

Domestication as a model system for niche construction theory

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Abstract Niche Construction Theory (NCT) provides a powerful conceptual framework for understanding how and why humans and target species entered into domesticatory relationships that have transformed Earth's biota, landforms, and atmosphere, and shaped the trajectory of human cultural development. NCT provides fresh perspective on how niche-constructing behaviors of humans and plants and animals promote co-evolutionary interactions that alter selection pressures and foster genetic responses in domesticates. It illuminates the role of niche-altering activities in bequeathing an ecological inheritance that perpetuates the co-evolutionary relationships leading to domestication, especially as it pertains to traditional ecological knowledge and the transmission of learned behaviors aimed at enhancing returns from local environments. NCT also provides insights into the contexts and mechanisms that promote cooperative interactions in both humans and target species needed to sustain niche-constructing activities, ensuring that these activities produce an ecological inheritance in which domesticates play an increasing role. A NCT perspective contributes to on-going debates in the social sciences over explanatory frameworks for domestication, in particular as they pertain to issues of reciprocal causation, co-evolution, and the role of human intentionality. Reciprocally, domestication provides a model system for evaluating on-going debates in evolutionary biology concerning the impact of niche construction, phenotypic plasticity, extra-genetic inheritance, and developmental bias in shaping the direction and tempo of evolutionary change.

Keywords Domestication · Niche Construction Theory · Co-evolution · Ecological Inheritance · Cooperation · Extended Evolutionary Synthesis

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Introduction

Domestication represents a *prima-facie* example of niche construction in which niche-modifying behaviors alter selection pressures on organisms living within the niche that shape their own and other organisms' evolutionary trajectories (Laland and O'Brien 2010, 2012; Crawford 2011; Smith 2012, 2015a; Zeder 2012a, 2015a). Domestication is the result of co-evolutionary mutualisms that develop in the context of active niche-construction by both humans and their plant/animal partners (Zeder 2015a). Humans utilize their capacity for goal-directed behavior to engineer environments in ways that enhance the productivity and predictability of economically important species (Smith 2007). Plants and animals undergoing domestication also engage in ecosystem engineering, as well as “re-locative” niche-construction, and niche alteration through developmental plasticity (Smith 2006; Donohue 2005; Odling-Smee et al. 2013). These activities have profound ecological effects that modulate energy and resource availability within engineered environments. They also influence selection pressures on humans and emergent domesticates that evoke demonstrable evolutionary responses in both. These co-constructed niches, moreover, have knock-on effects on organisms not directly involved in the evolving relationship that affect their own evolutionary trajectories. Niche construction theory (NCT) would, then, seem to have a lot to offer to domestication research, while domestication provides a model system for examining many of the core components of NCT.

The utility of NCT as a framework for domestication research is underscored by the close correspondence between insights held to provide “unambiguous evidence that niche construction is of considerable ecological and evolutionary importance” that qualify NCT as “serious body of evolutionary theory” (Odling-Smee et al. 2013: 5–6; Laland et al. 2013a: 74) and central features of domestication and the subsequent emergence of agricultural economies based on domesticates (Table 1). I explore three of these here—co-evolution, ecological inheritance, and cooperation—to investigate the relevance of NCT to the study of the plant and animal domestication. Next, I turn to a broader consideration of the value of a NCT explanatory framework for initial domestication. Finally, I discuss the potential of domestication for evaluating the impact of processes such as niche construction, phenotypic plasticity, extra genetic inheritance, and developmental bias on the direction and tempo of evolutionary change.

Co-evolution

Niche-constructing activities have “ecological spill-over” effects that alter niches and selective environments, often resulting in co-evolutionary relationships between niche-constructing species and other species living in the constructed niche (Odling-Smee et al. 2013: 6). Co-evolutionary responses to niche-construction are “pairwise” when they involve two interacting niche-constructing species, or “diffuse” when the evolutionary response of a second species is mediated by some change in abiotic conditions or intermediary biota caused by the activities of the niche-constructing species (Odling-Smee et al. 2013: 14; Matthews et al. 2014: 248–249). These relationships are central to domestication in which co-evolutionary mutualisms are defining features (Zeder 2015a).

Niche-construction plays a role in each of three distinctive pathways that humans, plants and animals follow into domestication (Zeder 2012b). Humans initiate the prey/harvest pathway through ecosystem engineering activities that manipulate the conditions of growth

Table 1 Insights from NCT as they relate to central features of domestication (following Odling-Smee et al. 2013:5–6)

Niche Construction can:	Domestication results in:
Fix genes or phenotypes that would, under standard evolutionary theory, be deleterious (Kerr et al. 1999)	Fixation of indehiscent seed dispersal traits in cereals and pulses (Fuller and Allaby 2009). Reduction in size and shape of horns in caprines no longer needed in mate competition (Zeder 2015a)
Affect evolutionary rates, both speeding up and slowing down responses to selection under different conditions (Laland et al. 1999, 2001; Odling-Smee et al. 2013)	Differential rates in the development of key domestication traits in plants (Fuller and Asouti 2012)
Cause evolutionary time lags, generate momentum, inertia, and autocatalytic effects (Erwin 2008)	Record of lags and sudden acceleration in the pace of culture change during the period of initial domestication and agricultural emergence in the Near East (Byrd 2005; Kuijt and Prentiss 2009; Zeder 2009)
Drive niche-constructing traits into fixation by creating statistical associations with recipient traits (Rendell et al. 2011)	‘Domestication syndrome’ of linked traits in plants (Smith 2006; Fuller and Allaby 2009) and animals (Zeder 2012b; Larson and Fuller 2014)
Be favored, even when costly, because of the benefits that will accrue to distant descendants (Lehmann 2007, 2008)	Development of dispersal mechanisms in sown seeds that confer greater advantage to descendants than to free-living individuals displaying these traits (Fuller and Allaby 2009)
Allow for the persistence of organisms in currently inhospitable environmental conditions that would otherwise lead to their extinction. Favors range expansion (Kylafis and Loreau 2008)	Dispersal of crops and livestock out of the Near East through Europe and Africa (Fuller 2015; Zeder 2008, 2015b). Dispersal of maize from Mesoamerica into North and South America (Smith 2015c)
Regulate environmental states, keeping essential parameters within tolerable ranges (Kylafis and Loreau 2008)	Human managed environments that buffer plants and animals from external climatic perturbations (Asouti and Kabukcu 2014)
Facilitate the evolution of cooperative behavior (Lehmann 2007, 2008, Sterelny 2007; Krakauer et al. 2009; Van Dyken and Wade 2012)	Increase in social mechanisms promoting cooperation and community cohesion coincident with initial domestication and agricultural emergence (Kuijt 2000; Sterelny and Watkins 2015)
Drive co-evolutionary events and affect the likelihood of coexistence (Krakauer et al. 2009; Post and Palkovacs 2009; Kylafis and Loreau 2011)	Domestication is a co-evolving mutualism between humans and plant/animals (Rindos 1984; O’Connor 1997; Zeder 2015a)
Affect carrying capacities (Krakauer et al. 2009)	Explosive human population growth with agricultural emergence (Bocquet-Appel 2011)

of an organism or its environment in order to increase its relative abundance and predictability (Zeder 2015a). These activities include alterations to the physical environment (i.e., burning, preparing soil substrates, channeling water, expanding habitats, building traps or corrals), as well as to biotic communities (i.e., moving plants or animals into new environments, selectively culling competing species or specific sex and age classes within an animal population) (Smith 2011; Zeder 2015a). Plants and animals following the commensal pathway, in contrast, initiate the relationship by moving into anthropogenic environments, practicing “relocative” niche-construction to take advantage of new opportunities offered by these environments. These activities include the colonization of

disturbed soils by “weedy” plant species that move on to become domesticates (Smith 2006), invasion of anthropogenic environments by animal species that feed off human refuse or on other animals that do so (Weissbrod 2010; Zeder 2012b), and the exploitation of anthropogenic habitats to enhance competitive advantage within a larger guild of species (Elmhagen and Rushton 2007). Humans take a more direct role in the third directed pathway that may involve deliberate breeding for specific traits or, more recently, manipulation of specific genes. This pathway also includes knock-on effects as evidenced by size reduction in the area of the brain that controls motor functions in domestic mink (Kruska 1996), or changes in brain size and function in farmed fish (Marchetti and Nevitt 2003) that can both be seen as responses to human constructed niches (cages and enclosures) that enhance captive animals’ reproductive fitness and thus their value as domesticates.

Co-evolutionary relationships resulting from these niche-constructing activities do not automatically lead to domestication. Elephants used as beasts of burden in South and Southeast Asia, for example, cannot be considered to be true domesticates since they are not bred in captivity but are instead captured as young animals from free-living populations and tamed (Barker and Manwell 1982). Restocking managed populations from free-living ones may also delay the manifestation of key domestication traits as has been argued for cereals and caprines in Near East (Wilcox et al. 2008; Fuller and Asouti 2012; Zeder 2001). Constructed niches that do not vary significantly from natural environments may not confer sufficient change in selective pressures to induce modifications in either humans or target species needed for domestication, as seems to have been the case with the rock mulching and habitat expansion of agave by pre-Hispanic populations in the southwest US (Fish 1995; Smith 2011). Species that practice relocative niche-construction by moving into anthropogenic niches and developing either neutral commensal (i.e. mice or weedy plants) or negative parasitic (i.e. lice or kudzu) relationships with humans will not move on to become domesticates without reciprocal niche-constructing activities by humans that encourage and deepen the relationship.

In order for niche-construction to result in domestication, a sustained, multi-generational relationship must develop from which both humans and target species gain mutual, though not necessarily symmetrical, benefits. Maintaining the relationship over the long term requires both partners undergo modifications (genetic or facultative) that enhance the benefits each accrues. Sowing seeds in prepared substrates, for example, induces changes in germination and dispersal mechanisms (Fuller and Allaby 2009) that confer advantage to tended plants by increasing their likelihood of being included in the next season’s seed stock. These traits also boost the plants’ productivity and hence their economic importance to humans. Animals moving into anthropogenic niches experience selection for reduced reactivity to humans that enhances their reproductive success in that environment, potentially benefitting humans by increasing the supply of a targeted resource (e.g., meat, pest-control, labor, assistance in hunting) and encouraging more intervention by humans in their care, protection, and breeding (Zeder 2012b; Larson and Fuller 2014). Such modifications not only increase mutual benefits, they also deepen the dependence of one or both partners on the other—sometimes resulting in obligate domesticates that cannot survive outside the relationship.

The majority of co-evolutionary interactions in domestication, then, should be considered pairwise responses between two active niche-constructing species, regardless of whether the relationship was initiated by humans (through the prey/harvest or direct pathway) or the plant/animal (via the commensal pathway). Diffuse co-evolutionary responses are more likely in species living in anthropogenically engineered environments

that are not targets of resource enhancement or that do not actively take advantage of these environments through their own niche-constructing activities. Human engineered environments often support higher bio-diversity (Blondel and Aronson 1999) or modified biotic communities (i.e. distinctive weed complexes found in cultivated fields, Colledge 2002) that may be considered examples of diffuse co-evolutionary responses to constructed niches. Organisms living in these niches that are not the direct targets of human resource management may also engage in niche-constructing activities in ways that take advantage of these novel environments, but will not move on to domestication without a reciprocal response from humans.

The potential for eco-evolutionary feedbacks between niche-sharing species also depends on their evolutionary potential to respond to organism-modified environments (Matthews et al. 2014: 260). This is certainly true in domestication where capacity to respond to selective pressures created by niche-constructing activities plays a major role in shaping domesticatory relationships. There are a number of traits that make species suitable candidates for domestication—the ability to colonize disturbed habitats in plants (Smith 2006), or hierarchical herd structures and a lowered reactivity to environmental stimuli in animals (Price 2002; Zeder 2012b). In humans, investment in the management of a species depends on the returns and demands of other potential resources, technological capacities, distribution of humans and resources across the landscape, as well as human physiological capacity to utilize these resources. Some species present insurmountable barriers to domestication, at least in the absence of more sophisticated technologies for breeding in captivity. Early steps toward management that in sheep and goats led to their domestication in the Early Holocene Near East, for example, did not have the same result with gazelle, another heavily exploited ungulate with a herd structure and flight reflex less amenable to human management (Rowley-Conwy and Layton 2011). The failure of an otherwise suitable species to move on to domestication may also be attributable to a lack of follow-through by humans, as may have been the case with wild oats that were intensively collected in the Early Holocene southern Levant but, unlike other economically important wild cereal species (i.e. barley and emmer), did not move on to domestic status at that time (Weiss et al. 2006).

Genetic variability also plays a role in the evolutionary potential of an organism to respond to niche-altering activities. Species with low genetic variation and trait heritability, for example, are predicted to be less likely to display co-evolutionary responses to niche-construction (Post and Palkovacs 2009), as demonstrated experimentally for algal-rotifer systems in which the lack of variation in single clone algal cultures had a significant impact on eco-evolutionary feedbacks shaping predator–prey dynamics (Yoshida et al. 2003). In contrast, species with high degrees of genetic variation, especially those that display plasticity in the expression of phenotypic traits, are thought to be more likely to respond to changes in selective environments caused by niche construction (Donohue 2005; Boogert et al. 2006: 575; Laland et al. 2008; Moczek et al. 2011).

There is a great deal in the recent NCT literature on the extent to which altered selective environments resulting from niche construction foster the accumulation and expression of cryptic phenotypic variation and the subsequent conversion of phenotypically plastic traits into genetically fixed traits (Laland and Sterelny 2006; Laland et al. 2008, 2011; Laland 2014). Developmental plasticity in reproductive phenology is argued to be a primary way that plants engage in niche-construction. Experimental studies with a weedy mustard species, for example, suggest that plasticity in seed dispersal, flowering time, and germination serve niche-constructing functions by shaping selective environments that influence the evolutionary dynamics of key reproductive traits (Donohue 2005; Donahue et al. 2005;

see also Laland and Sterelny 2006; Nicotra et al. 2010). Cryptic variation is thought to be especially likely to accumulate under circumstances of relaxed selection on environment-specific genes that can be released during shifts to novel environments in rapid bursts of adaptive evolution (Moczek et al. 2011). Although stressful conditions are argued to facilitate the expression of environmentally triggered developmental traits (Moczek et al. 2011), factors mitigating stress in novel environments may actually be more likely to promote both the accumulation and expression of phenotypic plasticity. For example, the lack of natural enemies is argued to promote increased adaptive plasticity in invasive species introduced to novel environments by reducing the costs of plasticity and increasing its benefits (Huang et al. 2015).

Phenotypic plasticity is just beginning to surface as an area of inquiry in domestication research, which to date has focused primarily on the effect of climate change on developmental plasticity in domesticate progenitors (Gremillion and Piperno 2009; Piperno 2011). Experimental work conducted by Piperno et al. (2014), for example, has demonstrated that teosinte grown under reduced CO₂ atmospheric conditions similar to the Late Pleistocene/Early Holocene exhibit a number of maize-like traits not seen in teosinte grown under modern CO₂ levels. These traits would have made these plants easier and more productive to harvest by Early Holocene foragers in southwestern Mexico leading to co-evolutionary relationships between humans and certain teosinte morphotypes that resulted in the fixation of these traits in domesticated maize.

Largely unexplored, however, are the potentially more powerful impacts of niche construction in setting parameters for the accumulation and expression of phenotypic plasticity in emergent domesticates. A particularly promising area for future research will involve the extent to which human niche-constructing activities affect phenotypic plasticity in target species, as well as the role of plasticity in enhancing the co-evolutionary relationships leading to domestication. Are, for example, domesticate progenitors more likely to exhibit plastic responses to altered environments than other species also subject to human niche-constructing activities that did not go on to become domesticates? How do variables such as the duration and intensity of modification stimulate plastic responses in managed species? Equally interesting are opportunities that anthropogenic environments offer species for shaping their own selective environments through developmental plasticity in ways that deepen mutualisms with humans. Are, for example, the changes in seed size, burial depth, and germination timing observed in domesticated annuals (Fuller and Allaby 2009: 262) plastic responses to high density in human prepared seedbeds similar to those seen in experiments with free-living annuals (Donohue et al. 2005).

Interactions between niche-constructing species may also be responsible for the expression of pleiotropic constellations of traits, with plastic responses in single genes influencing the expression of multiple traits across the life cycle of an individual (Chaing et al. 2012; Donohue 2012). This observation has special relevance to selection under domestication in which epistatic responses are held to be a key feature in domestication (Doebley et al. 2006; Fuller and Purugganan 2009; Larson and Fuller 2014; Wilkens et al. 2014). Pleiotropic cascades in the expression of seemingly unrelated traits are common among domesticates. In annuals these include larger seed size, thinner seed coats, changes in inflorescence architecture, increased yield, and lowered dormancy rates (Fuller and Allaby 2009; Meyer and Purugganan 2013:845). In animals, reduced reactivity to environmental stimuli, paedomorphic behaviors, changes in heterochrony, mottled coat colors, and lop ears are all argued to be pleiotropic traits (Trutt 1999; Price 2002; Zeder 2012b; Larson and Fuller 2014). While earlier studies suggested domestication traits in multiple species were attributable to mutations in a limited number of regulatory genes (Koinage

et al. 1996; Jensen 2006), more recent research has shown that the origins of these traits is more complicated than originally thought (Albert et al. 2012; Zhao et al. 2008; Fuller and Allaby 2009; Meyer and Purugganan 2013; Carneiro et al. 2014; Wilkens et al. 2014).

Studies seeking to unravel the complicated history of genetic change in domesticates, however, have generally not explored the nature and source selective pressures operating on target species undergoing domestication. NCT brings a much needed focus on the processes that alter selective environments of emergent domesticates responsible for the manifestation of domestication traits. Viewing these traits within a NCT framework as constellations of environmentally mediated genetic associations (EMGAs) arising in the context of altered environments (Odling-Smee et al. 2013) broadens attention from discovering how solutions to changed selective environments were achieved (i.e. on whether these traits arose through parallel changes in the same genes, or through changes in different genes that converge on the same adaptive solutions), to a consideration of how the altered features of the selective environment that produce the constellations of domestication traits arose in the first place. Refocusing attention on the role of niche construction in altering selective environments allows us to ask how co-constructed niches resulted in the same constellation of domestication traits in different domesticates, and to investigate the conditions that trigger plastic responses and pleiotropic cascades in certain species within certain co-constructed environments but not in others. Understanding how humans modified environments to encourage target species, as well as the capacities of species to respond to and reshape these environments, may shed new light on variations in the timing and sequence of trait expression, allowing us to more effectively address why, for example, grain size increases precede the evolution of non-shattering dispersal mechanisms in Near Eastern cereals by hundreds of years, while the reverse is true for pulses (Fuller and Allaby 2009; Asouti and Fuller 2013).

Ecological inheritance

Niche-constructing activities often leave lasting imprints that persist beyond the lifetime of the original niche-creator, bequeathing a “legacy of modified selection pressures” to subsequent generations (Laland et al. 1999: 10242, Erwin 2008: 304). This “ecological inheritance” is thought to be responsible for a number of time-lagged, directional trends in the evolution of descendant organisms living within the modified niche (Laland et al. 2008; Krakauer et al. 2009) that drive even costly niche-constructing traits into fixation due to the benefits they accrue to subsequent generations (Laland et al. 2008: 556). This legacy is strongest when feedbacks generated by modified selective environments encourage continued regulation and enhancement of modified niches by the organism and its descendants (Jones et al. 1994; Laland et al. 2009: 201). The evolutionary impact of ecological inheritance is so great, it is argued, it should be recognized as a general inheritance system that, along with genetic inheritance, serves as a major driver of evolution (Odling-Smee et al. 2003; Laland and Sterelny 2006: 1758; Laland et al. 2008: 556).

These concepts have special relevance to domestication. The niche-constructing activities of humans and target species that promote co-evolutionary domestic relationships leave an ecological inheritance that shapes the evolutionary trajectory of both. Human sowing of selected seed stock and the methods used to harvest mature seeds, for example, create a legacy that promotes the development of plants with traits that would make them unviable in a free-living state (Smith 2006; Fuller and Allaby 2009; Fuller et al. 2014).

Landscapes modified by burning, terracing, and mulching to enhance yields of target plant species continue to shape the selective environment of descendent populations, evoking adaptive responses that make managed plants more successful in these environments and more attractive to humans, but less viable outside this relationship. The lowered reactivity that makes animals living in close proximity to humans more productive, and easier to manage, would render animals living outside anthropogenic environments more vulnerable to predation and less successful in mate competition. The protection afforded by corrals and pens and the decrease in competition for mates resulting from selective culling is part of an ecological inheritance afforded to subsequent generations of managed animals that continues to strengthen the mutual benefits enjoyed by animals and humans alike. Engineered ecosystems constructed to encourage certain species, investments in built environments, and new social mechanisms developed by humans in response to growing reliance on managed resources make it increasingly difficult for descendant communities that inherit these altered social and physical environments to abandon them for something else.

Ecological inheritance is transmitted over multiple internal (e.g., genetic and epigenetic) and external channels (e.g., modified selective environments, acquired behaviors), potentially resulting in a loss of transmission fidelity, especially when compared to the template copying system of genetic inheritance (Laland and Sterelny 2006: 1758; Odling-Smee 2010; Odling-Smee and Laland 2012). One way to enhance fidelity is through improvements in the transmission of acquired behaviors. In animals, this can be accomplished through mechanisms that enhance animals' ability to learn from one another and allow novel learned traits to spread widely through populations (Laland and Boogert 2008). Humans' capacity for social learning using language and other symbol systems vastly increases the fidelity of information transmission, making it possible to modify and fine-tune these behaviors and thus "ratchet" up their complexity and efficiency (Dean et al. 2013). Since cultural processes generally operate more quickly than natural selection, cultural transmission is argued to eventually overwhelm natural selection as a primary factor maintaining and perpetuating ecological inheritance in human-altered niches (Kendal et al. 2011; Laland et al. 2010; Laland and Rendell 2013).

The primary way humans bequeath engineered ecosystems to descendants is through transfers of ecological knowledge about their environment, its resources, and the methods developed to enhance returns of important species (Sterelny 2007; Smith 2012). These stores of Traditional Ecological Knowledge (TEK) are continuously modified and updated bodies of "knowledge, practice, and belief, evolving by adaptive processes and handed down through generations by cultural transmission," (Berkes 2008: 7). TEK is transferred in stories, myths, ritual performance, and symbolic repertoires, often translated into elements of the built environment, that disseminate the cumulative understanding of the local environment and how to enhance its returns (Reide 2012), providing a "coherent overall framework" of how the world works and how humans fit within it (Smith 2012: 263). Fostering deepening mutualisms between humans and emergent domesticates relies in large measure on the accumulation and transmission of TEK as an enduring cross-generational user's manual that contains essential information on where and when resources can be found and how to maintain the modified environments and management strategies needed to ensure their continued productivity. Over time investment in this body of information becomes a key component in protecting and preserving the resources and the modified environments that support the community. The accumulation and transmission of TEK in communities embarking on domestication, then, provides a powerful case-study example of how, from a NCT perspective, cultural transmission of acquired behaviors

plays a central role in the transmission of ecological inheritance that drives evolutionary trajectories of humans, emergent domesticates, and other organisms swept up in the accelerating process of niche-alteration leading to domestication.

Cooperation

Niche-constructing activities that modulate resource availability create potential for some individuals to benefit from the resource enhancing activities of others without contributing to them (Van Dyken and Wade 2012). This “tragedy of the commons” would seem to create considerable disincentives to engaging in niche-constructing activities at the cost of investing in one’s own reproduction if others are able to invest more in their reproductive success by taking advantage of the enhanced resources produced by niche-constructors. The perpetuation of altered niches that forms the basis of the ecological inheritance bequeathed to subsequent generations, then, requires conditions that favor cooperation within niche-constructing populations that compensate for the selective advantages enjoyed by free-riders.

By broadening the focus of fitness beyond individual actors and their contemporaries to include the individual’s descendants, the concept of ecological inheritance carries clues as to how niche construction facilitates the evolution of cooperative behaviors (Lehmann 2007, 2008). Widening the lens of kin selection pressures to include future generations means that the individual actor also benefits from activities that benefit descendants. Benefits accrued by descendants are enhanced in populations with overlapping generations in which parents interact with off-spring, expanding the network of interrelatedness on which kin selection operates (Lehmann 2008: 557). These benefits are even greater among philopatric populations that make long-term investments in altered-niches allowing them to continue to reap advantages of niche-constructing activities of both the original niche-constructors and their descendants (Lehmann 2008: 558). In contrast, descendant benefits from niche-improving activities decreases under conditions of high population dispersal, low density, and high mobility that reduce or even eliminate benefits of altruistic cooperative behaviors. Monopolizing local environments through spatial proximity or preferential access further selects for cooperative behaviors by ensuring that niche-constructing populations continue to benefit from collective actions, as well as minimizing degree to which interlopers are able to take advantage of resource enhancing activities (Kylafis and Loreau 2008; Krakauer et al. 2009).

Niche-constructing activities that create the context for domestication depend to a large degree on cooperative behaviors of both humans and their plant/animal partners. When plants and animals move into anthropogenic niches, for example, there is a premium on monopolizing these new niches to prevent “cheaters” from reaping the benefits of their investment in these environments. The cultivated field can thus be seen as a “botanical battleground” (Jones 1988) in which morphotypes able to germinate quickly and dominate prepared seedbeds gain considerable advantage over conspecific competitors that do not show the same plastic responses to altered environments (Fuller and Allaby 2009). Once humans augment the ability of affiliate species to monopolize these environments by enhancing availability of essential resources and discouraging interlopers (i.e., weeding invaders from tended seedbeds or protecting animals from predators), they further promote cooperative behaviors in emergent domesticates that reinforce their commitment to the anthropogenic niche.

The pressure on humans for cooperative behaviors is even more evident. By engaging in niche-constructing activities leading to domestication, humans run the risk that others in the group will benefit from resultant enhanced returns without having contributed to their production (Bettinger et al. 2010). Pressure for cooperative relationships within the group increases as ecosystem engineering activities responsible for enhanced yields require collaborative actions of larger groups, thereby increasing potential benefits to cheaters. It is likely no accident, then, that initial domestication usually arose in the context of semi- to fully sedentary groups that had a long-term investment in the exploitation and improvement of abundant, diverse resources that could be reliably found within circumscribed catchments (Zeder and Smith 2009; Smith 2012; Zeder 2012a)—environments predicted to encourage reduced mobility and increased territoriality among foragers (Dyson-Hudson and Smith 1978). Following NCT insights about the importance of cooperation in preserving ecological inheritance, these are the types of environments that could be monopolized and defended in ways that encourage cooperative behaviors needed to perpetuate niche-constructing behaviors and set co-evolutionary processes leading domestication into motion.

Increasing investment in niche-altering activities and reliance on managed resources promotes notions of proprietary ownership of managed resources and the manipulated environments in which they grow (Bowles and Choi 2013), making group members who benefit more from these labors less inclined to cooperate with others who might not have been as industrious or as lucky. The inherent tensions arising from increased dependence on resource management, then, create additional pressures for cooperative behaviors that promote community cohesion and keep it from splintering into competing sub-groups. Inclusion of cultural niche construction in the tenets of NCT promises special insights into the ways that societies on the threshold of domestication maintain the cooperative social environment required for continued investment in managed resources and environments, despite increasing disincentives for cooperation. It is argued that cooperative behaviors in small-scale societies are not sustained through a process of reciprocal altruism involving continuous calculation of self-interest and punishment of non-cooperators (Sterelny 2007). Instead, as a result of their long history of food sharing to compensate for stochastic variations in foraging success, humans have evolved to be “default cooperators”, in which cooperative interaction is assumed rather than enforced. This default reciprocal behavior is maintained by shared customs, norms, and values (a body of cultural niche-constructing behaviors) that set unambiguous, widely acknowledged rules for cooperative behavior that make the failure to abide by these standards expensive. These behaviors are augmented by accumulated bodies of ecological and social expertise embedded in shared societal norms and played out in quotidian and ritual activities (Sterelny 2007: 725). As groups size increases and the complexity of niche-constructing activities needed to sustain the group grows, these same sets of rules and shared values make it possible for different individuals to engage in more specialized tasks, while ensuring that the group as a whole continues to reap the benefits of this collective labor (Sterelny 2007: 727).

These behaviors are plainly evident in the archaeological records of small-scale societies on the threshold of food production. In the Epipaleolithic and early Neolithic Near East, for example, increasing commitment to resource management within circumscribed catchments is accompanied by a ramping-up of social and ritual activities evidenced by the construction of megalithic structures, communal houses, ritual, and feasting activities (Hodder 2001; Watkins 2006, 2015; Schmidt 2012). These new social behaviors can be interpreted as evidence of cultural niche construction involving the transmission of norms of behavior in ways that reinforced cooperative aspects of core subsistence activities

(Asouti and Fuller 2013). These behaviors also likely helped maintain social cohesion among larger, more sedentary groups increasingly dependent on the production of managed/domesticated resources (Sterelny and Watkins 2015). NCT, then, provides fresh insight into how the social mechanisms promote cooperative behaviors required to sustain niche-constructing activities, ensuring that these activities produce an ecological inheritance in which domesticates play an increasing role (Zeder 2015c).

NCT as an explanatory framework for domestication

In the last two decades archaeologists have employed somewhat traditional readings of neo-Darwinian evolutionary theory to construct “overarching framework[s]” for the explanation of domestication (Gremillion et al. 2014: 6171). One version of this approach advocates a literal application of the neo-Darwinian Modern Synthesis (Mayr 1961) to the study of cultural evolution. This “Selectionist” school of archaeologists maintains that culture is shaped by forces analogous to selection, drift, and gene flow operating on individual culture traits, and proceeds in a gradual and incremental pace as these shaping forces operate on variation in individual traits (Rindos 1985; Leonard and Jones 1987; Dunnell 1989; O’Brien et al. 1998; Lyman and O’Brien 2001). The classic Selectionist account of agricultural origins was proposed by Rindos (1984) who argued that domestication arose as a gradual process of symbiotic co-evolution no different from similar processes that drive parallel relationships between social insects and other non-human species.

A more recent application of neo-Darwinian principles to domestication is grounded in Optimal Foraging Theory (OFT), which is itself borrowed from micro-economics and folded into neo-Darwinian theory on the thesis that foragers who optimize for returns enjoy selective advantage over those who do not (Smith 1983: 626). While a variety of OFT models have been applied to the incorporation of domesticates into foraging economies (Gremillion 1998, 2006) and the emergence of agricultural economies (Barlow 2002; Kennett et al. 2006), the only OFT model applied to initial domestication has been the Diet Breadth Model (DBM). A classic foraging theory model (MacArthur and Pianka 1966; Emlen 1966), the DBM predicts the types of resources incorporated into forager diets based on a formal ranking of net energetic returns after search and processing costs (Hawkes and O’Connell 1992; Winterhalder and Kennett 2006). Progenitors of domesticates (plants and small to medium-sized mammals) are generally classified as low-ranking, only utilized in the context of reduced availability of higher ranked resources (Gremillion et al. 2014). The DBM also predicts that delayed-return strategies involved in the production of domestic resources, indeed resource management in general, are only adopted when immediate return strategies are no longer as productive (Bettinger 2006; Winterhalder and Kennett 2009). These models, then, automatically cast inclusion of domesticate progenitors into forager diets and adoption of delayed-return resource management strategies as adaptive responses to resource depression.

Proponents of OFT explanatory models of have been dismissive of more recent NCT informed explanatory frameworks, asserting that “niche construction is not a theory, but a common biological process” that fails to provide a “general theory of behavior to explain why individuals would alter environments” (Codding and Bird 2015: 12). This general theory, they maintain, is to be found in behavioral ecology, more particularly in human behavioral ecology, arguing that insights derived from NCT are nothing new and can be easily be accommodated by existing approaches (Broughton et al. 2010; Gremillion et al. 2014; Codding and Bird 2015; Molenhoff et al. 2015). There are, however, three areas

where Selectionist/OFT explanatory frameworks differ in fundamental ways from those grounded in NCT (Zeder 2015d).

The first is the portrayal of the role of niche-modification in initial domestication. Selectionist/OFT approaches subscribe to an asymmetrical view of adaptation in which “organisms adapt to their environment, never vice versa” (Williams 1992: 484). Human modification of the environment, when acknowledged, is commonly characterized in negative terms as “anthropogenic reductions in prey abundances” (Broughton et al. 2010: 373) that lead to the broadening of the resource base to include lower return resources, thereby lowering foraging efficiency. Even when recognized as enhancing resource returns, human ecosystem engineering is cast as a response to either anthropogenic or environmentally caused resource depression resulting in an intensification of resource extraction strategies such that “individuals must work harder to extract more resources” (Coddig and Bird 2015: 15; see also Gremillion et al. 2014: 6175). Human niche-constructing activities, as well as those of plant and animal species involved in domestication, are viewed in the same way as other non-anthropogenic environmental perturbations that serve as background conditions for selection, but not as independent evolutionary processes.

A NCT framework recognizes that the niche-altering activities of humans, and partner species, are not simply adaptive responses to environmentally induced selective pressures, but are instead dynamic evolutionary forces (Odling-Smee et al. 2013: 17). Activities such as ecosystem engineering, relocation, and niche alteration through developmental plasticity are seen as vehicles by which humans, plants, and animals alter selective factors in their shared environment to their mutual benefit. While humans may initiate or intensify niche-constructing activities under conditions of persistent stress and resource depression, such contexts are not likely conducive to the kind of co-evolutionary processes that lead to domestication. NCT insights on co-evolution, ecological inheritance, and cooperation would predict, in fact, that the long-term, reinforcing niche-constructing activities leading to domestication are more likely to evolve in relatively stable environments, especially ones with abundant, diverse resources found within well-defined catchments (Smith 2012). Not only are these environments more easily monopolized and defended, they also provide opportunities for experimentation with productivity enhancing techniques that effectively audition resources for those that respond to human attention with the most predictable and productive yields (Smith 2012: 267). These environments are also targets of opportunity for receptive plants and animals that move into anthropogenic niches where, increasingly buffered from selective factors experienced by free-living conspecifics, they are able to accumulate and express a range of plastic responses that confer advantage over populations living outside of a co-evolutionary relationship with humans. In effect, humans and emergent domesticates co-construct environments that enhance and perpetuate their mutual investment in each other and their shared niche, serve as buffers to outside perturbations, and build an ecological inheritance in which they and subsequent generations have an increasing stake.

The second major difference between these explanatory scenarios is how they account for co-evolutionary interactions that lead to domestication. OFT based scenarios purport to explain how domesticate progenitors enter forager diets (i.e., through broadening the resource base to compensate for reductions in higher-ranking resources). Other than claiming that this contact between humans and progenitor species led, in some unspecified way, to the initiation of co-evolutionary interactions (Winterhalder and Goland 1997; Piperno and Pearsall 1998; Piperno 2006), these scenarios fail to explain how domesticatory relationships actually unfolded (Smith 2015a: 225). Even Selectionist accounts that center on co-evolutionary interactions (Rindos 1984; O’Brien 1987) do not detail how these interactions led to domestication.

The above discussion on co-evolution provides a number of concrete examples of NCT provides insights into how niche-constructing behaviors initiate and further pairwise co-evolutionary interactions between humans and emergent domesticates, as well as into pre-requisite characteristics that define prospective candidates for domestication (on both the human and plant/animal side). NCT also accounts for mechanisms (genetic and facultative) that shape these relationships, showing how altered selective environments of modified niches promote the accumulation and expression of plasticity and the selection for constellations of linked traits responsible for the genetic transformation of free-living organisms into domesticates. In addition, NCT has bearing on cumulative cultural traits that reinforce the niche-altering behaviors that promote these genetic developments.

The final major area of departure between these approaches is in their treatment of the role of human intentionality. Selectionists argue that intentions behind human actions are irrelevant since behaviors resulting from intentional actions are simply another source of random variation on which selection operates (Lyman and O'Brien 1998: 619; O'Brien and Holland 1992: 450; Rindos 1984, 1985). While OFT scenarios allow for a degree of short-term intentionality in discrete choices about which resources to exploit and which to pass over (Bettinger 2006; Piperno 2006:164; Winterhalder and Kennett 2006), these choices are ultimately guided by optimizing rules dictated by natural selection (Hawkes and O'Connell 1992; Zeder 2012a: 257). Human intentionality, or agency, is relegated to "one of any array of historical processes and proximate mechanisms" (Codding and Bird 2015: 13) that fail to rise to the level of ultimate causes of evolution, a province restricted to identifying how "natural selection (the ultimate cause) shapes the way people make decisions (the proximate cause)" (Gremillion et al. 2014: 6175).

The rejection of human intentionality as a causal factor in cultural evolution may be one of the reasons social relations seldom figure into Selectionist/OFT accounts of initial domestication (Rindos 1984; Stiner 2001; Piperno 2006; Stutz et al. 2009), as well as why archaeologists who focus on social organization, ritual, and symbolic behaviors tend to relegate human/environmental interaction to an ancillary supporting role in their accounts of Neolithic emergence (Hayden 1995; Cauvin 2000; Hodder 2001; Watkins 2010; Zeder 2012c, 2015c). NCT provides a way to bridge this divide by including cognitive abilities among the suite of mechanisms that humans use to shape selective environments and co-direct their evolution (Laland and Brown 2006; O'Brien and Laland 2012; Flynn et al. 2013; Laland et al. 2013b). Far from arguing for some form of "human exceptionalism" that makes humans answerable only to powers outside the constraints of biological evolution as some critics have suggested (Codding and Bird 2015: 12), NCT sees human cognitive capacities as an extension of the use of acquired knowledge and social learning by non-human animals to transmit the ecological inheritance of modified selective environments (Odling-Smee 2010; Odling-Smee and Laland 2012). Beneficial behaviors arising in the context of social networks that brought individuals into frequent contact where they could observe, imitate, and modify innovations (Hill et al. 2011), encouraged information transfers through otherwise costly social learning mechanisms and contributed to the evolution of human cognitive capabilities that, though originally derived from social-learning capacities in non-human animals, have come to exceed them (Sterelny 2007). Human cognitive capabilities, enhanced by higher fidelity information transfers afforded by language and symbolic communication, have fostered the development of "cumulative culture" traits built by multiple interacting individuals and transmitted through social learning mechanisms that are far more complex than one individual could invent on their own and that ramp-up the evolutionary impact and tempo of human niche-altering activities (Dean et al. 2012, 2013). A NCT perspective, then, provides novel

insight into how human cognitive capacities (1) protect and enhance the ecological inheritance of altered niches, (2) promote cooperative behaviors needed to perpetuate niches and preserve social groups that serve as a nexus for innovation and transmission, and (3) play central roles in the interplay among environments, plants and animals, and humans leading to domestication. NCT uniquely integrates ecological and social components of domestication, incorporating human capacity for goal-directed behavior into a theory of evolution that recognizes the role of human agency in the evolutionary interactions of humans and non-human species (Zeder 2015d).

Contra Codding and Bird (2015: 12), NCT is, in fact, a body of formal mathematical theory with specific assumptions and predictions about the evolutionary consequences of environment-altering behaviors (Odling-Smee et al. 2003). True, NCT focuses on evolutionary outcomes of these behaviors rather than the rules that shape them. But NCT's explicit linkage between acquired behaviors, social learning, and evolutionary process, and its acknowledgment of the importance of human capacity for goal-directed behavior in evolutionary process, has considerable bearing on factors guiding behavior in human and non-human animals that has a great deal to offer both behavioral ecology in general and human behavioral ecology (HBE) in particular (Laland et al. 2009: 208–210). Specifically it challenges HBE to move beyond its current preoccupation with optimization molded by natural selection toward a body of theory that acknowledges the role of human intentionality in forging a flexible behavioral repertoire that both responds to and alters environmental conditions in goal-directed ways (Laland and Brown 2006; Laland et al. 2007; Zeder 2012a, 2014, 2015d).

These fundamental differences make it possible to develop different sets of predictions about the conditions and contexts that result in initial domestication under NCT and Selectionist/OFT frameworks that are readily testable with available data (Table 2). In Selectionist/OFT framework domestication arises in the context of resource depression, resulting from deteriorating environmental conditions or population increase, with niche-altering behaviors, if utilized at all, adopted only after less costly resource acquisition strategies are no longer effective. Social behaviors play a relatively minor role, more likely to amplify the competitive advantage of more successful members in the group. A NCT explanatory framework places initial domestication in the context of environments where diverse and abundant resources can be reliably found within defined catchments capable of fostering both co-evolutionary interactions leading to domestication and cooperative behaviors in humans and target species needed to sustain and further those interactions. Niche-altering behaviors should be evident throughout the process, as should corresponding adjustments in social behaviors that reinforce intra-group cooperation. Head-to-head comparison of these two different explanatory frameworks has only just begun (Zeder and Smith 2009; Lee 2011; Smith 2012, 2015a, b; Zeder 2015a), and it is hoped that this healthy dialog will continue as the archaeological record of this key transition becomes more finely resolved in multiple world areas.

Domestication as a model system for evolutionary biology

As is often the case in cross-disciplinary incursions, social science applications of evolutionary biology to cultural evolution frequently lag behind developments in biology and are framed in ways that miss the nuance and middle-ground between differing viewpoints. But in a number of ways debates among archaeologists over the merits of neo-Darwinian

Table 2 Test Implications and data sets of explanatory frameworks for initial domestication. (following Smith 2015a)

	Test Implication— events occurring prior to or concomitant with initial appearance of domesticates ^a	Selectionist/OFT	NCT	Data
1a	Climate/ environmental change	Climate/environmental change resulting in reduction in relative biomass	Climate/environment stable or change resulting in increase in relative biomass	Paleo-environmental proxies (e.g. lake cores, speleothermes, pollen data)
1b	Population levels	Marked increase in population levels reaching or exceeding carrying capacity	Little to no change, with population levels remaining below carrying capacity	Number and size of sites in a region and intensity of site occupation
2	Mobility patterns	Decrease in mobility due to population packing. Catchment areas of groups within region do not necessarily map on resource rich areas	Decrease in mobility due to targeting resource rich catchment areas with abundant, predictably available resources within a relatively circumscribed area, without evidence of population packing	Settlement pattern data and the correlation of settlements with regional resource mapping
3	Resource availability	Decrease in high ranking resources (i.e., large game and high yield plant resources). Increase in food processing to extract nutrients	Broadening of resource base to include greater diversity of plant and animal species with either no net reduction in available biomass or change in processing	Archaeological plant and animal remains (e.g. ubiquity and diversity of taxa, evidence of processing methods and intensity)
4	Niche construction activities	Intensification of human alteration of landscape or manipulation of biotic communities and species demography, if practiced at all, only following evidence of dramatic drop in availability of high ranking resources	Continuous and intensifying evidence of human alteration of landscape or manipulation of biotic communities and species demography in the context of resource rich catchment areas and in the absence of evidence of resource pressure	Evidence of forest clearing through burning (i.e. charcoal in cores), increased patchiness in environments, changes in weed assemblages associated with cultivation, appearance of plant and animal species outside of their natural habitats, evidence of changes in age and sex of prey

Table 2 continued

	Test Implication— events occurring prior to or concomitant with initial appearance of domesticates ^a	Selectionist/OFT	NCT	Data
5	Social behaviors and ritual activity	Any intensification of social and ritual activities more likely to promote competitive advantage of more successful foragers (i.e., competitive feasting, costly signaling)	Intensification of social and ritual activities that enhance shared sense of community and cooperation, and that level intra- community differences in access to resources	Evidence of feasting, changes in community structure, evidence of differential access to resources and social status through burial practices

^a Initial appearance of domesticates as evidenced by genetic, archaeobiological, or archaeological markers following Zeder 2015a

and NCT derived explanatory frameworks for initial domestication echo on-going debates within evolutionary biology—especially on whether evolutionary impacts of developmental processes are easily accommodated by Standard Evolutionary Theory (SET), or whether the importance of these processes in evolution calls for a major “rethink” of SET and its enhancement by an Extended Evolutionary Synthesis (EES) (Laland et al. 2014a, b; Scott-Phillips et al. 2014; Wray et al. 2014; Laland et al. 2015).

Perhaps the primary overlap between these debates in archaeology and evolutionary biology is on the distinction between ultimate and proximate causes of evolutionary change. Polarized statements of positions within evolutionary biology have SET advocates arguing that the status of ultimate causes of evolutionary change should be reserved for those “evolutionary processes ... that change gene frequencies” (i.e. natural selection, genetic drift, mutation, and migration), with genetic inheritance the only mechanism responsible for a unidirectional causal process, in which, taking an expressly “adaptationist stance”, natural selection serves “as the ultimate source of organism-environment fit” (Scott-Phillips et al. 2014: 1239). EES advocates argue that notions of evolutionary process need to be broadened to include developmental processes relegated in a SET framework to playing proximate, background, and largely ancillary roles in evolution (Laland et al. 2015). EES advocates also argue that, in addition to genetic inheritance, extra-genetic modes of inheritance (i.e., ecological and cultural inheritance) should be acknowledged as having significant influence over the direction and pace of evolutionary change through a process of reciprocal causation in which developmental processes both shape and respond to selection (Laland et al. 2013b, 2015; Laland 2014). As we have seen, debates among neo-Darwinian and NCT camps in archaeology have taken similar positions on the importance of niche-altering behaviors and human intentionality, directionality in evolutionary process, and the primacy of natural selection as the ultimate causal mechanism that shapes both the human and the plant/animal sides of evolving domesticatory relationships.

Domestication serves as a model system for evaluating core issues in this ongoing debate. All of the four developmental processes EES advocates argue require more recognition (Laland et al. 2014a, 2015) are in play in the process of plant and animal

domestication involving humans. They are apparent (1) in the ways in which humans and plants/animals modify environments (niche construction), (2) in the developmental constraints that channel the direction of modifications that humans and plants/animals make to further this co-evolutionary process (developmental bias), (3) in how all partners use the capacity for plastic variation to respond to and shape environmental conditions (plasticity), and (4) in the transmission of these responses through ecological and cultural inheritance (extra-genetic inheritance).

The role of cultural inheritance, in particular the importance of learned behaviors and cumulative culture in initiating and perpetuating co-evolutionary domesticatory relationships, is of particular interest here. Traditional readings of SET by biologists, and indeed as we have seen by some social scientists, treat culture as a proximate causal process. According to this view, although culture might help “fine-tune” the variation on which natural selection acts, it has little influence on directional change in evolution (Laland et al. 2013b; Laland 2014)—a position that may serve to alienate human scientists from contributing to evolutionary theory (Odling-Smee et al. 2003: 380; Reide 2012: 90). The inclusion of cultural behavior in evolutionary process is a special strength of NCT, one that offers a bridge to the human sciences and a way to better understand the interface between human and natural systems (Laland et al. 2009: 209–210). The extent to which humans have used their capacity for acquired and socially transmitted behaviors to manipulate environments and biotic communities for tens of thousands of years makes it impossible to isolate “natural” populations of plants and animals as the focus of evolutionary or ecological research. The incorporation of human cognitive abilities and modes of extra-genetic inheritance into a body of evolutionary theory promises a more holistic understanding of evolutionary process and ecological relationships in a world in which humans have played an increasing role in influencing both. Domestication offers a concrete example of how human capacities for inventing and transmitting acquired behaviors restructured ecological relationships and resulted in dramatic evolutionary change in target species. It also provides corollary insight into how constructive and developmental processes of non-human partners in domestication played shaping roles in cultural evolution. Domestication is, then, an ideal system for exploring the role of acquired behaviors and cultural transmission in the profound evolutionary changes that transformed both plant and animal domesticates and human domesticators.

Domestication also offers an opportunity for exploring the rate and tempo of evolutionary change. EES advocates argue that developmental processes both constrain and, especially, speed-up evolutionary change (Laland et al. 2008: 556, 2015; Odling-Smee et al. 2013: 9), harkening to earlier debates over whether evolution proceeds in gradual, microevolutionary steps of selection operating on random variation in individual traits versus a view that envisions evolution in terms of major events of directional, multi-scalar change punctuating long periods of stasis (Gould 1989; Gould and Eldredge 1993). Documenting the rate of evolutionary change is not easy. Studies seeking to do so with contemporary organisms are limited to short generation, relatively simple systems such as bacteria, yeast, flies and other insects (Saltz 2011; Snell-Rood 2012; Glenney and Kerr 2013; Buser et al. 2014). While paleontological studies add deep time perspective on the role of constructive activities in complex eco-systems (Erwin 2008), they still face considerable challenges due to the paleontological record’s patchiness and poor temporal resolution.

Initial domestication of plants and animals, that occurred independently in multiple areas beginning about 12,000 years ago, seems ideal for examining the impact of reciprocal causation on the pace, tempo, and direction of evolutionary change. AMS dating of

the remains of humans, plants, and animals involved in emergent domestication provides tight temporal control, while more complete archaeological records and the growing number of analytical techniques for documenting domestication (Zeder et al. 2006) allow researchers to more closely track the complex cultural and biological relationships involved in domestication. Recent research on pre-agricultural societies of the Early Holocene Near East, for example, have been increasingly successful in melding genetic analyses with archaeobiological studies of plant and animal remains, along with paleo-environmental data, and data on ancient settlement patterns, built environments, and artifact complexes to achieve a increasingly granular understanding of the rate of change of species undergoing domestication (Wilcox et al. 2008; Fuller and Asouti 2012), the environmental context and ecological impacts of human niche-constructing activities (Roberts et al. 2011; Asouti and Kabukcu 2014; Asouti et al. 2015), and the social behaviors that perpetuate these emergent domesticatory relationships (Asouti and Fuller 2013; Sterelny and Watkins 2015), all set within a relatively tight temporal framework (Byrd 2005; Asouti and Fuller 2013). The increasingly well-resolved records of initial domestication in multiple regions makes comparative studies possible in contexts where localized differences in resource availability, environmental conditions, and cultural capacities resulted in different rates and trajectories of change (Zeder 2009).

Conclusions

This paper has explored the ways in which recent NCT research offers novel insights into initial plant and animal domestication—a key transition in Earth history that transformed biota, landforms, and atmosphere, and shaped the trajectory of human cultural development. The relevance of NCT insights into fundamental components of domestication have been outlined, from core mechanisms of the co-evolutionary pathways that humans and their plant/animal partners traveled into domestication, to the lasting legacy of these interactions and the mechanisms of its inheritance by descendant populations, to how human capacities for creating and transmitting goal-directed behaviors helped shape this process. In so doing NCT provides an important conceptual bridge between often-disassociated ecological and social components of this important transition. This paper has also examined how NCT contributes to on-going debates in the social sciences over explanatory frameworks for domestication. Reciprocally, it has considered how domestication offers a model system for evaluating core elements of debates within evolutionary biology over the role of developmental processes in shaping the direction and pace of evolutionary change. Clearly these research domains—NCT and domestication—have a lot to offer one another. Exploring the symbiotic relationship between them promises to have an increasing impact as researchers across a wide spectrum of biological and the human sciences exploit their potential for cross-illumination in understanding core processes of both biological and cultural evolution.

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