutionary processes. Here I argue that niche construction provides an important evolutionary and behavioral context for understanding one of the major transformations in the history of our species, the initial domestication of plants and animals.

As outlined earlier, observations and arguments in support of the proposition that the human societies that initially domesticated plants and animals worldwide did so within a preexisting broad context of environmental engineering can be organized under at least eight different categories of general observations and arguments. First, niche construction by a large number of other animal species has been documented across all of the earth's ecosystems and biotic communities. Given that so many different animal species manipulate their environments, it is reasonable to assume that human populations have been actively managing environments to varying degrees for tens of thousands of years. Second, It is also reasonable to assume that such past patterns of human resource management were both sophisticated and constantly being refined. Humans, after all, are acknowledged to be the ultimate niche constructors, both in terms of the diversity of different ways in which we manipulate the world around us and the magnitude of our resultant impacts. Third, ethohistorical and present-day studies have documented a growing inventory of the different ways in which human societies actively intervene in their local environments in an effort to shape them more to their liking. Fourth, recent research is beginning to provide much more fine-grained and comprehensive understanding of the overall coordinated management strategies employed by human societies, strategies that embrace many different forms of environmental manipulation and involve a variety of different organic and inorganic ecosystem components. Fifth, archeologists and archeobiologists continue to look for and find increasing evidence of a range of forms of human niche construction in the archeological record, extending across many of the world's terrestrial ecosystems. Sixth, the widely dispersed and isolated record of domestication of different species of plants and animals, globally scattered in time and space, suggests the existence of an underlying shared general pattern of human behavior. Seventh, domestication of hundreds of species, with different species-specific management or manipulation challenges, called for a wide variety of human behavior sets. Eighth, increasing documentation of multiple efforts to establish relationships of domestication, which sometimes were not sustained, underscores the extent to which human societies, with a diverse array of skills, were consistently experimenting across a broad range of species in an effort to enhance their environment. Based on these supporting arguments and observations, a plausible case can be presented that domestication quite likely occurred within integrated strategies of ecosystem engineering based on a comprehensive storehouse of knowledge about local biotic communities that had been acquired over hundreds, if not thousands, of years of direct experience.[43,44]

Whatever the exact nature and role of the particular macroevolutionary causal factors that may have been in play in independent centers of domestication, human societies responded not in terms of spontaneous and anomalous acts of isolated inventive genius, but rather within a coherent and broadly based approach to managing and enhancing their environment.

How then, does this recognition that relationships of domestication were forged within a broad behavioral context of coherent environmental management strategies add to our understanding of this major developmental episode? First, and perhaps most importantly, by situating domestication within a broad and well-documented category of general human behavior we remove, to a considerable extent, the proximate mystery surrounding exactly how domestication was accomplished. Whatever the exact nature and role of the particular macroevolutionary causal factors that may have been in play in independent centers of domestication, human societies responded not in terms of spontaneous and anomalous acts of isolated inventive genius, but rather within a coherent and broadly based approach to managing and enhancing their environment. Domestication was not the product of unusual "outside the envelope" behavior patterns, but emerged out of coherent preexisting resource management systems. Macroevolutionary forces did not directly cause domestication, but rather resulted in human societies intensifying their niche-construction efforts. The human societies that initially domesticated different species in different world regions, I argue, were involved in the active, ongoing manipulation of many species in a variety of ways. As macroevolutionary variables caused overall expansion and intensification of efforts at resource manipulation, a few of the varied efforts at manipulation of different plants and animals produced an advantageous enhancement of abundance and productivity far beyond what was achieved with the vast majority of other species being managed. Niche construction thus provides a general universal context for domestication that is, in fact, relevant across a wide range of different environmental zones and within a broadly diverse set of cultural developmental trajectories. Even though human societies in very different ecosystem settings, from south China to the highlands of South America, independently domesticated a wide range of different species of plants and animals at different times and in different sequences, they all share a common behavioral strategy of niche construction. Recognition of this broad context of human ecosystem engineering also underscores the general manner in which human societies identified and targeted certain species and species groups for further intervention and manipulation and, in the process, highlights several interesting related issues that may represent promising future areas of research.

When initially established, for example, relationships of domestication cannot be assumed to have differed from other forms of niche construction either qualitatively, for example in terms of inherent intellectual complexity, or in terms of required human labor investment. The specific human behavior patterns that comprised relationships of domestication with managed species were not necessarily either more challenging or more labor intensive initially than were other niche-construction activities carried out by human populations. Within such long-term sustained strategies of ecosystem engineering, human societies carried out "trial and error,"[1] "tinkering,"[18] or "experimentation"[31] that involved repeated auditioning of a wide range of species with a constant stream of different forms of management in an effort to identify new and better ways of shaping and enhancing their niche. Most such ecosystem engineering by human societies, and most species they manipulated, had inherent limitations, and did not hold the promise of open-ended expansion or lead to impressive returns, even though they were integral components of successful, sustainable, long-term human adaptations to local environments. Placing those particular behavior patterns that produced domesticates within the broader comparative context provided by other parallel human efforts at landscape management may offer clues to other relevant aspects of the process by which humans shifted to a greater economic reliance on domesticates. Ongoing consideration of why some species went on to have long and illustrious careers as domesticates while others did not[3,4,6,33] holds the promise of continuing to provide substantial new insights regarding the particular attributes and profiles of preadaptation that humans were able to recognize during broad-scale niche-construction auditioning for potential star performers.

Situated at this interface of macroevolutionary causation on the one side and the formation of a multitude of species-specific relationships of domestication on the other, human niche construction also provides a vantage point for speculation on two other major and widely recognized aspects of the initial domestication of plants and animals: the extent to which the "broad-scale revolution" may reflect intensified resource management by human societies and the potential application of niche-construction theory in gaining a better understanding of the apparent "rich resource zone" context of domestication of plants and animals worldwide.

Establishing the structure, complexity, and impact of human niche construction strategies back into the Pleistocene remains a challenging and potentially rewarding area of inquiry. The very early domestication of utilitarian species such as the dog and bottle gourd, along with tantalizing evidence of possible deliberate burning of vegetation, provide most of the admittedly limited direct evidence that human societies were active ecosystem engineers well back into the Pleistocene and likely had the potential for establishing relationships of domestication.

Interestingly, both the dog and bottle gourd fall toward the lower end of the scale of required human intervention in establishing and sustaining such new relationships. As the search for evidence of niche construction is extended back into the Pleistocene in a more concerted manner, it will be interesting to see to what extent the "broad spectrum revolution"[69] may be associated with intensification of human efforts at resource management. Reflecting a dramatic increase in the range of species being exploited by human societies and documented in many world regions as overlapping with and immediately preceding domestication, the broad-scale revolution is often identified as evidence of a growing human population, with resource imbalance that necessitated increased human reliance on higher cost, lower yield resources.[37] This dramatic increase in the number and diversity of species, whatever its cause, may also reflect an associated expansion and intensification of human niche construction activities. At the same time that human societies were working their way down the preferred species list and increasing their diversity index of exploited species, they could well have also been expanding and intensifying their ecosystem engineering efforts. It will be interesting to see to what extent new markers of human resource management may be hiding in plain sight within the increasingly well documented developmental patterns of the broad-scale revolution.

Niche-construction theory also provides an interesting new perspective on why a variety of the world's first food crops appear to have been domesticated in relatively similar habitats. Species that were initially domesticated for their food value, rather than utilitarian uses, and which involved more capital investment in terms of human effort in intervention, first appear as domesticates in very similar environmental settings in many of the independent centers of domestication so far identified worldwide. In the Yangtze River Valley corridor in China, for example, as well as in the Near East, Sub-Saharan Africa, eastern North America, and Mexico, very early evidence domestication of a range of different species comes from settlements situated in very rich resource zones associated with river valleys, lake margins, and springs.[6,33,70] In none of these areas did relationships of domestication appear to have developed within a "necessity is the mother of invention" context as population growth forced humans into marginal environmental zones.[69,70] Rather, these relationships developed within rich resource situations that enabled expanded and sustained human experimental intervention in the life cycle of a broad spectrum of different species and the adoption of a sedentary, logistically based economy.

This rich environmental context for initial human domestication of plants and animals fits comfortably within the expectations of niche-construction theory.[1] Local habitat settings that were rich in biotic resources (species abundance and diversity, as well as species with high biotic potential) would have provided the greatest opportunity for human societies to expand and enrich their overall integrated resource-management strategies. The greater the range of species included in human efforts at intervention auditions, and the wider the range of different potential forms of intervention that could be attempted, the greater the likelihood that relationships of domestication would have been successful and sustained.

According to niche-construction theory, within the context of post-Pleistocene climatic improvement and the associated increase in resource gradients within spatially heterogeneous environments (increasingly nonuniform distribution of resources), the richer resource zones, those that exhibited a greater capacity for supporting more people in more permanent settlements, could be expected to have witnessed stronger sustained niche-construction efforts. Trajectories of change would have been "channeled toward adaptation to those regions of niche space in which abundance is greatest, rather than to other regions."[1] Similarly, with increased sedentism and sustained niche construction over many generations, the impact and potency of human ecosystem engineering, with the sheer persistent repetition of the same niche-construction activities, "might act like a persistent unidirectional 'pump,'"[1] directing trajectories of human development toward greater investment in and dependence on intensified niche-construction activities. While it is, of course, dangerous to place too much reliance on "unidirectional pumps" and "channeled" adaptation, any more than on climatic "triggers," niche-construction theory can be considered to provide additional conceptual insight regarding why domestication appears to have occurred within rich resource zones in many different world regions.

The apparent shared environmental setting of initial domestication of food crops across a wide range of ecosystems worldwide provides a third common aspect of this major developmental shift in human history. Human domestication of crop plants and livestock species appears to have occurred in many different world regions, in resource-rich environmental zones, within a broad general behavioral context of niche-construction strategies and nested in an associated broad-scale revolution in subsistence economies.

In conclusion, while not meant to represent any sort of overarching explanatory framework for domestication, these proposed common aspects of human domestication of plants and animals worldwide, when taken together, do provide new ways of looking at one part of this complex process: the environmental and behavioral interface between macroevolutional causal factors and the establishment of new relationships of domestication. This discussion also helps focus attention on many central and still-open questions regarding the relative importance and origin of environmental or cultural circumscription in the initial domestication of plants and animals. The resource-rich river valleys and lake or spring margins that witnessed much of the early domestication of plants and animals existed within regional mosaics of habitats of varying biotic abundance, with environmental gradients forming natural clinal boundaries. Within the rich resource-zone pieces of the mosaic that could support greater residential stability and "logistical" subsistence strategies, it is still difficult to establish exactly why stronger and less permeable cultural territorial boundaries may have been established around the resource catchment areas of different communities. Was the apparent formation of strengthened and sustained cultural boundaries in such resource-rich zones the result of population growth, peer polity packing, and intergroup competition for resources? Or is it possible that such "affluent" and "logistically" organized communities more firmly defined their own territorial boundaries as an aspect of an ongoing process of investment in, enhancement of, and conceptual attachment to an ever-improving anthropogenic landscape?

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