



Niche Construction and Long-Term Trajectories of Food Production

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Abstract

Niche construction theory has played a prominent role in archaeology during the last decade. However, the potential of niche construction in relation to agricultural development has received less attention. To this end, we bring together literature on the forms and sources of agronomic variability and use a series of examples to highlight the importance of reciprocal causation and ecological inheritance in trajectories of agricultural change. We demonstrate how niche construction theory can inform on emergent mutualisms in both inceptive and established agronomic contexts, the recursive relationships between humans and their agronomic environments, and bridges between the past and present.

Keywords Niche construction theory · Emergent mutualisms · Archaeology of food production · Ecological inheritance · Coevolution

Introduction

Niche construction theory (NCT) brings attention to the ways that organisms co-create their own selective environments (Odling-Smee 1988; Odling-Smee et al. 2003), purposefully or inadvertently, and in so doing initiate or direct evolutionary change (Odling-Smee et al. 1996). These are not new concepts in biology or archaeology (see Lewontin 1983; Spengler 2021; Waddington 1959), but NCT formalizes these ideas and has brought them to the forefront of these and other

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disciplines (Laland and O'Brien 2010; Matthews et al. 2014). The significant influence of NCT in archaeological discourse is illustrated by the voluminous literature on the subject, especially over the last five years. Niche construction has encouraged many archaeologists to think differently about how they approach the analysis and interpretation of causation, emergent social phenomena, and the cascading effects of reciprocal human–environmental interactions. Niche construction theory both overlaps with but also is distinct from other recent theoretical developments in archaeology that privilege agency and emergent outcomes (e.g., Hodder 2012; Fitzhugh et al. 2019; Fuller et al. 2012, 2016), as the long-term entanglements of societies, organisms, and landscapes are recognized by NCT. We argue that what NCT does differently, or more effectively, is situate anthropology within the broader biosciences: it highlights the place of humans in and as part of natural systems; demonstrates the scale, scope, and importance of ecological inheritance; and transcends time, illuminating complex causal relations between past and present states.

The evolutionary success of humankind stems in large part from our ability to intentionally modify the world around us in strategic ways (Ellis 2015; Odling-Smee et al. 2003; Smith 2007). Among the most consequential activities are those related to food production. Plant and animal mutualisms, agricultural practices, and especially the development of intensive, large-scale agricultural systems, have dramatically altered the planet through cumulative, persistent, and often irreversible changes. It is NCT's attention to these processes, including ecological, social, and historical contexts, that makes it a particularly useful framework from which to evaluate long-term trajectories of agricultural change. The analysis of agricultural practices as emergent, continuously unfolding, but historically situated phenomena, as NCT holds, has particular promise for new insights into the complex causal networks of past ecological relations and land use, and may contribute to addressing future challenges. Furthermore, it facilitates investigation of the full continuum of food production practices, from early, small-scale, nonintensive behaviors to larger, more complex agricultural systems deeply entangled with sociopolitical institutions. In so doing, it improves understanding of the cumulative outcomes of such processes over centuries and millennia.

In this review, we bring together a growing body of literature relating to niche construction. Our aim is to consider what has been learned from NCT-driven analyses of agricultural change thus far and to identify useful directions for future study. A major theme is the importance of emergent symbioses, as manifested through ecological inheritance and evolutionary feedback mechanisms, and their potential to enhance or inhibit future outcomes—pivotal in the context of agronomic processes. We begin by situating agricultural change within NCT and introducing key concepts. We then explore the ways that humans can alter their selective environments through agricultural practices and illustrate these ideas and evolutionary scale outcomes through examples from Amazonia, island Polynesia, Mesopotamia, and northern China. We end with a discussion of issues, theoretical and substantive, that warrant further exploration.

Niche Construction Theory and Agriculture

For social scientists, NCT is both distinctive and advantageous in drawing serious attention to the role that organism agency plays in evolutionary trajectories. This agency not only produces behavioral variation that may be shaped by natural selection (external environmental forces) but also, in and of itself, contributes to an organism's selective environment and that of other species. In considering NCT, an important distinction lies between (a) niche construction behaviors or activities that modify the environment (Laland et al. 2007; Ready and Price 2021) and (b) niche construction as a macroevolutionary evolutionary process—the long-term and cascading effects of niche-constructing behaviors (Laland et al. 2019; Post and Palkovacs 2009). The former is a well-recognized phenomenon most strongly allied with the concept of ecosystem engineering (Jones et al. 1994; Odling-Smee et al. 2013; see also Lewontin 1983, 2000). With respect to the latter, NCT theory recognizes that some (but not all) niche construction behaviors drive evolutionary change when the transformed or engineered ecosystem alters the selective environments of conspecifics and other organisms. As argued by Odling-Smee and Laland (2011, p. 222), “[u]nlike ecosystem engineering, niche construction must be evolutionarily as well as ecologically consequential.”

A critical element of NCT is ecological inheritance (Mesoudi et al. 2013; Odling-Smee and Laland 2011), which is the mechanism through which environmental consequences and ecological outcomes of prior niche-constructing activities are transmitted by an organism. Ecological inheritances are passed on, continuously, to multiple organisms who occupy those same environments, within and between generations (Odling-Smee and Laland 2011). Such transmission may be vertical (from one generation to another) or horizontal (between “ecologically related organisms” that share a common ecosystem) (Odling-Smee 1988; Odling-Smee and Laland 2011). It can include both inherited ecologies and inherited knowledges relating to environmental manipulation and management. The latter contribute to a given set of practices being reproduced repeatedly through time, which can strengthen ecological linkages and firmly imprint environmental modifications. As the foregoing suggests, environmental transformations and attendant ecological impacts are often cumulative, building up over time (Ellis 2015; Odling-Smee and Laland 2011). Ecological inheritances may override natural selection processes and direct populations down alternative evolutionary trajectories (Odling-Smee and Laland 2011, p. 234). Importantly for archaeological studies, ecological inheritances can persist for millennia, altering the evolution of an array of organisms that successively inhabit those spaces, and affecting the structure and function of ecosystems over considerable periods of time (Foster et al. 2003; Ziter et al. 2017).

By privileging the active role of organisms and highlighting another form of evolutionary inheritance, NCT challenges conventional definitions of adaptation (Day et al. 2003; Lewontin 2000) and evolutionary causation (Laland 2015; Laland et al. 2011, 2013). Traditionally, adaptation sees the fit between an organism and its environment as the result of *only* natural selection. Proponents of NCT

argue that adaptations can also be the result of recursive relationships between the organism and organism-driven modifications of the environment (Laland et al. 2017); in other words, the recursive relationships themselves become evolutionary forces alongside natural selection (Odling-Smee et al. 2013, table 2). The coupling of organism and environment can lead to directed evolution, and thus a fit partially determined by the organism itself (Lewontin 2000). Understanding the causes of evolutionary change necessitates investigation of the evolution of selection pressures and focuses attention on feedback relationships (Laland and Sterelny 2006). While organisms modify their environments in response to current selective conditions, they are constrained by both prior modifications (created by previous generations) and by behavior transmission processes.

Niche construction theory has appealed to social scientists because of its ability to integrate diverse disciplinary questions relating to the intersection of natural selection, human agency, and human/nonhuman entanglements (Fuentes 2016; Laland and O'Brien 2010). This is especially useful in the study of subsistence economies where humans intentionally modify their environments—generally with positive outcomes, at least in the short term (Smith 2015; Zeder 2016). Beginning with foraging, humans instigated processes that fundamentally changed the selective environments of other organisms and themselves and increased the availability of resources. For example, the use of fire creates environmental mosaics and can concentrate preferred resources (Bliege Bird et al. 2013; Erickson 2008; Pyne 2019). Other small-scale environmental modifications can also accumulate over time. Examples include the tending and protection of favored plants leading to intensified mutualisms (Lepofsky and Lertzman 2008; Turner and Peacock 2005), or the incremental enhancement of “persistent places” (after Schlanger 1992) through active translocations and/or incidental dispersal of preferred plants and animals (Denham 2011; Hofman and Rick 2018; Hynes and Chase 1982).

These and other practices are part of the complex history of human–biota interactions, cultural management, and coevolutionary relationships that ultimately led to domestication and agricultural systems (Smith 2015, 2016; Zeder 2016, 2017). A definition of agriculture that has currency within the NCT literature was originally offered by Rindos (1980, p. 752), who defined it as “a set of integrated activities which affects the environment inhabited by the domesticated plant throughout its life cycle.” Agriculture is often further characterized by landscape-scale production (Harris and Fuller 2014) and distinctive cultivation practices (tilling, tending, etc.) (Smith 2001). It is these varied practices across landscapes that foster symbioses with other organisms and, over time, forge agricultural trajectories. The latter are embedded in local landscape histories, involve interrelationships with different forms of production, and are shaped by long-term socioecological feedbacks, which are simultaneously both the consequences and causes of agricultural change (Morrison 2006).

The products of ecological inheritance—modified landscapes and ecosystemic relationships—are the context for the practice of agriculture at any given time (O'Brien and Laland 2012; see also Morrison 2015). While niche construction activities relating to agriculture are often learned, the inheritance of modified environments is a form of transmission that occurs independently of genetic inheritance but can, over time, induce

genetic responses (Laland and O'Brien 2012; Odling-Smee et al. 2003). As such, and perhaps most importantly, the inheritance of modified environments and the associated ecosystemic relationships is a process that is constituted by the activities of *multiple* organisms that inhabit the same location. Not only are humans and domesticates able to exert influences on the long-term evolution of agricultural systems, but other non-domesticated species (e.g., birds, bats, and rodents) also may shape the anthropogenic niche through seed dispersal, pest predation, nutrient contributions, etc. More generally, biotic and abiotic modifications arising from agricultural activities may result in new kinds of environments, leading to multidimensional ecosystemic relationships that persist and become selective forces.

Archaeologists around the world have documented an enormous variety of environmental and ecological phenomena that are the outcomes of past agricultural behaviors (e.g., Altman and Mesoudi 2019; Boivin et al. 2016; Ruddiman et al. 2014). The legacies of past land use and ecological relationships include but are not limited to intentionally constructed geomorphic features, modified soils, constructed vegetation formations, and genetic changes to plants (e.g., Arroyo-Kalin 2019; Morrison 2014). Fixed landesque capital investments are a particularly enduring form of cultural modifications (Blaikie and Brookfield 1987; Håkansson and Widgren 2014). Such capital investments were often made across many generations, creating highly engineered landscapes from the bottom up (Erickson 1993; Lansing 1991). Other long-term effects of agricultural land use are often more subtle and unintentional, such as erosion or soil creep, which may both constrain or augment agricultural productivity over long time periods (e.g., Kirch 1988, 1994; Spriggs 1981). The accumulation of modified environmental characteristics, whether intentional or otherwise, results in agricultural practices having substantial downstream effects through time, on subsequent generations of agricultural practitioners, on other cultural activities, and on other organisms. Even subtle changes to the environment have the potential to scale up and become influential through time as they accumulate and become intertwined with other niche construction behaviors or natural processes (see Doolittle 1984; Ullah et al. 2019). Thus, agricultural practices offer enormous opportunities for ecological inheritance, more so than almost any other kind of human activity.

While other perspectives usefully organize and explain shorter sequences and more specific phenomenon (e.g., emergent political economies), NCT integrates and builds on these ideas by exploring multidimensional systems across centuries and millennia. It recognizes that the selective environments of agricultural behaviors are complex, including the place of agricultural strategies within systems of production, the influences of accretionary landscapes, and the cultural contexts under which production is practiced. These all are subject to variability and are inheritable—key ingredients of evolutionary change.

Forms and Sources of Organism-Driven Change

Niche construction theory partitions behaviors into two broad forms: perturbations and relocations (Odling-Smee et al. 2003, p. 47). *Perturbational niche construction* is organism-driven modification of the environment; in the context of agricultural

activities, this might include vegetation (re)structuring, earth moving, or water manipulation. *Relocational niche construction* involves organisms “actively” moving in space, dispersing or migrating, as for example, in response to climatic change or adaptive range expansion (Odling-Smee and Laland 2011, p. 222); in so doing, they typically encounter new selective environments.

A second dimension of niche construction behaviors relates to the source or driver of change, external versus internal. *Counteractive niche construction* occurs when an organism responds to changing external environmental conditions (e.g., forest fires, arrival of new predators, climate change). These kinds of niche construction behaviors tend to be conservative or stabilizing, typically arising when organisms attempt to restore a match between previously evolved features and altered environmental conditions, either by relocating or through niche construction behaviors aimed at alleviating the newly generated selective conditions (Odling-Smee et al. 2003). In contrast, *inceptive niche construction* involves organism-initiated change that exposes themselves, or ecologically related organisms, to novel selective conditions. Inceptive niche construction may take the form of either relocation or perturbation, the latter potentially involving novel behaviors (e.g., innovations) (Laland et al. 2017). The intersection of these two dimensions of niche construction, the form and source of change, give rise to varied selection conditions and shape long-term ecological inheritances. Below, we examine forms of perturbation and relocation in relation to agricultural practices and consider how they may arise from counteractive or inceptive niche construction. In the case of humans, such niche-constructing behaviors often involve conscious choices and may be facilitated or constrained by a variety of environmental, economic, social, and political conditions; we focus here on the first, while alluding to and acknowledging the importance of other conditions. Critically, to qualify as a macroevolutionary process, regardless of form or source, the environmental and/or ecological change must give rise to at least one new selection condition, for at least one recipient population in an ecosystem, and have one or more evolutionary consequences (Odling-Smee and Laland 2011).

Perturbation

Agricultural behaviors can involve a host of environmental modifications aimed at supporting the growth, reproduction, harvesting, and storage of plants on which people rely for sustenance (O’Brien and Bentley 2015; Rindos 1984). Initially inceptive, perturbations create new selective environments for humans, the organisms they cultivate, and others that share a given agricultural niche. Counteractive perturbations may follow in response to the changing selective conditions. Human populations, through habitation and the generation and transmission of ecological knowledge, come to recognize local environmental possibilities and limitations, including specific kinds of microhabitats that are suitable for a variety of cultigens. Purposeful perturbations frequently regulate conditions that might inhibit or slow the growth of target species, affect their productivity, or shape desired end products (see Rindos 1984; Smith 2011). Other noncultivated organisms may benefit from these environmental modifications or their legacies (Bogaard et al. 2018; Eriksson and Arnell

2017), though novel selective environments are deleterious for some. For humans, niche construction by perturbation is often aimed at making the targeted resource more reliable and/or exploitation more efficient.

Agricultural infrastructure, in the form of landesque capital, plays an important role in the formation of novel microenvironments and ecosystems. It may be undertaken simply to expand the productive space or to enhance or ameliorate specific environmental conditions. Infrastructure not only creates novel habitats for target plants and other organisms but may also have consequential impacts on local sedimentary processes, nutrient cycling, and microclimates. Agricultural terraces provide a useful example of how infrastructure both creates novel ecosystems and forges ecological inheritances, which can endure for generations and may transcend sociocultural boundaries (Fig. 1). Terracing has been documented across the globe, crosscutting a range of environments, and varying in size, form, construction, and function (Denevan 2001; Treacy and Denevan 1994). Dryland terraces stabilize slopes, while also capturing run-off and sediments, thereby trapping nutrients, retaining moisture, and increasing soil volume (Beach et al. 2002; Chase and Weishampel 2016; Sandor 2006; Sandor and Homburg 2017; Varisco 1991). In these respects, terraces counteract factors that constrain plant growth, such as aridity or low soil fertility. Some terrace systems have persisted for generations as unique microenvironments that continue to support distinctive vegetation communities



Fig. 1 The Mayoyao Terraces. The terraces are part of the Ifugao agro-ecocultural system, which includes swidden fields, house gardens, private and communal forests (agroforestry), complex irrigation system, and house platforms (Acabado and Martin 2022). Photograph courtesy of Stephen Acabado

(Hightower et al. 2014). Terraced landscapes may also attract subsequent generations of cultivators, even when the original production activities have ceased (see below), as the presence of infrastructure serves to reduce labor demands for subsequent generations of prospective agriculturalists (Bevan et al. 2013).

Other forms of infrastructure may also enhance agricultural productivity. In the Hawaiian Islands, modeling demonstrates how extensive networks of stone walls and earthen embankments, laid out across dryland slopes, would have ameliorated the effects of persistent, drying trade winds by reducing wind flow, which in turn helped retain soil moisture (Ladefoged et al. 2003). Rock and earthen mounds in these field systems probably reduced and suppressed weeds as well. Experimental plantings in the mounds demonstrate significantly higher returns relative to plantings in nonmounded spaces (Marshall et al. 2017). Other infrastructural features alter local environments even more dramatically, as for example qanats in arid North Africa and the Middle East, where novel ecosystems were created by transporting water from wells and aquifers to large areas of otherwise arid plains (Manuel et al. 2018). Some of these systems produced oasis environments and enhanced biodiversity (Rezaei Tavabe and Azarnivand 2013). One of the most enduring kinds of agricultural infrastructure are irrigated terrace systems, particularly taro (*Colocasia esculenta*) pondfields and rice (*Oryza sativa*) paddies. These artificial wetlands not only provide novel environments for agricultural production but often expand the habitat of wetland species, including birds and fish, which may be resources themselves, or enhance ecosystem productivity (e.g., Gee 2007; Malachowski and Dugger 2018).

Raised bed systems can function in a similar manner. Well-known examples come from the Andes, Amazon, and Mesoamerican lowlands, where they were sometimes constructed to reclaim otherwise unproductive lands (Denevan 1970). The periodic deposition of organic-rich canal sediments onto the raised beds enhanced soil fertility, while the canal waters likely acted as a heat sink, regulating temperatures across such systems in the Andean highlands (Erickson 1988, 1992). In the southwestern Amazon, raised beds effectively mitigated both flooding (by channeling water) and periods of drought (by retaining moisture) in conjunction with a diversity of other landscape modifications and management practices (Duncan et al. 2021). As with irrigated terraces, raised bed systems can increase landscape heterogeneity and support nonfood organisms (McKey et al. 2010). Some organisms that adapted to these constructed environments have come to depend on them and act to regulate ecosystem functioning even after their abandonment by people (Renard et al. 2013).

Another important agricultural perturbation is the purposeful or incidental modification of soils. A variety of soil additives have been used in traditional food production systems to enhance productivity, particularly stone and shell. Lithic mulches improve moisture capture, reduce evapotranspiration from solar radiation and wind stress, control erosion, and improve soil nutrient content (Ladefoged et al. 2010; Lightfoot and Eddy 1994; Maxwell 1995; Wozniak 2001). In arid environments, lithic mulches can also limit the formation of soil crusts (Lightfoot 1996). Experimental work shows the effectiveness of stone mulching. Alderfer and Merkle (1943), for example, demonstrated that bare plots can lose up to 60% of incoming rainfall to run-off, while rock-mulched plots lose only 3–10%. Shell mulches can

also moderate soil temperature (Lightfoot 1996) and in New Zealand allowed for sweet potato cultivation in otherwise marginal areas (Barber 2013).

Inputs of green waste, principally manure and vegetation, also alter soil temperature and moisture, but they are best known as ways to enhance soil fertility. High-intensity refuse disposal, whether intentional or otherwise, can result in the formation of anthrosols—human-formed soils with distinctive chemical properties, pH, color, and clast inclusions (Pears 2012; Richter 2007; Siderius and de Bakker 2003). Purposeful mulching and soil conditioning are well documented from the European Neolithic forward (Bogaard et al. 2013), and some anthrosol formations are even associated with foraging communities (Guttmann 2005; Turner et al. 2011). The legacy of soil enhancement is especially well demonstrated by Amazonian brown and dark earths (ABE and ADE; also known as *terra preta*). These productive soils were created by multiple generations of human inhabitants and their past cultivation practices, which included mulching and burning (Arroyo-Kalin 2010, 2019; Heckenberger and Neves 2009; Robinson et al. 2020). While the history and importance of anthropogenic soils is perhaps best documented for the Amazon, these kinds of fertile, anthropogenic soils have a broad global distribution (e.g., Frausin et al. 2014; Hejzman et al. 2013).

Agroforestry practices are another form of “perturbation” often aimed at creating cultivated environments that mimic the structure and ecological relations of “natural” forests. Anthropogenic forests are found in several regions of the globe (e.g., Ford and Nigh 2015; Latinis 2000; WinklerPrins and Levis 2021). The spatial scale and temporal persistence of anthropogenic forest modification is a matter of empirical debate (e.g., Piperno et al. 2015, 2017), but human-induced forest development wholly transformed some tropical environments on centennial to millennial scales (Clement et al. 2020; Ford and Nigh 2015; Heckenberger and Neves 2009; Roberts et al. 2017). Even after the cessation of active human management, past agroforestry practices often continue to influence the composition and structure of contemporary forests across temperate and tropical environments (Arnell et al. 2019; Dupouey et al. 2002; Levis et al. 2018; Quintus et al. 2019; Ross 2011). In the Amazon, empirical research demonstrates that anthropogenic forests can increase the provisioning of ecological services and enhance biodiversity relative to non-domesticated bioscapes (Levis et al. 2020; Lins et al. 2015; Maezumi et al. 2018; Odonne et al. 2019). Thus, over time, these domesticated landscapes (*sensu* Levis et al. 2018) become evolutionarily important via their effects on resource distributions, vegetation structure, and energy flows. They can also profoundly affect the subsistence strategies of later groups, in some cases persisting to the present day (e.g., Leitão-Barboza et al. 2021) where they may be important reservoirs of famine foods (Minnis 2021).

Some of the “perturbations” described above were undertaken with clear intent on the part of past human cultivators, aimed at providing larger or more predictable yields. However, intent is not a necessary condition of niche construction processes. Indeed, incidental niche construction outcomes, sometimes referred to as “byproducts” (Laland and O’Brien 2012), can be equally consequential (Post and Palkovacs 2009). These unintended outcomes can alter the nature and distribution of resources available to human populations and other organisms over time (Turcotte et al. 2017).

As noted above, habitation and refuse disposal can produce anthrosols that mimic the effects of green manure and are utilized by subsequent generations of farmers (Guttmann 2005; Guttmann et al. 2008; Kirch 1988). Indeed, habitation-derived anthrosols are influencing the loci and productivity of small-scale farming around the world today (Glaser 2007; Hejcman et al. 2011, 2013; Solomon et al. 2016). While the foregoing kinds of perturbations are often beneficial, they may increase the vulnerability of any given agricultural system (Rindos 1984, p. 274). Increased reliance on cultivated resources, for example, is often linked with demographic change and/or increasing sociopolitical complexity and may contribute to a series of self-reinforcing feedback loops known as “runaway niche construction” (Ellis 2015, 2016). These kinds of “byproducts” are common features of constructed niches generally (van der Leeuw 2012).

The social impacts of niche construction activities should also not be overlooked. The construction of infrastructure across a landscape often modifies the social relations of production, which in turn gives rise to new conditions for agriculture change. Agricultural outcomes may ramify through a social system and across generations, differentially enhancing wealth and affecting intergenerational property rights, as evidenced during the European and Near Eastern Neolithic periods (Bentley and O’Brien 2019; Shennan 2011). Shennan argues that these developments often have cascading effects over time, even influencing human reproductive strategies (e.g., polygamy, monogamy, etc.), as for example those designed to keep wealth intact across generations. Infrastructural investments also tie farmers to specific locales and render them more susceptible to taxation and sociopolitical tributes (Earle 1997; Erickson 1993; Kirch 2010; Morehart 2010). Furthermore, the alleviation of localized environmental selection pressures may lead to regional variability in agricultural strategies and long-term outcomes. Those that produce more regularly or at higher yields relative to others may foster emergent leaders or give rise to production bottlenecks, which can be capitalized on by elites (Earle 2011).

Relocation

Agricultural practices provide useful examples of relocational niche construction. The agricultural niche is readily transported (Shennan 2018), in that it is often focused around a relatively small number of species that are under strong controls (Rowley-Conwy and Layton 2011). Nonetheless, while relocation may alleviate challenging conditions of the prior environment, it not only exposes organisms to novel opportunities but also to constraints. This often gives rise to agricultural innovations, such as new planting technologies, infrastructure experimentation, and/or sometimes new coevolutionary relationships (e.g., Fuller and Lucas 2017; O’Brien and Laland 2012; Quintus and Cochrane 2018).

Useful examples of some of these relocational processes come from Polynesia (Quintus and Cochrane 2018). As human settlers spread across the Pacific, they colonized numerous archipelagoes where they encountered markedly different environments, from large, high volcanic islands to low coralline atolls that are only a few meters above sea level. Despite a broadly shared set of agronomic techniques and

cultigens, place-based adaptations arose as populations responded to variations in island geology, soils, freshwater resources, and biota (e.g., Gumbley 2021; Kirch 1994; Ladefoged and Graves 2000; Quintus and Lincoln 2020; Weisler 1999).

Research in temperate regions demonstrates other agricultural techniques aimed at counteracting cold temperature regimes, marked seasonality, and short growing seasons (Donoghue 2008; Fuller and Lucas 2017). The use of shell mulch in New Zealand is one such innovation in Polynesia that may have allowed Māori cultivation to extend into colder environments (Barber 2013). Innovations also evolved at landscape scales, as for example the development of ridge-and-furrow systems in the American Midwest (Fig. 2). Simulations and experimental studies suggest these extensive furrows systems promoted “frost drainage” (Riley and Freimuth 1979). In Europe, Groenman-van Waateringe and van Geel (2017) hypothesize that Iron Age Celtic fields followed a similar design and function, counteracting lower temperatures in the ninth century BC.

Genetic research has been particularly valuable in identifying sequences of change that arose in domesticated plants as they were carried beyond their natural ranges and centers of domestication. Cockram et al. (2007, 2011) suggest that variability in genetic controls on barley (*Hordeum vulgare* ssp. *vulgare*) flowering times preadapted it to successful relocation into higher latitudes by agricultural peoples. Subsequent artificial selection produced landraces and cultivars with flowering times that avoided the harsh winters of northern Europe and took advantage of



Fig. 2 Ridge and furrow system from Kletch Park, Milwaukee, Wisconsin. Ridges, which are roughly 50–60 cm above the furrows, are visible above the snow, and the top of ridges are roughly 1 m apart. Photograph was taken in 1978 and is courtesy of Thomas Riley

long, cool, and often wet summers. Another well-documented example is maize (*Zea mays* ssp. *mays*). The development of flowering traits to accommodate longer day lengths also was key to its expansion, again the result of both natural and artificial selection (Huang et al. 2018; Hung et al. 2012). The genetic plasticity of maize made it especially well suited for relocation to areas outside its tropical homeland (Huang et al. 2018) and led to a cascade of changes that had considerable economic, political, and social impacts (e.g., Smith 2017).

Relocation, however, need not be spatially expansive to have evolutionary consequences. Birds, for example, routinely select nest locations in specific trees, and particular areas within forests, to decrease the risk of predation and enhance offspring survival (Odling-Smee 2003 et al., pp. 64–65). Similarly, human food producers adjust crop locations to increase the productivity of a given cultivated species, for example, by extending plantings into new habitats (O'Brien and Laland 2012, fig. 1). Use of different environments, even when they are not especially distant, offer alternative conditions that can alleviate adverse impacts or enhance crop success, and such behaviors may become fixed over time.

Spatial diversification demonstrates how populations can operationalize inceptive niche construction at multiple scales and over an annual cycle. The exploitation of multiple environments taking advantage of different environmental characteristics is well documented for several geographical regions and time periods (Drennan et al. 2020; Marston 2011). Use of diverse environmental settings, with variable selective conditions, may offset or redistribute environmental risks. In essence, these communities are “hedging their bets” by diversifying the selection conditions under which they operate. The character of these niche construction activities is shaped by the nature of hazards, including their periodicity, magnitude, and duration, but it is their differential long-term evolutionary outcomes that are of critical importance (Allen 2004). In many localities, agricultural communities took advantage of seasonally or geographically contrasting environments, often with markedly different opportunities and constraints (e.g., Kirch 1994; Ladefoged et al. 2009; Morrison 1995). In the Hawaiian Islands, for example, farmers staggered planting and harvesting across dispersed locations to take advantage of seasonal and elevational variations in temperature and rainfall (Kagawa and Vitousek 2012; Kagawa-Viviani et al. 2018). Spatially dispersed fields can function in a similar manner, with different microenvironments offsetting hazards and mediating interannual variability (Ladefoged and Graves 2000; Marston 2011, p. 193). The inheritance of these modified locations by subsequent generations of producers can have substantial downstream consequences (Morehart 2018).

Still, relocation of the agricultural niche is a complex process with variable long-term outcomes. Increases in productivity brought about by relocation may render agricultural systems unstable (Rindos 1980, 1984; see also Ammerman and Cavalli-Sforza 1984; Rowley-Conwy and Layton 2011). This instability arises from several factors, including the often-narrow focus of agricultural systems on a limited number of species, specialized cultivation requirements, loss of genetic diversity, and declines in soil fertility over time. The latter is an especially common deleterious effect of relocated agricultural systems that populations attempt to counteract through further movement (Shennan 2018). Declines in soil fertility can be a strong

incentive to relocate or adapt, not only with swidden (slash-and-burn) technologies but also in fixed field contexts (Roos et al. 2016; Wood et al. 2016). These processes are perhaps best documented for Neolithic Europe, where boom-and-bust demographic patterns are recorded. Populations often increased substantially following relocation (Shennan et al. 2013). Populations decreased, however, as soil fertility declined and climate deteriorated, often accompanied by increased investments in barley and the use of less-intensive food-production techniques (Colledge et al. 2019), including foraging and pastoralism (Bevan et al. 2017). In these cases, the success of a relocated agricultural niche set the stage for change and produced selective pressures that required subsequent adaptation.

Population growth may also facilitate relocation and exportation of the agricultural niche by providing novel sources of labor. The *japonica* subspecies of Asian rice, originally a wetland grass of southern China, was domesticated between 7400 and 6500 BC (Long et al. 2022). Although highly successful in this locality, there appears to have been a pause between rice domestication, the development of paddy-field infrastructure, and the spread of irrigated rice technologies further afield. Fuller and Qin (2009) attribute this pause to the labor requirements of paddy-field agriculture and the need for administrative oversight to coordinate the requisite labor. The inception of irrigated systems of rice agriculture in the lower Yangtze River likely led to some population growth, but it may have been the combination of rice and millet (*Setaria italica* and *Panicum miliaceum*) cultivation that facilitated the population levels necessary for the spread of paddy-field rice cultivation outside its core (see Long et al. 2022). Population growth also preceded the arrival of rice in several areas of Asia, which may have created ideal conditions for the subsequent adoption of more-intensive forms of cultivation. Although these processes remain to be fully demonstrated, the available evidence suggests that even though wetland rice cultivation was highly productive, the spread of the formal irrigated rice technologies were feasible only after population growth had reached certain thresholds. This example illustrates emerging mutualisms and dynamic feedback relationships, as well as shifts between perturbational and relocalational niche construction behaviors.

The Process of Agricultural Niche Construction

Long-term agricultural change is coevolutionary in that agricultural practices are evolving in concert with the environment, which includes abiotic and nonhuman biotic components and cultural phenomena (e.g., demography, social organization, labor and management, worldviews, etc.). Such evolutionary sequences, historically actualized through ecological inheritance, speak to the role of reciprocal causation in agricultural trajectories. The global archaeological record of agricultural change usefully illustrates how anthropogenic niches are constructed, evolve, and endure. Myriad cases show how biota, soils, and geomorphology are manipulated by human societies for the purposes of food production in myriad ways and across diverse settings. These records also demonstrate several key concepts of niche construction. Here we review three geographic contexts that illustrate a diversity of evolved agricultural behaviors: Amazonia, island Polynesia, and the floodplains of Mesopotamia

and northern China. These examples illustrate how NCT can provide unique insights into human symbioses with other organisms (targeted and otherwise), intergenerational ecological inheritance, and processes of runaway niche construction, which can sometimes lead to path dependencies, where opportunities are constrained by earlier choices. While not all the studies reviewed herein have explicitly drawn on NCT, their findings can be accommodated within a niche construction framework.

Emergent Mutualisms in Amazonia

In the jungles and savannas of Amazonia, a diversity of food production practices was born out of ecological and cultural inheritances that accumulated over millennia (Clement et al. 2021; Neves and Heckenberger 2019). The multiplicity of coevolutionary relationships identified in this region are intriguing, reflecting ecological inheritances from both other species and human foragers, domestication practices across a range of scales (from individual to landscape), and both formal and informal landscape management practices (Clement et al. 2020). These coevolutionary relationships are not restricted to any given time or place, and their continued emergence alongside more formal agricultural practices extend from the ongoing process of niche construction.

Human food-production practices in the Amazon have resulted in “domesticated” landscapes (*sensu* Clement 1999; Levis et al. 2018)—defined by and the outcome of multiple symbioses between people and organisms, as well as more general human landscape modifications *at regional scales* and over *evolutionary time frames*. This occurs as humans alter landscape components and processes, including plant propagation, regional hydrology, and soil formation. Such systems often change the demographic characteristics of biota, resulting in environments more conducive to human populations of variable configurations. These kinds of food production systems are also found in Papua New Guinea, Southeast Asia, Mesoamerica, and indeed probably many tropical ecosystems (Roberts et al. 2017). However, the Amazon is the best-known example and potentially provide expectations for the character, functioning, and evolution of domesticated landscapes elsewhere (Arroyo-Kalin 2017, 2019; Erickson 2008; Levis et al. 2018).

Amazonia is now well recognized as a center of plant domestication, and landscape modifications in forested and savannah environments included vegetation restructuring and plant translocations from the early Holocene onward (Clement et al. 2021). There are also suggestions that some of these processes are linked to pre-adaptations in trees with large fleshy fruits, which derive from earlier mutualisms with megafauna who served as seed dispersers (Neves and Heckenberger 2019; Spengler et al. 2021). Following early Holocene extinctions, humans began to fill ecosystem services once provided by megafauna (McKey 2019; Neves 2016; Spengler et al. 2021). In essence, ecosystem engineering by megafauna resulted in food-rich niches that were inherited by humans and led to new coevolutionary relationships between humans and former megafaunal dependents. The large fleshy fruits, however, were only part of the extensive roster of plants cultivated and domesticated in the Amazon. While some underwent significant morphological changes, many

were largely physically unchanged but now have broader distributions and are more abundant as the result of intensive management (Clement et al. 2021).

Human cultivation and plant management continued to modify the composition and structure of tropical Amazonian vegetation through the early and middle Holocene (Lombardo et al. 2020), with extensive transformations occurring after 4000–5000 BP as farming became more widespread (Duncan et al. 2021; Roosevelt 2013). Diverse management techniques were used, most notably fire, which created forests gaps in rainforests and forest islands in savannas, along with the tending, weeding, and harvesting of useful nondomesticates, and the creation of house gardens (Erickson 2008). The contemporary environments of the Amazon are thus the outcome of millennia of human management that resulted in significant regional heterogeneity (Clement et al. 2015; Levis et al. 2018; Maezumi et al. 2018), although there is ongoing debate about the intensity, persistence, and spatial extent of human impacts (e.g., Piperno et al. 2015, 2017).

Perhaps the most iconic components of domesticated Amazonia landscapes are their anthropogenic soils: Amazonian dark earths (ADE). These fertile soils formed over long periods of time through both in situ occupations and concentrated deposition of refuse in areas peripheral to camps and settlements (Erickson 2008; Roosevelt 2013; Schmidt et al. 2014). The lighter soils (*terra mulatos*), typically some distance from settlements, are thought to be the outcome of soil management and fertilization practices associated with cultivation (Arroyo-Kalin 2019; Fraser et al. 2011). These anthropogenic soils served to increase the amount of arable land, and economic trees are today disproportionately represented in these locations (Levis et al. 2020). Levis et al. (2020) further argue that anthropogenic activity increased the heterogeneity of soils across local landscapes in ways that supported a diverse range of food production strategies. De Oliveira et al. (2020) highlight how ADE and non-ADE soils in combination contributed to increased species richness, as floristic compositions are somewhat dissimilar on the two soil types due to slightly different growing conditions (i.e., pyrogenic carbon in ADE). Importantly, ADE supported the cultivation of key crops that are difficult to grow in lower fertility areas, including maize (Fraser et al. 2011). Ethnographic data further demonstrate that contemporary communities continue to target specific anthropogenic soils, including ADE, for a variety of landraces (Fraser 2010). Unsurprisingly, areas of ADE are today reservoirs of traditional forms of agro-diversity (Clement et al. 2003). This may be because ADE relaxed certain selection pressures that otherwise prohibit the spread of some species. Some even argue that human management practices fostered and maintained plant genetic diversity in many parts of the Amazon, diversity that was greatly diminished in the aftermath of early contact period depopulation (Clement 1999).

Symbioses were also created through geomorphological engineering in savanna areas of the Amazon. Raised bed systems are perhaps the best-documented form of infrastructure in this region (Denevan 2001; Rostain 2013; Walker 2018) and were often used alongside other landscape modifications (e.g., ADE) (Walker 2011). These are in seasonally inundated savannas, which are themselves partially the result of anthropogenic burning that was presumably undertaken to keep the forest at bay (Erickson 2008). The raised beds effectively circumvented the risk of flood

inundation (Lombardo et al. 2011), and experimental studies suggest that raised bed soils were enriched by sediments from the canals (Erickson 2006). As Duncan et al. (2021) note, landscape modifications of this kind, along with fire, and other agronomic techniques, created productive locations in environments that have historically been considered “wastelands.” Importantly, these systems created habitats for other organisms, probably expanding their natural ranges (Erickson 2008). Although no longer in production, the raised beds and canals continue to be important points of concentrated resources and are often occupied by nonhuman ecosystem engineers (i.e., ants and termites) today (Renard et al. 2013). The engineering of other organisms contributes to the persistence of these structures, which have become biodiversity refugia in the contemporary landscape (McKey et al. 2010). In short, these extensive raised beds systems were both sites of human food production and novel anthropogenic environments that fostered human–animal symbioses, not only when initially constructed but over time.

This regional-scale construction myriad food-producing ecosystems and large networks of symbioses produced novel selective environments that had profound effects on resident human populations. In contrast to regions of the world where intensive human–plant mutualisms centered on a limited number of plant species, many Amazonian groups managed and relied on a diversity of taxa and over time transformed whole ecosystems (Clement et al. 2021; Denevan et al. 1988; Levis et al. 2017). The success of this strategy in alleviating challenges of previous selective conditions (low soil fertility, dense primary forest), and a material consequence of niche construction (see Odling-Smee et al. 2013), was population growth, especially in the late Holocene (Arroyo-Kalin 2017; de Souza et al. 2019). Arroyo-Kalin (2017) outlines a sequence wherein initial land use created productive patches characterized by fertile anthrosols and stands of economic plants. These resulted in higher levels of food production, which in turn supported larger populations in the first millennium AD; later in time they were in some cases even defended. These examples highlight the evolutionary role domesticated landscapes and ecological inheritance can have on the long-term evolutionary fitness of human groups in tropical regions in the absence of formal agricultural practices. The success of communities in the Amazon is due to the development and maintenance of multiple mutualisms and low-intensity environmental management practices undertaken at a regional scale (Levis et al. 2018).

The human niche construction activities and coevolutionary relationships that emerged in the Amazon continue to be important for contemporary groups, who often acknowledge their reliance on products of the past, particularly the productivity of old settlement sites (Arroyo-Kalin 2019; Balée 1989, 2010; Erickson 2008). ADE and other anthropogenic soils are still regarded as agricultural capital by local populations (Schmidt et al. 2014). Walker (2011) notes the preferential use of anthropogenic soils by some farmers in the central Llanos de Mojos, where these soils are associated with nearly continuous cultivation. Further, high-value crops, such as exotic domesticated vegetables, can be grown on ADE without chemical fertilizers (Kawa et al. 2011). Clearly, past niche construction behaviors in the Amazon are continuing to shape modern food production, albeit conditioned by both contemporary social and technological conditions (German 2003).

The process of niche construction in the Amazon led to substantial human–environment interdependencies. As noted by Allaby et al. (2022), human management across large landscapes can result in protracted human–plant entanglements. They argue that such long-term landscape-scale relationships are important to understanding domestication globally; the Amazon presents an excellent example of the key processes (see Clement et al. 2021). However, the Amazon also demonstrates well how landscape-scale management created and maintained diverse mutualisms across multimillennial time frames. These included the formation of microenvironments that drove crop and agricultural diversity, as well as engineered ecosystems that modified the demographic characteristics of plants and animals and created new dependencies. Such processes led to human population growth as they enhanced the economic potential of the regional landscape.

The persistence of mutualisms across the Amazon is an important source of contemporary population resilience and has implications for contemporary environmental management (Peters et al. 1989). In many Amazonian environments sustained niche construction activities have not only promoted robust mutualisms but also created distinctive environmental structures (e.g., hyper-dominance patterns in trees) and shaped ecosystem functioning (e.g., Balée 2010, 2013; Neves and Heckenberger 2019). The persistence of these unique anthropogenic environments requires ongoing human management with Indigenous peoples, without which the long-term mutualisms, associated forest structures, and novel ecosystemic properties will be lost (see Clement et al. 2020).

Ecological Inheritance in Polynesia

The foregoing illustrates how food production practices can create a diversity of perturbations with multifaceted impacts. It is the totality of the accompanying changes, including the “dramatically altered community of microorganisms, insects, plants, and animals,” that constitute ecological inheritance (Odling-Smee and Laland 2011, p. 223) along with archaeologically tractable landscape modifications. Importantly, to be considered ecological inheritances, these myriad changes must be transmitted to successive generations and create novel selective environments for humans and/or other organisms. However, disentangling these kinds of evolutionary feedback relationships is challenging, especially when multiple interacting agents are responding to both organism-driven environmental modifications and other selective conditions. One approach is to use “model systems,” which are often characterized by boundedness, small size, isolation, reduced complexity, and/or the speed of key processes (e.g., reproduction). An effective model system is “an integrated, functional, and persistent example of the larger set of systems whose functioning they are meant to illuminate” (Vitousek 2002, p. 574), such as an organism, ecosystem, lake, or island (see also Matthews et al. 2014, p. 260). Comparative methods are another useful way to test alternative scenarios of ecological inheritance (e.g., Laland et al. 2017; O’Brien and Laland 2012). Both approaches have proven useful for understanding socioecological processes in Polynesia, where closely related human populations, sharing broadly similar agricultural practices, crop inventories, and ethnobiological

knowledge systems, are spread across environmentally diverse islands (e.g., Allen 2015; DiNapoli and Leppard 2018; Kirch 2007).

Human settlement in Polynesia began around 2850 years ago in a process that involved the translocation of numerous species. These included dozens of economic plants (of which carbohydrates were critical), three animal domestics (*Sus scrofa*, *Canis lupus familiaris*, *Gallus gallus*), the commensal Pacific rat (*Rattus exulans*), and anthropophilic weeds, land snails, and arthropods (e.g., Anderson 2009; Kahn et al. 2015; Prebble and Wilmshurst 2009). Yen (1973, p. 76) referred to these translocations as “detachable parts of former environments which became the founding endowment” on newly settled islands. As Polynesians spread across this oceanic region, they were exposed to a diversity of new environments; at the same time, they and their transported associates also changed the selective environments of newly encountered native species, in innumerable ways and with evolutionary consequences that continue to the present (see Odling-Smee et al. 2013, p. 8). One way was through local extinctions, of both individual native taxa (e.g., Steadman 2006) and sometimes whole plant communities, such as the endemic lowland palm forests of Hawai‘i, Rapa Nui (Easter Island), and elsewhere (Athens 2009; Hunt 2007; Prebble et al. 2019), presumably along with many of their microorganisms, invertebrates, and avifauna.

Polynesians generated novel ecological inheritances in many other ways as well. For example, traditional crop inventories were sometimes incompletely transferred or failed to establish (e.g., in New Zealand, Rapa Nui). This led to new mutualisms with native species that were essential to human livelihoods (e.g., as sources of food, fiber, and timber). Their fitness, in turn, was enhanced through range expansions, artificial selection, and/or specialized cultivation (e.g., Funk 1982; Leach and Stowe 2005; Shepherd et al. 2016). Translocated domesticates also underwent further selection following island settlement, with varieties developed to counteract new kinds of perturbations (drought, pests, etc.) and/or different environmental constraints (infertile soils, low temperatures, aridity, seasonality, etc.) (see Handy and Handy 1972; Yen 1974).

Polynesian colonists also affected the selective environments of their successors (and other organisms) through disruptions and realignments of long-established biogeochemical webs (see also Odling-Smee et al. 2013, p. 8). For example, local processes were altered by biotic introductions (e.g., predatory rats), native biotic extinctions (e.g., guano-producing seabirds), and soil degradation (e.g., deforestation and extractive agricultural practices)—often with sustained, intergenerational effects on agricultural productivity and fitness implications for humans, their domesticates, and other co-inhabitants of the anthropogenic niche. Understanding of these impacts is nascent, but studies of soil fertility (e.g., Ladefoged et al. 2010; Vitousek et al. 2014) and isotopic records of humans and their faunal associates (e.g., Allen 2015; Richards et al. 2009; Swift et al. 2016) are providing insights into long-term variability in biogeochemical webs in relation to agricultural practices.

Colonists reshaped the physical landscapes of Polynesia as well, altering geomorphic processes and through formally constructed features. An example of the former is human-aided sediment mobilization and redeposition, sometimes on a massive scale. Such processes sometimes created fertile lowland plains that became

the focus of intensive cultivation for generations (e.g., Kirch 1994; Lepofsky and Kahn 2011, pp. 323–326; Quintus 2018a; Spriggs 1997). Formal agricultural constructions are also widely evidenced, varying considerably in form, size, and complexity (Fig. 3). The most significant engineering is seen in irrigated taro pond-field systems, designed to maximize planting areas, control water flow, and enhance production. Many such systems represent incremental investments, accumulated over time, by multiple generations of cultivators (e.g., Allen 1991; Kirch 1994; McElroy 2007). Large-scale, rain-fed, dryland field systems are another impressive form of landscape modification, best known from the leeward areas of younger Hawaiian Islands, where networks of terraces, walls, and elongate mounds extend over extensive areas. These speak to varied production and management strategies, as known through archaeological stratigraphic sequences, modeling, and remote-sensing studies (e.g., Allen 2004; Dye 2014; Kirch 2011; Ladefoged et al. 2008, 2011). Extensive dryland field systems are also found in New Zealand, where cultivators positioned their fields to take advantage of fertile volcanic tephra or alluvial outwash fans (e.g., Barber 2004; Leach and Leach 1979). The contribution of these kinds of highly varied and complex landscape investments to ecological inheritances is reflected in well-documented archaeological histories from across the region, albeit usually discussed through other theoretical lenses.



Fig. 3 Coastal swamp cultivation of taro in raised beds with intervening reticulate drains on Aitutaki in the Cook Islands. Note the presence of palm fronds used as mulch. Photograph by Melinda Allen

Another example of ecological inheritance comes from the Marquesas Islands, where Polynesian colonists introduced an array of economic plants (both root and tree crops), anthropophilic arthropods, and probably weedy plants around the 11th to 12th centuries AD (Allen et al. 2022; Huebert and Allen 2020). To make way for shifting cultivation, the indigenous forest was cleared, initially from lowland regions and often assisted by firing, a common Polynesian technology. This created open areas for crop plants and weedy associates (with positive fitness outcomes for both), but it also led to geomorphic instability. As native trees declined, so did native avifauna, with numerous extinctions (see Steadman 2006). Given the crucial role of birds in pollination and fruit/seed dispersal in the absence of native mammals, these losses undoubtedly disrupted ecosystem functioning, with potential cascade effects across trophic levels and food webs. Extinctions in herbaceous and arborescent plant taxa would have further weakened ecological webs in ways not yet fully understood (Allen et al. 2022). As an example, one originally widespread lowland forest species (*Sideroxylon* sp.) initially favored as a fuel wood was greatly reduced within the first few centuries of Polynesian arrival, eventually going extinct (Huebert and Allen 2020). Its demise required Marquesans to find alternative fuels, which were sometimes more costly to acquire (i.e., distant) and less efficient.

This suite of adverse feedbacks created novel selective environments for Marquesan people and native biota; within a few centuries of human arrival, counteractive niche construction was underway. Although this may have taken varied forms, the most archaeologically visible manifestation is the rapid dispersal and uptake of tree cultivation, dominated by breadfruit (*Artocarpus altilis*), a Polynesian introduction with a large, starchy, syncarpous fruit. These processes were repeated across multiple valleys, and over time the inventory of tree crops expanded to include other arborescent Polynesian introductions (e.g., Tahitian chestnut, *Inocarpus fagifer*) and at least one native tree, Pacific rosewood (*Thespesia populnea*). This evolving arboricultural system had several advantages: structurally it mimicked the original native lowland forest, mature trees stabilized soils, and forest habitat was restored for native land birds. In time, breadfruit became the mainstay of the Marquesan subsistence economy. Its fruits were not only highly nutritious but could be processed into a readily storable product that was a crucial food source during the archipelago's sometimes crippling droughts (see Allen 2010). A related outcome was specialized storage facilities that allowed for long-term preservation (up to decades), at both household and community scales. This example illustrates some of the biological components of ecological inheritance and provides a foundation for further study and modeling of behavioral, ecological, and genetic interactions over time in this locality.

Two other island sequences demonstrate the interplay between agricultural niche construction and sociopolitical processes, one speaks to competitive outcomes (Mangaia, southern Cook Islands) and the other suggests community-scale cooperation in (Ofu, Manu'a Islands, Sāmoa). The distinctive landscape of Mangaia (51.8 km²) features a highly weathered central volcanic cone surrounded by a massive ring of upraised karstic limestone. Polynesian settlers arrived roughly a millennium ago, cleared the interior volcanic hillslopes of native forests with fire, and initiated shifting cultivation (Kirch 1996, 2017, p. 19). However, erosional processes quickly

followed, stripping away the thin topsoils and further depleting the naturally infertile substrates; even today this area remains unsuitable for cultivation (Kirch 2017, p. 23). While the agricultural potential of the interior hillslopes was significantly diminished, sediment redeposition in valley bottoms created rich alluvial terrain. These areas were particularly well suited to irrigated taro cultivation in raised beds and inundated fields but constituted only two percent of the island's overall usable land (Kirch 2017, pp. 22–23). Irrigated production was supplemented by shifting cultivation and tree cropping, now repositioned to the rugged karstic makatea and lower colluvial slopes. Over time, the limited fertile valley bottoms, with their accumulated agricultural investments, became the focus of intense, cyclical, intertribal warfare, which was marked by rituals of human sacrifice. A complex and distinctive ideology emerged, dominated by warriors and priests, diverging from the chiefly inheritance systems more commonly seen in Polynesian societies (Kirch 1994, 2017). The ecological inheritances were thus two-fold: (a) degraded and nonproductive interior hillslopes and (b) considerable investments in irrigation architecture in the small, circumscribed valley bottoms. The latter were central to elite competition, with significant flow-on effects to the population at large.

Elsewhere, agricultural developments resulted in rather different downstream sociopolitical effects. In Sāmoa populations initially settled on the coast of the volcanic doublet of Ofu-Olosega (13 km²), but around the 11th century AD there was relocation into interior Ofu, where populations faced different selective environments (Quintus 2018a; Quintus et al. 2016). This steep interior region is particularly vulnerable to the region's high rainfall (more than 3,000 mm per year), torrential downpours, and periodic but severe cyclones. The high-intensity run-off associated with such events often strips away crops or buries them under sheetwash. To counteract these conditions, cultivators constructed simple drainage features, initially around household-scale cultivation plots. Subsequently, larger ditches and more complex ditch networks appeared, suggesting changes in the organization of labor and community-scale investments. The effectiveness of these features against known hazards has been tested through hydrological modeling, while their long-term success is suggested by increases in their size, distribution, and complexity over time. Changes in the scale of this risk management infrastructure also coincided with the appearance of other community-scale architecture. Quintus et al. (2016) argue that these innovative water control devices allowed for a stable productive system despite periodic perturbations. This in turn created conditions favorable to community integration, the emergence of suprahousehold leadership, and ongoing investments in larger facilities. Such changes in labor organization and management strategies can impact on agronomic success—increasing both production efficiency and productivity (Athens 1999; Brookfield 1972).

As these examples suggest, heavily modified landscapes often became “attractors” for successive generations of cultivators, engendering further agronomic and social investments. Archaeological excavations reveal that the surface structures visible today are often the outcome of accretional investments, sometimes built on earlier architectural investments, as is the case globally (e.g., Doolittle 1984). Transmission to successive generations is clear, but relatedness is often uncertain, and community, tribal, or cultural “boundaries” are sometimes crossed over time.

For example, terraces and walls in the field system of Kona, Hawai'i were adopted (rather than dismantled) by 19th century commercial coffee farmers (Allen 2004). Elsewhere centuries-old Hawaiian taro terraces were converted to rice paddies by 20th century Asian immigrants (Jones et al. 2015). In many rural Polynesian communities, traditional agricultural sites are still in production, using centuries-old traditional ecological knowledge. Ethnobiological knowledge has been lost in other places, but the physical sites are being reclaimed by descendant groups who are benefitting from the investments of their ancestors (e.g., Lincoln et al. 2018; see also Morrison 2014, 2015).

These examples demonstrate dimensions of ecological inheritance that are common to many places. Among these are the extinction of species, from habitat loss, novel predators, and sometimes new competitors. Biogeochemical webs are also frequently disrupted by the emplacement of agricultural niches, with evolutionary effects that may reverberate to the present day (see also Odling-Smee and Laland 2011, p. 227). Other outcomes of these novel niches were the rise of new co-evolutionary relationships and subsequent intergenerational transmission. Moreover, as earlier investments compound and congeal, there is often increasing articulation with larger-scale social, political, and demographic processes. A key distinction on islands, perhaps, in the Pacific and elsewhere, is that such ecological inheritances are not only powerful but often inescapable.

Runaway Niche Construction in Mesopotamia and Northern China

Runaway niche construction refers to situations where long-term cycles of environmental manipulation essentially lock populations into specific trajectories of change and further investments in niche construction (Ellis 2015, 2016). These trajectories are self-reinforcing, initially maintained by positive evolutionary feedbacks but ultimately limiting alternative trajectories and never reaching evolutionary stable solutions. While not using a niche construction framework, van der Leeuw (2012) demonstrates this phenomenon in his aptly titled article, "For every solution there are many problems." Agricultural systems in arid and riverine environments, where the manipulation and control of water are central, provide particularly clear examples of these dynamics.

The lengthy sequence of irrigated agriculture in southern Mesopotamia is one such case. While rain-fed agriculture is possible in northern Mesopotamia, irrigation is necessary in the south. The latter setting illustrates the role cumulative small-scale modifications played in the long-term development of intensive irrigation systems (Wilkinson et al. 2015). Irrigation took advantage of river levees to direct water to adjacent fields (Adams 1981). Early forms of irrigation are argued to have enhanced natural alluvial processes, taking advantage of easily worked crevasse splays that provided a fertile cultivation medium (Wilkinson et al. 2015). Over time investment in extant systems was more cost-effective than beginning elsewhere anew. Moreover, further investment was feasible because of the transgenerational transmission of the products of past labor. As Wilkinson and colleagues (2015, p. 410) observe, the initial irrigation systems provided the template for what would come. The architecture

and engineering of such systems is place-specific, highlighting the need for farmers to understand and respond to the specific selective conditions of local microenvironments for successful cultivation (Hritz and Pournelle 2016). To some extent, it was these locally specific requirements that gave rise to agricultural variants, which then became the raw materials of subsequent relocation, innovation, and/or elaboration.

Over time, the Mesopotamian systems were further developed, producing more complex technologies and creating extensive anthropogenic landscapes. This continual adjustment of infrastructure is a pervasive feature of niche construction, a situation that results from populations seeking to redress new cultural and environmental selective pressures that arise, sometimes from prior states. This process is not unique to human societies and their agricultural practices and is well documented in other species (Odling-Smee et al. 2003, pp. 79–84). In the case of Mesopotamian agriculture, as new canals were built on lower gradient slopes, additional labor was needed to maintain these systems and to avoid sedimentation. Ultimately, even further expansion of the system was required to support the labor force necessary for its maintenance. In essence, the combination of the labor demands of these new systems and their high productivity formed feedback loops that favored population aggregations as well as the continued expansion of the irrigated agricultural complexes (Wilkinson et al. 2015, pp. 411–412).

The irrigation systems of southern Mesopotamia were successful in mitigating the region's arid conditions, expanding cultivatable land through the transport of water and fine sediments. However, these cultural transformations intersected with larger-scale natural processes, such as climatic variability, which brought about large-scale geomorphic changes and cascading effects (Hritz and Pournelle 2016; Jotheri et al. 2016, 2018; Walstra et al. 2010; Wilkinson 2003). Heyvaert and Walstra (2016) illustrate the multiple ways that local populations modified or interfered with the natural processes of river avulsion and alluvial fan development, with substantial and long-lasting flow-on effects for farming and human settlement in the region. Cultural elaborations redistributed key resources, which in turn changed the opportunities and constraints of communities at local and regional scales. Constructed canals, while providing irrigation water and flood control, at times became rivers or streams in their own right (Jotheri et al. 2016). The development of crevasse splays for irrigation systems likely contributed to alluvial fan development by restricting channel avulsion (Walstra et al. 2010). Moreover, the drainage of irrigation canals created artificial marshes and lakes, which became ecosystems for other organisms and novel resources for human communities (Eger 2011). The extraction of irrigation water on occasion resulted in reduced transport capacity and increased sedimentation in natural river channels. Such sedimentation can, eventually, contribute to channel avulsion, which in turn reshapes local and regional environments, with substantial impacts on human land use. Indeed, cultural modifications to channel avulsion are a major component of the ecological inheritance of contemporary Mesopotamian societies (Heyvaert and Walstra 2016, p. 2150).

Runaway niche construction is also apparent in northern China, where again there is a long history of landscape modifications in dynamic riverine settings (Lee et al. 2007). The Yellow River region is particularly well known. The river flows though the broad Loess Plateau, which is an especially fertile area but one that is

vulnerable to erosion (Rosen 2008), and the color of the river derives from such erosion (Fig. 4). Small-scale agriculture was practiced on the plateau from the Neolithic (before ca. 7000 BP) (Lee et al. 2007), with notable effects on local geomorphological processes (Rosen 2008; Rosen et al. 2015; Zhuang and Kidder 2014). During the Yangshao period (ca. 7000 to 5000 BP), for example, hillslope erosion increased alongside expanded and intensified agricultural production, concomitant with increased precipitation (Rosen et al. 2015). Increased sediment loads led to alluvial aggradation and floodplain buildup. As on some Pacific islands (e.g., Spriggs 1997), hillslope erosion seems to have been beneficial, and one consequence of these sedimentological changes was an opportunity for irrigated rice cultivation (Rosen 2008; Rosen et al. 2015).

The effects of increased sediment loads, induced by deforestation and other agricultural practices, were seen throughout the Yellow River basin by the Bronze Age, in the second to first millennia BC (Cao et al. 2010; Kidder and Zhuang 2015; Rosen et al. 2015). Neolithic populations made use of floodplain resources that were supported by regular river alluviation (Zhuang et al. 2013), but it was developments in irrigation during the Bronze Age that facilitated the expansion of human populations across the region (Storozum et al. 2018). Ultimately, however, increased sedimentation along the Yellow River increased the risk of flooding, first in the Bronze Age and then in later periods (Kidder and Zhuang 2015).

By the early Iron Age (first millennium BC), if not before, populations began constructing flood control infrastructure (Kidder and Liu 2017). This began a feedback loop. Initially, channelization of the river took place, resulting in siltation, which increased the base of the river and necessitated further construction of infrastructure aimed at flood protection. This served to reduce the frequency of floods but concomitantly resulted in higher amplitude events, because of the now elevated base of the river relative to the surrounding floodplain and the amount of water that could breach levees when those levees failed (Zhuang and Kidder 2014). Imperial incentives and coercion intensified and further expanded



Fig. 4 A view across the Yellow River (Huang He) at its southern bend. The photograph is taken from Henan Province looking toward the broad floodplain of Shanxi Province. The tablelands are roughly 50 m above the broad alluvial bottomlands. Note the high amount of sediment in the water. Photograph courtesy of Christian Peterson

production during the Dynastic period (end of the first millennium BC), when more effective tilling was made possible by iron implements; this again resulted in increased erosion and greater river sediment loads (Kidder et al. 2012b).

At the same time, growing populations from the mid-Holocene and a centralized, resource-consuming government sought increased production (Kidder and Zhuang 2015), often through investments in landscape modifications that reclaimed or enhanced floodplains (Zhuang and Kidder 2014). The effect was to concentrate populations in these low-lying environments: the past deposition of sediments, substantial infrastructural investments, and an increased focus on wheat made these areas especially attractive. This reclamation of land for farming exacerbated the threat of floods, while channelization required further modifications to replenish alluvial sediments for cultivation (Zhuang and Kidder 2014). By the Han period, in the first century AD, floods had become catastrophic, with sediment fans covering hundreds of square kilometers (Kidder et al. 2012a, b).

This sequence of agricultural change, population growth, and river avulsion continued through the last two millennia, with more substantial effects relative to those of earlier times. Erosion of the Loess Plateau seems to have been considerable during the 11th and 12th centuries AD due to the expansion of farmers into the region from elsewhere in northern China. These conditions were exacerbated by climate change and resulted in increased sediment deposition on the North China Plain (Storozum et al. 2018). As in the past, sedimentation combined with the continued use of fertile floodplains (themselves the result of previous floods) to increase the vulnerability of local populations to catastrophic inundations. However, because populations had become dependent on production from these areas, decision makers had few options other than continued cultivation in this niche. Eventually, however, geomorphic processes left the area unusable, and farmers migrated elsewhere (see Storozum et al. 2018, p. 1768). The long-term outcomes of niche construction, coupled with and exacerbated by natural environmental variability, created a selective environment that strongly favored relocation.

The Mesopotamian and northern China sequences clearly illustrate the process of runaway niche construction. Initial environmental modifications were small—mainly involving shifting cultivation or cultivation of naturally occurring wetlands. Cleared areas were built on by succeeding generations, who also inherited increased susceptibility to flooding and soil erosion. Attempts to mediate these adverse conditions led to innovations, as for example, the implementation of flood controls and the expansion of irrigation systems. These, in turn, altered the selective environment anew, allowing irrigated farming to expand and populations to grow. However, this created new risks and vulnerabilities, such as salinization, susceptibility to avulsions, and the need for additional labor. When coupled with high population densities, which had promoted expansion in the first place, additional investments were required to counteract emergent and unforeseen selective conditions. In short, local agricultural practices can become increasingly intertwined with natural processes, resulting in distinctive anthromes that are driven by complex socioecological processes (see Ullah et al. 2019) and lead to ongoing environmental transformations and a range of cultural adaptations (Ellis 2015).

Directions in Agricultural Niche Construction

The foregoing examples illustrate how niche construction theory directs attention to our relationships with other organisms and human populations, through space and time. It manifests important evolutionary processes and focuses on complex feedback loops generated through deep time. Critically, it reframes our place in the world, building an understanding of human behavior in the past, and potentially shaping how we envision our future. Understanding the histories of the constructed environments we have inherited is fundamental to building more sustainable and resilient futures. In this final section, we highlight issues for substantive and theoretical elaboration.

Operationalizing Agricultural Niche Construction

Researchers across both the biosciences and archaeology have stressed the importance of separating niche construction behaviors from the evolutionary process of niche construction (Odling-Smee et al. 2013; Ready and Price 2021; Stiner and Kuhn 2016). Niche construction theory, as a process, is concerned with long-term evolutionary outcomes and sequences of reciprocal causation; it is not a theory of short-term decision making. However, archaeologists have also asked how niche construction behaviors originated. Often intentionality is assumed, with the short-term goals of economic advantages or other positive outcomes. Building on this premise, there have recently been concerted efforts to integrate models from human behavioral ecology with niche construction theory (e.g., Haas and Kuhn 2019; Ready and Price 2021; Stiner and Kuhn 2016; Zeanah 2017). Drivers of short-term niche construction behaviors can be identified by recognizing and analyzing the economic trade-offs of different kinds of behaviors (Mohlenhoff and Codding 2017), and the use of formal models from human behavioral ecology (HBE) can identify specific kinds of environmental and social factors that affect human decision making (see Ready and Price 2021). Intentional niche construction behaviors are beneficial in only some circumstances, taking the form of practices that either enhance or stabilize production, and driven by a desire to increase the economic benefits of an environment relative to initial prehuman conditions. As illustrated by Mohlenhoff and Codding (2017), niche construction behaviors are potentially predictable and quantifiable within an HBE framework. Although the data requirements of these kinds of analyses are considerable, and the models involve simplifying assumptions, they provide testable hypotheses relating to short-term niche construction behaviors that are aimed at off setting particular selective conditions.

Some HBE models can account for long-term sequences of reciprocal causation, for example, ideal distribution models (Hale and Sanger 2020; Prufer et al. 2017; Weitzel and Codding 2022). Landscape suitability is a key component of these models, and for agriculturalists suitability is often defined by the presence of resources such as fertile soils and fresh water. These models typically examine how changes in settlement density, a condition that alters the selective environment, impacts the

suitability of a habitat. Such changes can be positive (the Allee effect), for example, increasing habitat suitability through cooperative behaviors. This could be in the form of a larger labor force or the construction of persistent infrastructure. Alternatively, changes in settlement density may have negative outcomes, such as intensified harvesting that results in resource depression. In each case, whether positive or negative, subsequent generations make decisions within a modified environment.

Still, defining changes in habitat suitability is challenging in many respects (Weitzel and Coddling 2022). Further consideration of ecological inheritance vis-à-vis the family of ideal free distribution models is useful in this regard (Bliege Bird et al. 2020). For instance, agricultural infrastructure (e.g., terraces) improves habitat suitability by reducing labor costs for subsequent users (see Bevan et al. 2013) and enhancing growing conditions (Sandor and Homburg 2017). The development of anthropogenic soils may have similar effects, replacing marginal substrates with fertile, productive ones. In contrast, niche construction behaviors can also be deleterious, rendering some environments less suitable over time and driving settlement elsewhere. For example, erosion and the loss of soil fertility would increase the benefits of relocation (counteractive niche construction). Testable predictions of when certain niche construction behaviors (e.g., perturbation or relocation) might occur can be usefully derived from ideal distribution models (Weitzel and Coddling 2022), and incorporation of niche construction processes into these could improve characterizations of habitat suitability and cost-benefit outcomes (see Thompson and Prufer 2021).

Additional factors also affect perceptions of habitat and landscape suitability (Prufer et al. 2017) and drive agricultural change (Morrison 2006), including food preference, land tenure, sociopolitical systems that shape ideas about where and how to engage in agricultural niche construction activities. Decisions about farming are driven by how and for what purpose the product is consumed (Morrison 1994, pp. 124–125). Food preferences and cultural values determine some forms of agricultural infrastructure, as in South India, where expensive canals and reservoirs were built to support rice cultivation in relatively arid and otherwise marginal environments (Morrison 2006, 2014). The continued maintenance of these features depended in part on the enduring social importance of rice, as well as sociopolitical conditions that ensured ample labor. Moreover, the construction of water control infrastructure served as displays of power, which led to their proliferation even though they regularly failed (Morrison 2015). In essence, it was the inherited social niche that drove some of the more prominent agricultural behaviors, and associated environmental reconfiguration, in arid India. More generally, sociopolitical needs can be powerful drivers of agricultural investment, or what Brookfield (1972) referred to as “social production.” Such practices often have legacies with substantial downstream effects (Morehart 2018). Agricultural change is often facilitated by political competition, wherein the expansion of landesque capital facilitates wealth assets and surplus production that can be socially deployed (Earle and Spriggs 2015). Taxation and tribute form part of the social niche, as do different forms of land tenure. The latter may enhance (or reduce) incentives to modify the environment (Netting 1993; Stone 1996), and tribute demands may change the calculus of agricultural activities (Erickson 1993; Morrison 1994), as farmers attempt to meet

both household and social demands. While variables such as social structure, land tenure, food preference, and the like are not frequently used in HBE analyses, recent work has shown how such variables may be included in models to provide a more nuanced and holistic understanding of human economic and settlement decision making (Prufer et al. 2017; Ready and Power 2018).

Human behavioral ecology models address different scales of socioecological processes relative to NCT and thus are complementary (Ready and Price 2021; Stiner and Kuhn 2016; Zeanah 2017). The former seeks to understand short-term decision making while NCT considers how such behaviors cascade and produce emergent evolutionary trajectories across evolutionary time. Such complementary frameworks can help operationalize niche construction and provide a more comprehensive understanding of subsistence sequences.

Ready and Price (2021, p. 76) provide formal equations through which dimensions of NCT and HBE can be jointly evaluated, illustrating the interplay between, and different scales of, the two theoretical frameworks. A useful example of this approach comes from Australia, where Bliege Bird et al. (2020) explore the interaction between landscape burning, resource abundance, and variance in mobility across Aboriginal foraging communities. Their research shows how anthropogenic fires create vegetation mosaics that act to concentrate resources and improve hunting returns, with positive cascade effects through time. More specifically, a positive relationship evolves between the extent of fire mosaics and habitat quality, leading to the development of persistent places. Likewise, Zeanah (2017) shows how foraging models can be used to explore occurrences of both resource enhancement and resource depression, providing opportunities to track processes of niche construction across the Eastern Woodlands during the emergence of agriculture.

However, for links between HBE and NCT to be useful, explanations developed using these approaches need to be falsifiable. O'Brien and Bentley (2015, pp. 374–575) suggest “construction chain analysis” can be a useful way forward. Causal relations in complex human eco-evolutionary systems, pathways, or networks might be progressively untangled by breaking down complicated network pathways into tractable components and subjecting each to analysis. Networks can then be reconstructed and the strength of interactions considered, as well as how they vary over time. O'Brien and Laland (2012, fig. 3) illustrate this approach with an example of Neolithic dairy framing (see Laland and O'Brien 2015). Brock and colleagues (2016) advocate the use of formal path analysis, an approach well established in other sciences. Hypotheses of causality between variables are graphically represented, requiring the analyst to specify how the variables relate to one another and potentially lead to specific outcomes. Using the available data, relationships between variables can then be statistically evaluated, for example, through Granger causality testing or linear vector autoregressions. Similarly, Ready and Price (2021, p. 76) advocate for formal analytical models where model predictions can be subjected to empirical testing. They draw on the concept of inheritance tracks—“a distinct physical system that transmits information through time.” These must contain heritable information that can be described and measured (e.g., genetic information or recurring patterns in artifacts), along with explicit specifications of how they evolve and their influences on behaviors. Computational modeling (e.g., agent-based modeling)

may also generate testable hypotheses by simulating systems with and without niche construction dynamics (Fogarty and Creanza 2017). These approaches build on and help formalize the cross-cultural comparisons advocated by Laland and O'Brien (2010) and have the potential to improve the rigor and quality of NCT explanations.

Secondary Symbioses

The recursive modification and inheritance of environmental characteristics is a powerful driver of novel coevolutionary relationships (Odling-Smee et al. 1996). In any shared niche, there is the opportunity for the development of a wide range of symbiotic relationships. This is especially true of agricultural niches (Bogaard et al. 2018; Fuller and Stevens 2017), which are formally constructed, intensively managed, and crucial to human health and well-being (O'Brien and Laland 2012; Rindos 1980, 1984). Many mutualisms between humans and plants were intensified over time, ultimately leading to new genetic and/or morphological traits and wider distributions and greater abundances of both relative to their ancestral forms (Bogaard et al. 2021; Denham et al. 2020; Smith 2015; Zeder 2016). However, there is increasing recognition of an array of symbioses that emerged in cultivated spaces but did not lead to domestication (Sugiyama et al. 2020; Terrell et al. 2003). Agricultural niches may not only foster the development of such mutualisms but also extend the ranges of nondomesticated agricultural associates (e.g., commensals and parasites), especially in 21st century contexts, and provide refugia for otherwise threatened taxa (Barthel et al. 2013). In short, agricultural niche construction has had evolutionary effects not only on the direct targets of cultivation but also on other organisms that share these ecological spaces and sometimes support cultivated species (e.g., through pollination, soil production, nutrient cycling, etc.)

An example is provided by domesticated squash (*Cucurbita pepo*) and its specialist pollinator, the squash bee (*Peponapis pruinosa*). Although this mutualism has long been recognized (Hurd et al. 1971), recent genetic work is revealing new facets of the coevolutionary relationship. Lopez-Uribe et al. (2016) used molecular markers to track range expansion in the squash bee, out of central and southern Mexico, and into and across North America, via multiple routes. The bee's massive expansion, well beyond its natural range, was facilitated by the human-aided spread of its *Cucurbita* hosts, despite multiple genetic bottleneck events. However, the strong mutualistic relationship with *Cucurbita* species may have come at an unexpected cost. The authors hypothesize that the low effective population sizes in this specialist bee are related to its nearly complete reliance on cultivated cucurbits throughout most of its current distribution. They also note the vulnerability of contemporary squash bee populations to the disturbances of modern agriculture, such as deep tillage (which can disturb their nesting sites), widely spaced crop rotation patterns, and use of insecticides.

Human–organism relationships are facilitated through local landscape modifications as well. Agricultural niches provide habitat for a variety of organisms, especially those that prefer open or mosaic environments (Bliege Bird et al. 2013; Eriksson 2013; Johnston 2005). Contemporary agricultural systems provide several

examples. In Spain, the configurations of agricultural landscapes reduce travel times and mortality risk for avian species, allowing them to efficiently link functionally diverse habitats (Camacho et al. 2014). Around the world bats both benefit from and service plantations, taking advantage of periodic insect outbreaks, while also serving as pollinators for crops like bananas, mangos, and guavas, with obvious benefits for farmers (e.g., Alpizar et al. 2019). In northern Europe, both constructed and informal field boundaries act as ecotones, enhancing biodiversity by providing refugia for useful insects (Kovar 1992; Marshall 1989; Marshall and Moonen 2002). The traditional infield–outfield farming systems of Scandinavia, where crop production and animal husbandry were closely integrated, also created high biodiversity through the use of manure as a fertilizer and the maintenance of open mosaic landscapes (Eriksson et al. 2021). Studies elsewhere show that active human management is often key to sustaining ecosystem productivity; when fields are abandoned or active management ends, reductions of commensal or mutualistic flora and fauna may follow (Bliege Bird et al. 2013; Clement et al. 2021).

However, environmental modifications can also be deleterious, driving some taxa to extinction. Anthropogenic extinctions contrast with those arising from climate change or natural catastrophes, where taxonomic turnover is generally slow or, in some cases, nonexistent (see Steadman 1986). As humans and the agricultural niche have dispersed across the globe, extinctions have greatly accelerated. Many Holocene extinctions are associated with habitat change and human-aided translocations of alien species that outcompete native taxa (Braje and Erlandson 2013). The effects of human niche construction activities on avian species are particularly well documented, arising from both habitat alteration and competition with introduced predators and competitors (Steadman 2006; Szabo et al. 2012). In some cases, adverse effects may persist even when native forests are replaced with arborescent economic species (Young et al. 2017), but in others new coevolutionary partnerships evolve. The variability in outcomes points to the important role played by historical contingencies, for example, the demographic and life history traits of the organisms involved. When extinctions occur, the effects may ramify through an ecosystem, leading to the loss of ecosystem services and disruption of ecosystem functioning, particularly in situations where functional redundancy is low.

Niche construction theory provides an exemplary framework for exploring these secondary symbioses as it links ecological and evolutionary processes (Matthews et al. 2014; Odling-Smee et al. 2013). It is often through the byproducts of agricultural activities and associated landscape modifications that “*many:many* relationships” develop (after Odling-Smee et al. 2013, pp. 5–6); these are instances where the selective environment is co-constructed by a multitude of organisms, leading to ecological “spillovers” that affect numerous organisms in the process. These *many:many* relationships are emergent phenomena in agricultural niches, with cascading effects through time and space. Niche construction theory also facilitates archaeological contributions to assessments of eco-evolutionary feedbacks, recognizing that humans are important elements of the environment, both in the past and at present. The role of humans in environmental modifications, and the transmission of those modified environments and attendant selective environments to other non-domesticated organisms, is increasingly acknowledged (Bogaard et al. 2018; Renard

et al. 2013). In short, NCT serves to integrate the differing vantage points afforded by archaeology, evolutionary biology, and ecology.

Long-Term Outcomes in Constructed Niches

The dynamic interactions between agricultural strategies and environmental, demographic, and sociopolitical processes are of longstanding interest to social scientists. Niche construction theory has the potential to provide new perspectives on these interactions and the differential outcomes that arise from the intersection of distinctive practices, ecological inheritances, and other selection processes. Niche construction behaviors are generally assumed to be adaptive in the short term, at least when they are intentional (Scott-Phillips et al. 2014). However, niche construction activities may alleviate or aggravate existing vulnerabilities over the long term, outcomes that often depend on the nature of the inherited environment and performance of agronomic investments. Here, we briefly consider a small number of studies that have considered these issues. Although none originate from a NCT framework, they bring into focus critical variables that might usefully be explored through a NCT lens.

Scarborough (2003, 2008; Scarborough and Burnside 2010) contrasts two pathways to sociopolitical complexity, both deeply intertwined with the management of biophysical environments: technotasking and labortasking. Technotasking societies, such as those from the Tigris and Euphrates drainages, are distinguished by their considerable investments in landscape engineering and technological innovations. They are strongly extractive, organized around short-term goals (e.g., growth and concentration of resources), and are typically regulated by top-down managerial controls. Technotasking societies can, over time, become overly dependent on built landscapes, economically, ideologically, or both, which can in turn drive further large-scale investments. However, such efforts may result in “path dependency” (Hegmon et al. 2008), a self-reinforcing process where initial decisions, for example, those relating to agronomic infrastructure and managerial practices, lock populations into particular trajectories. In these instances, when selective conditions change, effective agronomic responses may be constrained by prior developments, making some potentially effective solutions too costly or culturally untenable, as suggested above for northern China (Chen et al. 2012; Kidder and Liu 2017).

Labortasking groups, in contrast, are associated with heterarchical societies and structured around long-term sustainability. This pathway is distinguished by intergenerational transmission of skill sets, highly organized labor management practices, and close attention to ecological relationships, as exemplified by ancient Mayan and recent Balinese societies (Scarborough 2008; Scarborough and Burnside 2010). Change is often slow and incremental, with new agricultural practices being integrated into existing social practices and political institutions. Smallholders and householders typically have more independence in such systems, allowing for greater behavioral variability and encouraging cooperative relationships (see Bruno 2014; Netting 1993). These circumstances potentially enhance economic resiliency, even when the overarching political institutions fail. Of particular note are the ways

that labortasking reinforces interdependency between human societies and the built environment, through gradual, incremental environmental modifications and the intergenerational transmission of agronomic knowledge (Scarborough and Burnside 2010, p. 335).

Likewise, de Souza et al. (2019) distinguish two alternative models of land use, and their intersection with climate change, in late pre-Columbian Amazonia. One type of land use system was intensive, specialized, and focused on short-term goals of maximizing productive outputs (continuous high yields and surplus); the other emphasized resource diversity and long-term stability. The former was associated with centralized decision making, social inequality, and high interdependency of social components, along with significant investments in large-scale landscape modifications (earthworks and agronomic architecture). This system, they argue, was more vulnerable to climate change. In contrast, the alternative land use system was linked with decentralized political structures and a greater focus on minimizing risks. The latter was achieved through agronomic behaviors that sustained ecological services (i.e., regenerative soil practices, polyculture, forest management), therein contributing to long-term resilience.

More recently, Freeman et al. (2021) explore how variation in landscape engineering, dichotomized as “technological” versus “ecological” intensification, affects the stability of food production and population dynamics. Using multimillennial archaeological sequences from six regions, they model the impacts of these two strategies across evolving food production systems, from hunter-gatherers to intensified agriculturalists. Summed probability distributions of ^{14}C ages and PaleoView climate projections (Fordham et al. 2017) inform the model, along with inferences of political-economy complexity based on settlement size (Freeman et al. 2021, p. 380). The outcomes suggest that the intergenerational accumulation of landscape engineering leads to more stable food production systems, supporting population growth and demographic stability. However, during rare and large-scale environmental perturbations, societies highly dependent on landscape engineering appeared more vulnerable, relative to those engaged in ecological intensification strategies. The modeling raises interesting questions about how differential investments in landscape engineering might affect long-term outcomes and shows the potential for testing alternative hypotheses through modeling.

Environmental variability, and the nature, function, and performance of agricultural investments, are also important parameters affecting the stability of food production systems and population dynamics (Allen 2004). In relatively stable environments, where year-to-year variance is minimal, productive maximizing strategies may effectively support population growth and/or the generation of surpluses. However, in risky and unpredictable environments these same strategies can be disadvantageous or even catastrophic. Here, energetic investments that spread the impacts of risk, or reduce the occurrence and costs (e.g., infrastructure designed to manage erosion, water, or temperature extremes), act to minimize year-to-year variance, albeit with short-term costs—a strategy known as bet hedging (Frank and Slatkin 1990). Simons (2011, fig. 1) illustrates the long-term advantages of bet hedging in unpredictable environments, noting that although initially characterized by lower average fitness, bet-hedging strategies reduce variance in fitness across generations (i.e.,

geometric mean fitness). These outcomes drive home the importance of considering environmental variance alongside other parameters when we compare agricultural strategies and point to the long-term benefits of variance-minimizing investments in risky and unpredictable settings. Importantly, not only is a modified environment inherited but so too are the strategies of prior generations and the outcomes of those strategies.

Although the foregoing examples stem from different theoretical perspectives, they have multiple points of overlap. Variation in the character and magnitude of landscape investments is central to each. Environmental parameters are also seen as critical. These include the diversity, abundance, and distribution of resources—all combining to shape agricultural possibilities and initiate trajectories. However, the nature of the environment, particularly the magnitude, periodicity, and predictability of risks, are also crucial and may affect the rise and transmission of behavioral strategies, as well as long-term resilience. Sociopolitical structures also play a fundamental role in the foregoing examples, with a dichotomy drawn between extractive versus stabilizing or regenerative strategies. The importance of maintaining a pool of behavioral variability and organizational flexibility in terms of access to land, resources, and technologies is also highlighted. This has been demonstrated for food security under conditions of climate change as well (Nelson et al. 2016), where social groups with flexible management structures are better positioned to quickly initiate counteractive niche construction, relative to those with large and potentially cumbersome sociopolitical social institutions.

Communities inherit modified landscapes, social structures, and the outcomes of agricultural strategies implemented by prior generations (Morrison 2014). These inheritances, in turn, lead to new selective environments for subsequent generations of producers, which have different long-term outcomes. Still, and despite differing historical contingences, the foregoing examples demonstrate that large-scale patterns can be discerned and provide a foundation for deriving testable hypotheses. They point to ways that forms of ecological inheritance may systematically covary with environmental features and sociopolitical developments, potentially leading to shared fitness outcomes.

The Past in the Contemporary World

Archaeologists are increasingly calling for more cross-disciplinary engagement to inform contemporary policy and aid in the resolution of socioecological problems (Boivin and Crowther 2021; Foster et al. 2016; Logan 2020; Turner et al. 2020). Indeed, some have argued that such contributions should be a key goal of archaeology as we seek to maintain relevancy (Guttmann-Bond 2019; Kintigh et al. 2014). One impediment has been the difficulties of convincing those outside the discipline that archaeology has something to offer (Smith 2021). Building awareness of the temporal depth of human modifications to landscapes and the extent to which humans have influenced earth processes over thousands of years is crucial (see Clement et al. 2020; Ellis 2015; Ellis et al. 2021). Niche construction theory builds on research framed by historical ecology, human ecodynamics, and human

behavioral ecology (e.g., Balée 2006; Fitzhugh et al. 2019; Nettle et al. 2013)—but uniquely draws attention to the importance of ecological inheritances and the myriad impacts our behaviors have on other organisms. Many communities around the world are more intimately tied to local agricultural histories of the past than is generally realized (Morrison 2015), and in many ways, our ability to survive today is fundamentally shaped by agricultural processes of the past. Most notably, the persistent effects of past land use alter modern agricultural potential through the production of anthropogenic microenvironments (Vining 2018). While people have long appreciated their connection to the past in a historical sense, NCT calls attention to the tangible, physical connections between food producers of the past and those of contemporary societies.

Continuity and local ecological knowledge are especially respected and celebrated where long-term cultural connections persist (e.g., Balée 1989; Frausin et al. 2014). Researchers working in many areas are demonstrating the role that both physical manifestations of ecological inheritance and the knowledge produced through cultural inheritance can play in combatting the effects of climate change and issues of food security across the world (Glaser 2007; Logan 2020; Solomon et al. 2016). Connections between past and present-day environments are especially visible in islands where inherited ecologies are inescapable (Fitzpatrick and Giovas 2021; Quintus 2018b). Contemporary concerns over food security and food sovereignty often reflect a lack of lay appreciation for these inherited landscapes of production (see Kurashima et al. 2019). As global supply chains have become more complex and uncertain for remote or marginal locations, interests in local food production and traditional technologies are increasing. Landscape legacies take on added importance in such places, with the potential to reinvigorate successful place-based agricultural niches of the past.

Recognizing and adapting to the consequences of our contemporary anthropogenic niche is a pressing issue. Major impacts include greenhouse gas emissions, landscape alterations on a massive scale, and precipitous declines in biodiversity (Boivin et al. 2016). The deforestation of large swaths of the globe for agricultural endeavors over the course of human history has had profound effects (Burdanowitz et al. 2021; Ruddiman et al. 2014). The practices that contemporary food producers, from individuals to multinational corporations, develop going forward will be built on the cumulative outcomes of human niche construction activities across deep time (Altman and Mesoudi 2019). An emerging and considerable challenge is climate change, as contemporary food production systems are substantially constrained by temperature (Xu et al. 2020), and novel agricultural strategies will be needed to expand the temperature envelope. Indeed, Meneganzin and colleagues (2020) characterize our current climate change crisis as a monumental human niche construction process and a “self-endangering evolutionary trap.” The latter situation arises when organisms are constrained by their evolutionary histories to make inappropriate choices, even when suitable alternative pathways are available. They argue that new forms of counteractive and inceptive niche construction are needed to stabilize the current global niche and drive technological innovation for our species’ survival. Within this frame, farmers are likely to extend cultivation into new environments, perhaps assisted by novel technologies. Indeed, the extension of some cultivated

species into new niches is already underway (Chapman et al. 2012; Skarbø and VanderMolen 2016). This global movement is being underwritten by governmental organizations (i.e., USDA AIM for Climate Initiative) that seek to address the legacies and consequences of past and future environmental change through innovation. History reminds us that these investments will undoubtedly generate vulnerabilities in time, and it may be worthwhile to model long-term outcomes, consider a diversity of options, and build in flexibility. Archaeology stands to offer unique multicentury insights into the successes and failures of a diversity of food production practices across a wide array of environmental settings (Fisher 2020).

Conclusions

The historical study of agriculture has been part of the collective focus of archaeology for decades. A variety of theoretical perspectives have been applied, and this work has been fruitful substantively, theoretically, and methodologically (Marcus and Stanish 2006; Marston 2021; Morehart and De Lucia 2015; Thurston and Fisher 2007). However, investigations of causation frequently privilege proximate drivers, with more limited attention paid to the cascading effects of historical choices, or the incremental accumulation of changes. Moreover, attention has frequently been placed on specific kinds of production techniques, especially those considered “intensive,” in relation to demographic processes and the centralization of political authority; less-intensive agricultural practices, such as agroforestry, informal field systems, and small-scale gardens have, until recently, been understudied.

Niche construction theory offers some advantages in this respect. It has the potential to serve as an overarching theoretical framework to integrate diverse but overlapping perspectives, including human–organism entanglement, human and nonhuman agency, natural selection, nongenetic inheritance, and reciprocal causation. We argue that the niche construction lens is providing new and sometimes unexpected insights into our understanding of historical changes in human behavioral variability and the coevolution of humans, other organisms, and the abiotic environment. This is illustrated by the burgeoning literature reviewed herein. More specifically, NCT contributes to the study of agricultural histories and processes in six interrelated ways. First, NCT places the study of agricultural trajectories into a wider body of theory derived from both the biosciences and anthropology. This, in turn, conceptually integrates human societies into natural systems and facilitates investigation of humanity’s role in the evolution of ecological systems. Second, NCT places focus on emergent phenomena that are the result of the confluence of multiple causal trajectories, and thus shifts inquiry toward documenting sequences of causation rather than events. Third, NCT highlights human, animal, and even plant agencies and the place of humans in reciprocal and recursive interactions. In this way, humans are decentered and the role of other organisms in affecting human agricultural behaviors via the shared niche is recognized (see Bogaard et al. 2021). As humans become more dependent on constructed agricultural niches, the physical and ecological impacts of other organisms increase. Fourth, NCT places focus on a host of human—organism relationships, not only those that result in domestication. Both nondomesticates and

domesticates are affected by agricultural behaviors, and these behaviors, intentional and otherwise, have reciprocal and dynamic effects. Fifth, NCT demonstrates the scale, scope, and importance of ecological inheritance. While persistent landscapes are archaeologically recognized, NCT places these records within a formal causal framework of inheritance. Sixth, and finally, a niche construction perspective transcends time and allows for the elucidation of relationships between organisms, past and present. While specific predictions can be challenging, as niche construction is historically contingent, knowledge of different forms of constructed niches and patterning in their associated long-term outcomes is useful. It provides an opportunity to assess, among other things, potential future states, the drivers of runaway niche construction, and the kinds of symbioses that enhance sustainability.

The focus of NCT on long-term trajectories of human–organism–environment entanglements, technological developments, cultural context, and behavioral strategies makes it an ideal framework from which to investigate agricultural change. Agricultural trajectories are dynamic, produced within the context of changing socioecological structures and the result of accretionary histories. It is through the operationalization of NCT that we can more fully understand both the entangled histories of agriculture in particular places and the general macroevolutionary processes that create and sort agricultural behaviors over time. As we move into the future, we will continue to build on agricultural legacies of the past, but with increasingly global consequences.

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