The role of food storage in human niche construction: An example from Neolithic Europe

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Niche construction theory, a branch of evolutionary biology, places emphasis on the capacity of organisms, through their metabolism, activities and choices, to modify natural selection in their environment and thereby act as co-directors of their own evolution as well as that of others. Humans are potent niche constructors, and understanding how niche construction regulates ecosystem dynamics is central to understanding the impact of human populations on their ecological and developmental environments. A classic example is provided by the evolution of dairying by Neolithic groups in Europe and the significant role played by storage in the development of the dairying niche.

Keywords: Cattle, Dairying, Milk, Neolithic, Niche construction, Storage

Introduction

As the papers in this issue attest, storage, especially of food but extending to water, weapons and any number of other phenomena, is and always has been a key component of human society. Because of this centrality, storage has long been a focus of archaeological and ethnological interest. Drawing from Morgan's (2012) summary, storage has been seen as a necessary precursor to agriculture (Bender 1978); as an indicator of sociocultural complexity (Price and Brown 1985); as a concomitant feature (Testart 1982), if not a cause (Flannery 1972; Rafferty 1985; Yoder 2005; Pearson 2006), of sedentism; as an important step in conceptualising private property (Bettinger 1999); as a means of social control (Wesson 1999); as a form of shared knowledge (Hendon 2000) and as a motivation for the development of numerical counting (Divale 1999).

Despite long-standing interest in storage on the part of social scientists, Morgan (2012) pointed out that there has been only minimal quantitative assessment of the causes and effects of food-storage variability and how these might play out in evolutionary-ecological contexts. Our goal here is not to attempt to summarise all the varied opinions on the role(s) of storage in human societies but rather to consider Morgan's call in terms of the co-evolutionary nature of organisms and storage features and more specifically the downstream evolutionary and ecological *consequences* of storage. That perspective derives from *niche construction theory* (NCT), a branch of evolutionary biology that places emphasis on the capacity of organisms, through their metabolism, activities and choices, to modify natural selection in their environment, which food storage does, and thereby act as co-directors of their own evolution as well as that of others (Odling-Smee *et al.* 2003).

Anthropologists have long known the power that culture exerts in shaping the human condition, but it is becoming increasingly clear that the interactions of genes and culture – literally, their co-evolution – offer a faster and stronger mode of human evolution than either by itself (e.g., Aoki 1986; Durham 1991; Ehrlich 2000; Richerson and Boyd 2005; Hawks *et al.* 2007; Laland *et al.* 2010; Richerson *et al.* 2010; Ihara 2011; Rendell *et al.* 2011). Nowhere has gene-culture co-evolution happened faster than within societies whose subsistence economies fall somewhere on the broad spectrum that ranges from incipient plant and/or animal domestication to full-blown agriculture – economies that depend heavily on food storage as an adaptive strategy. The NCT approach to the evolution and development of agriculture has provided numerous opportunities to link the findings of human genetics with those of anthropology and archaeology and to generate novel hypotheses about human evolution (Itan *et al.* 2009; Laland and O'Brien 2010; Laland *et al.* 2010; Richerson *et al.* 2010; Gerbault *et al.* 2011; O'Brien and Laland 2012).

Humans are not the only animals to have evolved the ability to store food; food storage is practiced by

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literally tens of thousands of species of mammals, reptiles, birds and insects (Vander Wall 1990; Nowak 1991). These can be remarkably human-like behaviours: some animals hoard in central larders, which they often guard closely, whereas others scatter their hoards in order to minimise the risk of catastrophic loss from theft. Some species go to great lengths to hide or disguise caches whereas others are quite open as to location (Koenig and Mumme 1987). Some even tolerate pilfering, apparently following a tit-for-tat strategy that what they lose today they'll make up through their own pilfering tomorrow. Some species practice food sharing whereas most do not.

Even the size and complexity of storage structures can blur the lines between humans and animals, one example of which is seen in the enormously complex underground nest and storage facility of a leaf-cutter ant species shown in Fig. 1. As impressive as that facility is, humans, being the ultimate niche constructors (Odling-Smee *et al.* 2003), have gone to incredible lengths in constructing storage facilities, from the granaries of the earliest food-producing societies of the Near East, such as the 11,000-year-old sloped-floor structure at Dhra, Jordan, in Fig. 2, to the massive Roman granaries at Karanis, Egypt, in Fig. 3.

Out of the almost limitless examples of the role played by storage in human niche construction, we selected one that dates roughly between 9000 and 6000 years ago and took place over a region that encompasses much of modern-day Europe and Turkey (Anatolia). That period, referred to as the European Neolithic, witnessed the introduction of cattle from Anatolia northward into the hunting-and-gathering economies of Europe and the spread of domesticated cereals, longhouses and associated storage facilities, Indo-European languages, and cultural practices that included dairying (Renfrew 1987; Bogucki 1988; Whittle 1996; Weisdorf 2005; Edwards *et al.* 2007; Bramanti *et al.* 2009; Haak *et al.* 2010; Bickle and Whittle 2013). The Neolithic example provides an excellent opportunity to examine the ecology of food storage in several guises, all of which played key roles in the evolution of genetic change among Neolithic populations, especially the evolution of the capacity for adults to digest milk. The example illustrates not only the wide range of storage features that humans have created but also the role that storage behaviours play in effecting genetic change.

Niche Construction

Ecologists and evolutionary biologists have long recognised the complex interplay of animal behaviour and the physical environment, with Mayr (1973, 388) claiming that behaviour is 'perhaps the strongest selection pressure operating in the animal kingdom.' Despite this recognition, standard evolutionary theory often treats the interplay of behaviour and the environment as unidirectional, where 'adaptation is always asymmetrical; organisms adapt to their environment, never vice versa' (Williams 1992, 484). The standard evolutionary perspective that 'the environment 'poses the problem'; the organisms 'posit solutions,' of which the best is finally 'chosen'' (Lewontin 1983, 276) is shown in Fig. 4 (top). Notice that (1) niche construction is recognised as a product of natural selection but not as an evolutionary process and (2) inheritance is primarily genetic.

The missing element in this standard perspective is the fact that the selective environments of organisms are themselves partially built by their own niche-construction activities. Thus 'organisms do not adapt to their environments; they construct them out of the bits and pieces of the external world' (Lewontin 1983, 280). The adaptive fit between organism and environment involves the capacity of organisms to modify environmental states, often, but not exclusively, in a manner that suits their genotypes (Fig. 4 (bottom)). Such matches are the dynamic products of a two-way process that involves organisms both responding to 'problems' posed by their environments through selection – the standard view of evolution – and setting themselves new problems by changing environments through niche construction – the addition to the standard view (Lewontin 1983, 2000; Odling-Smee 1988; Laland and Sterelny 2006 (see also debate in Scott-Phillips *et al.* 2014)). Examples of niche construction include bacteria fixing nutrients (Wcislo 1989; Jones *et al.* 1994, 1997; Odling-Smee *et al.* 2003); fungi decomposing organic matter; plants changing levels of atmospheric gases and modifying nutrient cycles; animals manufacturing nests, burrows, webs and pupal cases; and humans constructing houses, animal pens and storage facilities and domesticating plants and animals (Smith 2007a; Odling-Smee and Turner 2011).

The Extended Phenotype: A Basis for Human Niche Construction

Standard evolutionary theory treats niche construction as phenotypic, or extended phenotypic (Dawkins 1982), consequences of prior selection, not as a cause of evolutionary change. Following Dawkins (1982), 'extended phenotype' is defined as an adaptation that is the product of genes expressed outside of the body of the organism that carries them – for example, a bird's nest, a spider's web or a caddis's house. As a result, there exists extensive theory within evolutionary biology and evolutionary ecology concerning how selection shapes the capacity of organisms to modify environmental states and construct artefacts (Alcock 1972; St Amant and Horton

Figure 1 Subterranean portion of a giant leafcutter ant nest in Brazil. Concrete was poured into the nest in order to create a cast of the inside. The nest branches out to cover more than 67 m^2 and contains 1920 chambers, 238 of which are occupied by fungus farms. The cut leaves are used as fertiliser for the fungus cultures. Courtesy Bilfinger Magazine.

2008; Shumaker *et al.* 2011) and structures (Hansell 1984; Turner 2000), but there is little theory concerned with how niche construction modifies natural selection, particularly selection acting at loci other than those expressed in the niche construction (Odling-Smee *et al.* 2003).

Likewise in archaeology, the notion of the extended phenotype has been applied to features such as ceramic vessels, stone tools and wattle-and-daub houses (O'Brien and Holland 1992, 1995), but again, there has been little or no discussion of the feedback effects of human artifacts on natural selection (Laland and O'Brien 2010, 2014; Odling-Smee and Turner 2011). As a result, there has been, for example, an underappreciation of the ability of humans to control temperature by manufacturing clothes and building shelters, which has damped selection favouring anatomical and physiological responses to temperature extremes and fluctuations and allowed us to inhabit colder areas of the world (Laland *et al.* 2007).

More significant for discussion here, the crops and animals that humans domesticate – aspects of a constructed niche – have substantially modified selection on alleles expressed in the ability of humans to store foods, to process novel diets and to resist inadvertently produced disease (Laland *et al.* 2010; Richerson *et al.* 2010; O'Brien and Laland 2012). This feedback from cultural processes is not restricted to the genetic level, given that pots, houses, storage facilities, crops and myriad other cultural products also transform the developmental niche (Sterelny 2009), altering learning environments and shaping local traditions (Talhelm *et al.* 2014). An important insight from

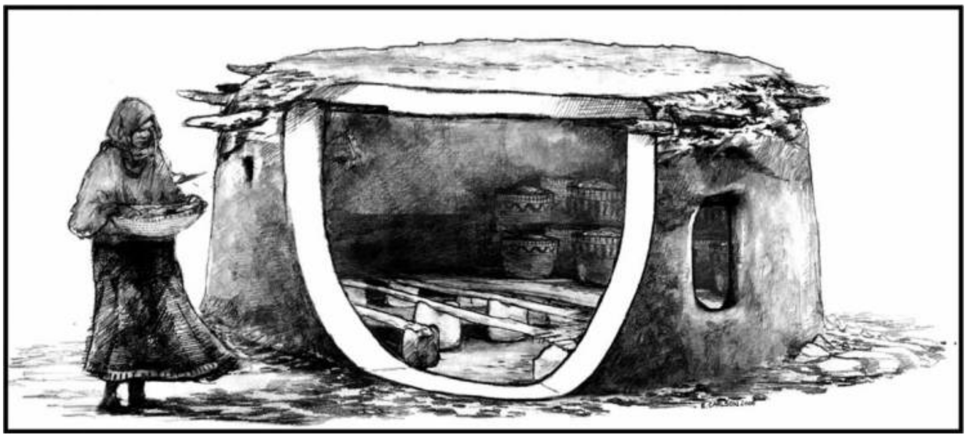

Figure 2 Interpretive reconstruction of an 11,000-year-old granary at Dhra', Jordan. The exposed area shows upright stones supporting larger beams, with smaller wood and reeds above, and finally covered by a thick coating of mud. The suspended floor sloped 7 degrees and served to protect stored foods from high levels of moisture and rodents. From Kuijt and Finlayson (2009).

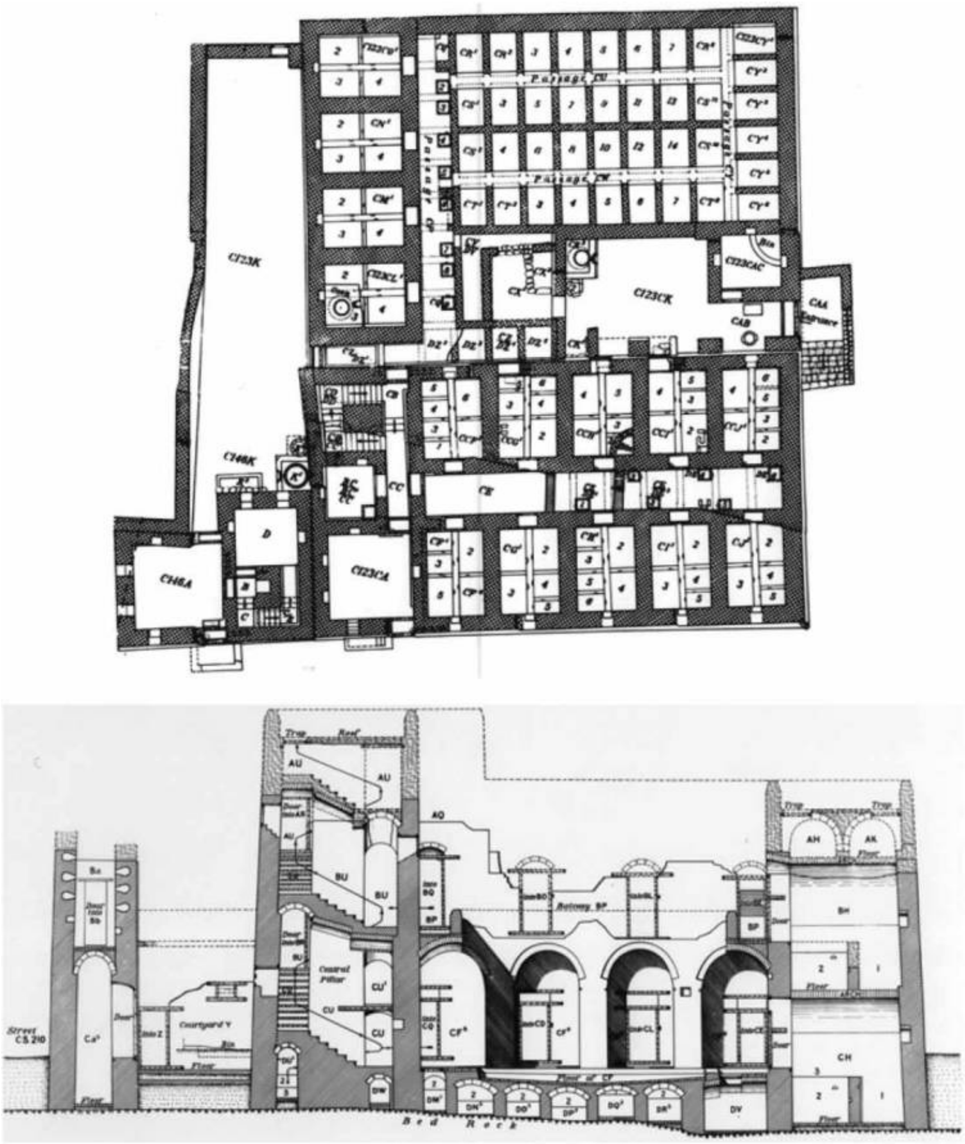

Figure 3 Views of two massive Greco-Roman granaries at the site of Karanis, Egypt: (top), plan view of granary C123; (bottom), sectional view of granary C65. Granary C123 occupied an area of about 22 × 28 m and was two stories tall, with vaulted storage rooms opening onto central corridors. Granary C65, a three-story structure, covered an area approximately 16 × 18 1 / 2 m. From Husselman (1952).

NCT is that acquired characters – Laland *et al.* (2000) lable them 'smart variants' – play an evolutionary role by transforming selective environments (Fig. 5).

Ecosystem Engineering: Modulating Energy and Matter Flow

An important concept in NCT, which comes out of ecology, is 'ecosystem engineering', by which organisms modulate flows of energy and matter through their environments (e.g., Jones *et al.* 1994, 1997; Jones and Lawton 1995; Cuddington *et al.* 2007; Cuddington 2011). Such engineering activity can have significant impacts on community structure, composition, and diversity. Young beavers, for example, inherit from their parents not only a local environment comprising a dam, a lake and a lodge but also an altered community of microorganisms, plants and animals (Naiman *et al.* 1988; Wright *et al.* 2002). Moreover, niche construction/ecosystem engineering can generate long-term effects on ecosystems. For instance, beaver dams deteriorate without beaver activity, but this leads to meadows that can persist for nearly a century and that rarely return to the original vegetation (Hastings *et al.* 2007). This kind of situation certainly is not news to anthropologists and other social scientists, who have long had an ecological perspective when it comes to humans and their interactions with natural and cultural environments (e.g., Steward 1955; Geertz 1963; Vayda 1969; Hardesty 1972; Diamond 1997). In fact, with anthropology characterised by polemical debate regarding evolutionary theory, it is worth noting that NCT offers common ground even to approaches that reject evolutionary approaches, such as structuration

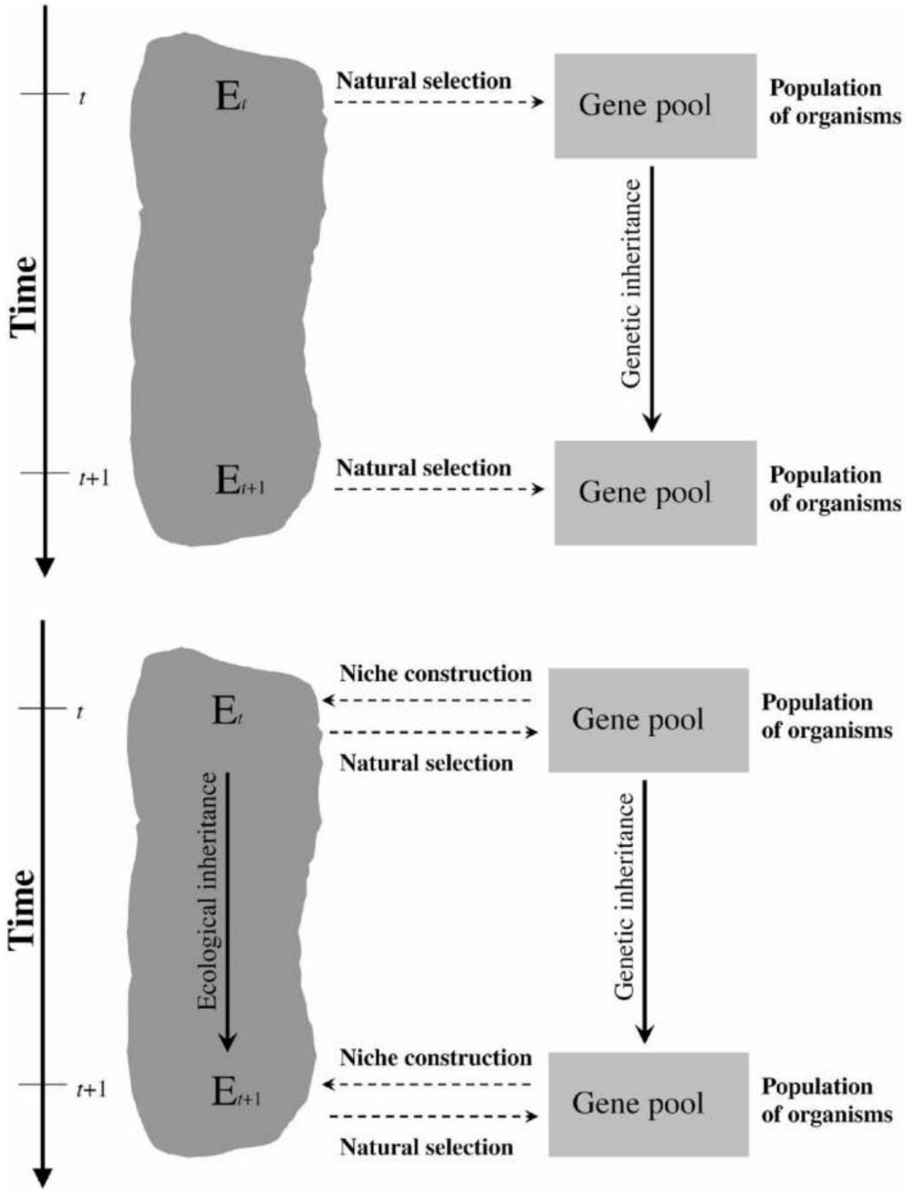

Figure 4 Two views of adaptation. Under the conventional perspective (top), niche construction is recognised as a product of natural selection but not as an evolutionary process. Inheritance is strictly genetic. Under the niche-construction perspective (bottom), niche construction is recognised as an evolutionary process. Here, ecological inheritance plays a parallel role to genetic inheritance. From Laland and O'Brien (2011).

theory (Giddens 1984), which emphasises the feedback among human actions, social organisation and built environments (O'Brien and Laland 2012).

Ecological Inheritance: Downstream Consequences of Niche Construction

The outcomes of previous niche-constructing behaviours – those that persist as a legacy to modify selection on subsequent generations – are known variously as 'ecological inheritance' (Odling-Smee 1988, 2007) or 'ontogenetic inheritance' (West *et al.* 1988). Ecological inheritance does not depend on the presence of environmental 'replicators' but merely on intergenerational persistence of whatever physical – or, in the case of humans, cultural – changes are caused by ancestral organisms in the local selective environments of their descendants. Through their niche construction/ecosystem engineering, organisms produce and destroy habitats and resources for other organisms, generating an additional 'engineering web' of inteconnected organisms and regulated ecosystems. Environmental changes that exemplify human niche construction, such as habitat degradation, deforestation and industrial and urban development, often destroy the control webs that underlie ecosystems, which motivates new conservation strategies to quantify the economic benefits of these 'environmental services'. Storage can, at times, act to damp some of these effects – for example, seeds can be stored, whether by Neolithic farmers for future plantings or by modern crop scientists interested in conserving genetically diverse germplasm.

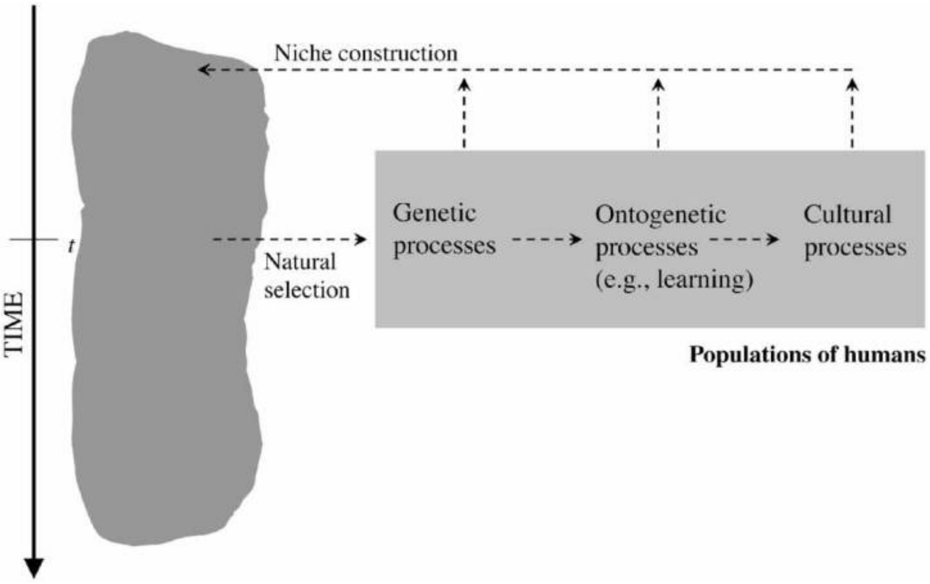

Figure 5 Interconnectedness of three domains of information acquisition and their roles in niche construction. Notice that in niche construction acquired characters have an additional evolutionary role. From Laland and O'Brien (2011).

NCT in the Human Sciences

Researchers in the social sciences have begun to find the NCT conceptual framework useful for framing testable hypotheses. For example, Smith (2007a, 2007b, 2009, 2011) proposes a cultural niche-construction model of initial domestication as a fresh alternative to optimal-foraging-theory accounts. Buchanan *et al.* (2011) applied NCT to ethnographic data to explore the causes of cross-cultural variation in the diversity of subsistence toolkits, finding that predictions from NCT provide a good fit to the data, unlike some established theories that view either risk or population size as the prime mover of toolkit diversity, regardless of subsistence strategy (Collard *et al.* 2013). Other successes of NCT relate to ecosystem and population dynamics, macroevolutionary change, cultural evolution and agriculture (Bleed 2006; Bleed and Matsui 2010; Broughton *et al.* 2010; Laland and O'Brien 2010; Riel-Salvatore 2010; Gerbault *et al.* 2011; Kendal *et al.* 2011; Riede 2011; Rowley-Conwy and Layton 2011; Shennan 2011; Wollstonecroft 2011; O'Brien and Laland 2012; Zeder 2012).

The example on which we focus concerns the coevolution of dairy farming and the allele for adult lactose absorption. Several lines of evidence now support the hypothesis that Neolithic dairy farming created the selection pressures that favoured this allele in pastoralist populations (Simoons 1970; Durham 1991; Holden

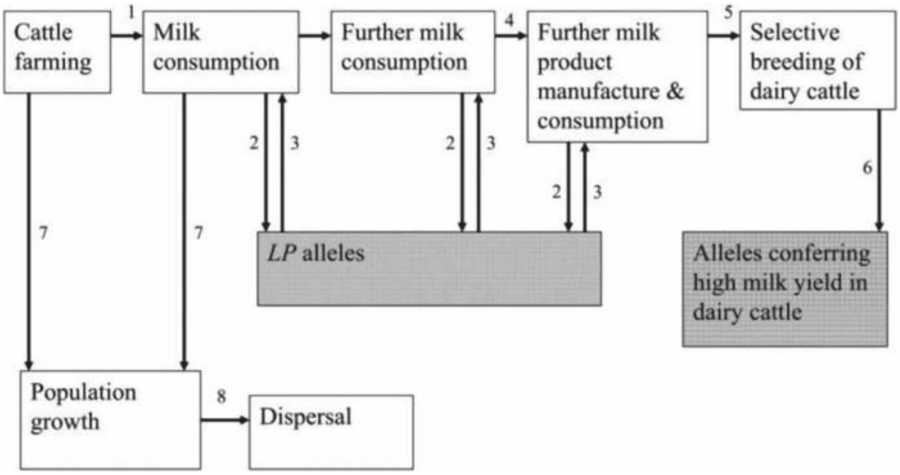

Figure 6 Construction chain depicting the flow of causal influences following a cultural niche-constructing practice for Neolithic dairy farming. Cultural processes are shown in white boxes, and genetic change is shown in shaded boxes. The domestication of cattle triggers (1) milk consumption, which (2) favours the spread of LP, (3) promoting further milk consumption, which (4) elicits further milk-product manufacture and consumption, which (5) leads to selective breeding of cattle, which (6) selects for alleles conferring high milk yield in dairy cattle. In addition, cattle farming and dairy-product consumption (7) lead to population growth, which (8) triggers dispersal into new environments. From O'Brien and Laland (2012).

and Mace 1997; Myles *et al.* 2005; Burger *et al.* 2007; Leonardi *et al.* 2012). This example shows food storage as a niche-constructing behaviour and also the wide variation in storage behaviours found in human societies.

The Coevolution of Cattle Husbandry, Storage and Lactase Persistence

Milk is often thought of as a nutritional bonus (Wooding 2007) because of its high content of fat, proteins, carbohydrates, vitamins and calcium. This rosy picture, however, overlooks the fact that much of the world – something on the order of 65% (Ingram *et al.* 2009; Itan *et al.* 2010; Leonardi *et al.* 2012) – cannot digest milk beyond the age of about eight (the digestion requires the body to break down the disaccharide sugar lactose into the two monosaccharides – glucose and galactose – from which it is synthesised). Most babies naturally produce the enzyme lactase (also known as lactase-phlorizin hydrolase or LPH) so that they can take advantage of the nutrients in mother's milk, but for most of the world's population, lactase production shuts down in the postweaning years. Drinking milk after that leads to a battery of symptoms, including diarrhea, cramping, gas, nausea and vomiting.

Simoons (1970) and McCracken (1971) were among the first to notice a pattern in the geographic distribution of lactose tolerance, usually referred to as lactase persistence (LP): populations that show high percentages of LP – those in northern Europe, for example, can exceed 95% (Ingram *et al.* 2009; Itan *et al.* 2010) – also exhibit a history of cattle dairying that goes back at least several millennia. As Simoons (1981, 29) put it, 'with the beginning of dairying … significant changes occurred in the diets of many human groups. In some of these, moreover, there may have been a selective advantage for those aberrant individuals who experienced high levels of intestinal lactase through life'. That advantage would have occurred in situations where milk was, or could be, an important part of the diet, where the group was under dietary stress, and where its members did not process all of their milk into low-lactose products such as cheese, yogurt and kumis.

As Gerbault *et al.* (2011) point out, the development and spread of LP is a good example of niche construction, a process that began with those Neolithic groups drinking milk gaining a selective advantage within their specific environmental conditions. The niche construction developed over subsequent millennia, as LP and dairying coevolved with the genetic diversity of human populations. The path diagram shown in Fig. 6 illustrates a hypothesised chain of causal influences (O'Brien and Laland 2012), with cultural processes in white boxes and genetic change in shaded boxes: The domestication of cattle triggers (1) milk consumption, which (2) favours the spread of LP, (3) promoting further milk consumption, which (4) elicits further milk-product manufacture and consumption, which (5) leads to selective breeding of cattle, which (6) selects for alleles conferring high milk yield in dairy cattle. In addition, cattle farming and dairy-product consumption (7) lead to population growth, which (8) triggers dispersal into new environments, such as the temperate forests of Europe (e.g., Renfrew 1987; Bocquet-Appel 2011).

As interesting and potentially informative as a path diagram might be, the real issue is the fit between expectations and data, the latter of which can be notoriously messy, especially when long time intervals are involved. Here, things are even more difficult because there is reason to suspect that there was no single path that the spread of LP took and that the strength of selection was not always the same. One might be tempted to think that a trait such as LP would occur only once and that its wide distribution would be a result of either diffusion – intergroup transmission of a trait – or demic spread – groups moving and taking their animal herds with them. At one time, genetic analysis made the single-appearance model appear likely, but recent work (Enattah *et al.* 2002, 2008; Mulcare *et al.* 2004; Tishkoff *et al.* 2006; Ingram *et al.* 2007; Itan *et al.* 2009; Gerbault *et al.* 2011; Nagy *et al.* 2011) has supported Holden and Mace's (1997) earlier conclusion that alleles for postweaning lactase production had multiple origins – perhaps as many as four (three in Africa and one in Europe) – and involved different animals. Despite the multiple origins, the pattern in Europe, which is tied to a single nucleotide polymorphism *(–13910*T)* located 13·9 kilobases upstream of the lactase (LCT) gene (Enattah *et al.* 2002), has been shown to explain most of the modern distribution of LP (Itan *et al.* 2010).

There are three complementary lines of evidence that make up the empirical underpinning of the path shown in Fig. 6 as it pertains to the spread of LP in Neolithic Europe – that obtained from modern genetics, from archaeology (including zooarchaeology), and from a combination of modelling and archaeogenetics. We consider each of these in turn below.

Modern Genetic Evidence

Based on a study of a Scandinavian population, Bersaglieri *et al.* (2004, 1111) estimated that the coefficient of selection associated with carrying at least one copy of the LP allele to be between 0·09 and 0·19 –'among the strongest yet seen for any gene in the genome'. Gerbault *et al.* (2011) make a similar point with respect to the estimated dates of origin of the (*–13910*T*) allele, which range from 2188–20,650 years ago (Bersaglieri *et al.* 2004) to 7450–12,300 years ago (Coelho *et al.* 2005). They note that these estimates are remarkably recent for an allele found at such high frequencies in multiple populations: 'it is easy to envisage recent alleles being rare since they change in frequency slowly, and in a directionless way, by genetic drift. However, a recent allele that has reached such high population frequencies requires more than genetic drift alone; it requires the extra 'kick' of natural selection (Gerbault *et al.* 2011, 864). Here, cultural evolution supplied the catalyst for the process.

Archaeological Evidence

A common feature of most populations with high frequencies of LP is a history of dairying activity (Gerbault *et al.* 2011). In terms of the timing of milk production, various lines of evidence derived from analysis of animal bones from Neolithic sites – age at death, presence of cutting marks, DNA analysis – together with precise radiocarbon dating of the bones, show that farmers began domesticating cattle, goats and sheep between 10,000 and 11,000 years ago in Anatolia, western Iran and northern Mesopotamia (Zeder and Hesse 2000; Troy *et al.* 2001; Helmer *et al.* 2005; Peters *et al.* 2005). At that point, selection would not have favoured LP, or only weakly so, because it was frequently damped by alternative activities of the niche constructors, who consumed the animals that would otherwise have been sources of selection. Slaughtering-age profiles derived from dated archaeological sites have demonstrated that animal exploitation in Mediterranean Europe and the Middle East is consistent with milk production from the early Neolithic onwards (Vigne and Helmer 2007).

In terms of artifactual evidence, Bogucki (1984, 1986, 1988, 1993) first proposed that perforated pottery found at early Neolithic sites in Poland had been used as cheese strainers. These sherds are now the world's oldest evidence of cheese production, dating to 6000–7000 years ago (Salque *et al.* 2013). The production of cheese was of critical importance because during its manufacture, lactose-rich whey is separated out. Thus, cheese production allowed the preservation of milk products in a nonperishable and transportable form and made milk a more digestible commodity for early prehistoric farmers (Lomer *et al.* 2008).

As for milk itself, residues on fragments of ceramic vessels (Dudd and Evershed 1998; Salque 2012) point to widespread occurrence of early milk exploitation across Europe, beginning as early as 8000–9000 years ago in southeastern Anatolia, a millennium or so later in Hungary, Romania and Slovenia, and in Britain by at least 6000 years ago (Copley *et al.* 2003, 2005; Craig *et al.* 2005a; Craig *et al.* 2005b; Evershed *et al.* 2008; Šoberl *et al.* 2008; Craig 2011).

Modeling and Archaeogenetic Evidence

In Europe, the spread of domestic animals is without question directly associated with the movement of the Neolithic cultural tradition from the Near East (Gerbault *et al.* 2011), but was it demic – a movement of people – or diffusion – a transmission of ideas? The speed of the wave suggests the former (Cavalli-Sforza *et al.* 1994), with a rate of 0·6–1·3 km per year (Fort *et al.* 2004; Pinhasi *et al.* 2005). Itan *et al.* (2009) used computer simulation to model the spread of LP, dairying and other subsistence practices across Europe and western Asia and estimated that the coevolution of European LP and dairying originated in a region between the northern Balkans and central Europe sometime between ca. 6250 and 8700 years ago. They proposed that after cattle herding and dairying became increasingly important components of southeastern European Neolithic culture, natural selection began acting on a few LP individuals in Neolithic cultures of the northern Balkans. After the initial slow increase of LP frequency in those populations and the onset of the LBK culture around 7500 years ago, LP frequencies rose more rapidly in a gene–culture coevolutionary process and on the wave front of a demographic expansion into central and north-central Europe that brought along cattle (Edwards *et al.* 2007; Bramanti *et al.* 2009; Haak *et al.* 2010). This led to the establishment of highly developed cattle-based (as well as goat-based) dairying economies throughout central and northern Europe by 6500 years ago (Collard *et al.* 2010). Burger *et al.* (2007) subsequently found that the LP allele was absent in ancient DNA extracted from early Neolithic Europeans, suggesting that it was absent or at low frequency 7000–8000 years ago. The spread of dairy farming also affected geographical variation in milk protein genes in European cattle breeds, which covary with present-day patterns of lactose tolerance in humans (Beja-Pereira *et al.* 2003).

The Role of Storage in the Neolithic Dairying Niche

Animal domestication provided almost unlimited avenues for niche construction among Neolithic groups. In addition to their meat and hide, which wild aurochs (*Bos primigenius*) also provided, domesticated cattle (*Bos taurus*) provided not only meat, milk, blood and labour but also a source of household differentiation, social capital and mobile wealth (Bogucki 1993; Conolly *et al.* 2012) – Sherratt's (1981, 1983) 'secondary products revolution'. Key to the success of the niche was food storage, or more properly, the storage of energy for both short- and long-term use. Numerous kinds of storage structures played important roles in the Neolithic dairying niche, all of which potentially left evidence in the archaeological record to one extent or another. Perhaps the most important storage 'structures' were the animals themselves. For the dairying niche to have evolved, there was a significant shift in perspective among Neolithic peoples from one that emphasised cattle as meat on the hoof – a short-term energy gain – to one that emphasised meat on the hoof *plus* milk in the bank – a much longer view of available energy sources.

It was quite a rich bank from the standpoint of energy because for each unit of food that ruminants consume, their milk yields four to five times the amount of energy and protein compared with meat (Salque 2010). However, it becomes complicated when we attempt to evaluate the precise role of milk production in a subsistence economy (McCormick 1992; Halstead 1996; Balasse and Tresset 2002; Craig 2011) because it requires estimating the amount of milk available for human consumption. This in turn requires knowing both the milk yield of primitive cattle, which itself is difficult to estimate (Gregg 1988; Peske 1994; Tresset 1996), and the amount of milk actually devoted to human as opposed to calf consumption. Modern U.S. dairy cattle produce something on the order of 60–70 pounds of milk per day; Indian and Chinese cattle, which are probably better analogs, produce around 7–15 pounds per day (FAOSTAT 2010). Neolithic cattle might have produced less, but milk would still have been a human 'nutritional bonanza' (Wooding 2007, 8) *if* it could be digested.

Without the shift in emphasis from meat to milk, selection would not have favoured LP and there would have been no dairying niche. The shift was not an overnight phenomenon, and neither was animal domestication itself. Nor was there a single trajectory toward domestication but rather considerable regional and temporal variation in the process (Rowley-Conwy 2004; Conolly *et al.* 2011). We tend to treat domestication as an either/or state, meaning either something is or is not domesticated, but there is a huge amount of grey area in between – more so in animals than in plants and more so in some animals than in others. Selective pressures on animals undergoing domestication focus on behavioural changes, some of which may leave physiological or morphological markers – for example, tooth-size reduction and juvenilisation of the skull – whereas others might not. Such markers can be considered signatures of cultural niche construction.

Multiple early Neolithic animal-bone assemblages from southwest Asia suggest it may have taken as long as 2000 years before domesticated cattle began to fix within agricultural communities as the dominant domestic animal (Conolly *et al.* 2011, 2012; Manning *et al.* 2014). Such a time span is predictable given an unfamiliarity with the intricacies of effective milk production and use on the part of Neolithic farmers. Just as cattle domestication was a lengthy process, so too was developing the knowledge and tools for tapping the resource effectively – an acquired knowledge that itself is a key component of the agricultural niche (O'Brien and Laland 2012).

To accommodate the new role of animals, Neolithic pastoralists needed reliable, year-round food supplies, which would have, at least on occasion, involved storage. Conolly *et al.* (2012) use a species-distribution model applied to zooarchaeological data to show that the process of cattle domestication involved a change in the types of environmental ranges in which cattle exploitation occurred. They convincingly demonstrate that there was an early Neolithic expansion of cattle rearing in temperate environments as opposed to drier environments – a conclusion also reached by Evershed *et al.* (2008). Even with more-temperate environments, however, there is no guarantee that conditions are stable. Open ranges are viable when conditions fall within certain parameters, but when conditions decline – periodic droughts, for example – cattle might require pasturing and alternate sources of water. With respect to niche construction, it is worth remembering that pastures are products of human, not natural activities (Milisauskas and Kruk 2002). This may well have limited herd sizes (Hüster-Plogmann and Schibler 1997). With respect to alternate sources of water, wood-lined early Neolithic wells have been reported from eastern Germany (Tegel *et al.* 2012). These could have served to water both plants and animals.

As cereal grains came under more intensive domestication (Colledge *et al.* 2005; Coward *et al.* 2008) across Neolithic central and northern Europe, they would have provided additional sources of animal food, just as they did human food. Carbon and nitrogen isotopic analysis of sectioned cattle teeth can reveal variation in cattle diets (Balasse *et al.* 1999; Craig 2011). This method could be particularly applicable to the identification of foddering regimes, such as the addition of C4 plants such as maize and millet. In turn, domesticated animals contributed back to the Neolithic agricultural niche by producing manure, which could be used on agricultural plots. Stable isotope determinations of charred cereals and pulses from 13 Neolithic sites across Europe demonstrated that early farmers used livestock manure and water management to enhance crop yields (Bogaard *et al.* 2013). Differential access to heritable lands, perhaps through patrilineality (Bentley *et al.* 2012), could have led to social differentiation in Neolithic farming communities (Bogaard *et al.* 2011, 2013).

Although they do not use the concept of niche construction, note the way in which Bogaard *et al.*'s (2013) discussion of the manuring of Neolithic fields parallels the earlier discussion of the path diagram in Fig. 6:

- Interpretations of weed evidence in southern and northern Europe suggest that early farmers invested considerable labor in the maintenance of long-established cultivation plots.
- Investigations of faunal assemblages indicate that small-scale intensive herding was the norm in various regions across Europe.
- Pasturing herds near hamlets and villages of early farmers would have enabled integration of cultivation and livestock keeping, with periodic stalling and use of crop material as fodder, introducing scope for use of manure on arable land.
- The practice of manuring to enhance soil productivity and tractability has implications for the long-term outlook of farmers on account of the 'slow-release' of essential macronutrients.
- Intensive manuring, therefore, has important implications for 'investment' in land and territorial claims by farming groups.

Neolithic niche construction is even more apparent in Bogaard's (2005, 179) statement regarding 'intensive mixed farming', which refers to intensive cultivation integrated with intensive livestock herding: 'Cultivation provides forage and fodder for livestock, while livestock provide manure for cultivated plots and regulate crop growth'. The functional interdependence between crop and animal husbandry in intensive mixed farming looks like this (Bogaard 2005):

Animal contribution to crop husbandry	Crop contribution to animal husbandry
• Manure to fertilise the soil, from either grazing animals or from collected manure • Grazing of unripe crops to prevent lodging and promote tilling	• Crop by-products (spoiled or surplus) used as fodder • Cultivation plots provide grazing

Not surprisingly, grain-storage structures – both cylindrical and bell-shaped pits and above-ground structures – became increasingly common features of European Neolithic communities (Tripković 2011). Although they are referring specifically to later Celtic pits, Audouze and Buchsenschutz's (1992, 129) description applies to earlier pits as well:

> Storage pits can be distinguished from innumerable pits found all over protohistoric settlements by their characteristic shape. They are usually circular in plan and generally small, being only rarely more than 3 m in diameter. The depth is usually equal to or greater than the maximum diameter. The opening was originally smaller in diameter than the maximum diameter of the pit. These characteristics stem from the need to have as large a storage capacity as possible with the smallest possible opening, which usually seems to have been worked out so as to allow a man to get inside.

Wood (2000, 98–99) provides one explanation of how the pits functioned:

> Grain is poured into the pit after the harvest and a plug of clay was used to cover it, with a layer of turf on top to stop the clay from drying out … The grain on the edge of the pit had contact with the damp earth. This grain then began to germinate, thereby utilizing all the remaining oxygen in the sealed pit, releasing carbon dioxide in exchange. When the oxygen was fully consumed, the germinating grain died and formed a crust on the outer edge of the pit. The grain within was sealed in a vacuum and would keep for years without deteriorating.

Discussion

It should be clear by now that it is difficult to overemphasise the role food storage played in the evolution of the Neolithic dairying niche, with the star of the show being the animals themselves and supporting roles being played by granaries, structures for fodder, corrals and protective sheds, wells, ceramic vessels in which to store milk products, and the milk products themselves. Of course, all of this is a moot point if one doesn't know how to process milk into products – an acquired knowledge that, as noted earlier, provided the initial kick to the dairying niche. Milk is host to a variety microorganisms – *Streptococcus*, *Lactobacillus*, *Bacillus*, yeasts and molds – and each plays a role in converting milk into milk products such as yogurt by breaking down lactose into lactic acid, which sours the milk and coagulates the milk protein, allowing yeast and mold to proliferate and reduce the acid. The fermented milk product can then be safely stored because it is still acidic enough to kill harmful microorganisms. Alternatively, cheese is made by adding the digestive enzyme rennet to acidified milk, coagulating it to the point that solids can be set aside and stored. Cheese making possibly was discovered by accident when milk was stored in a container made from the stomach of an animal, which still contained rennet. The heat from the sun turned the milk sour and the rennet turned the milk into curds and whey (Ridgwell and Ridgway 1986).

Here again is an illustration of long-term consequences of niche construction: keeping cattle for their milk, together with the spread of LP, created the developmental niche that scaffolded the invention of various processed-milk products and their associated technologies (O'Brien and Laland 2012). Again, it is unclear in some cases whether milk itself was being consumed or whether it was being processed into cheese or other products and stored in those forms. Itan *et al.* (2009) suggest that few early Neolithic individuals were lactose tolerant, which apparently is one reason why cheese, and probably other milk products, was manufactured. As Bogucki (1984) proposed 30 years ago, the cheese sieves identified from Neolithic Poland 'played an important role in early dairy production, for the manufacture of cheese was an essential step in the exploitation of milk by populations who possibly had a high level of lactose intolerance'. Whether or not the LP allele achieved high frequency depended on the probability of the offspring of milk *drinkers* – not just consumers of milk products – becoming milk drinkers themselves (Feldman and Cavalli-Sforza 1989). In other words, milk drinking had to be not just a learned tradition but a *reliably* learned tradition (see Aoki 1986). Here, then, is an excellent example of the strong role that cultural, as opposed to only natural, selection can play in shaping the genotype.

To sum up, NCT allows us to make an account of the full picture of how dairying co-evolved with its genetic and socioeconomic implications. Cattle are effectively portable storage vessels, not just nutritionally of meat, milk and blood but also of wealth and/or status for the owners (Bogucki 1993). Livestock ownership may well have been unequally distributed in the Neolithic (e.g., Bogucki 1993; Hayden 2001; Bentley *et al.* 2005). Also, cattle ownership is conducive to patrinineal kinship (Holden and Mace 2003). These patterns lead us to expect patrilocality and unequal access to resources in Neolithic Europe, for which there is increasing archaeological, genetic and linguistic evidence (Bogucki 1993; Haak *et al.* 2008; Bogaard *et al.* 2011; Fortunato 2011; Lacan *et al.* 2011; Bentley *et al.* 2012).

With a NCT perspective, we can hypothesise that owners of large dairy herds would have had a selective advantage over smaller owners or non-owners because wealth in agro-pastoralist societies predicts better reproductive success, that is, more surviving children (e.g., Holden and Mace 2003). Consider this along with the possibility that Neolithic populations experienced boom-and-bust cycles of growth and decline (Shennan *et al.* 2013). These population bottlenecks must have had substantial effect on the genetic and cultural diversity of each subsequent population growth period. Different niches may well have determined different survival rates, resulting in strong selective alteration of the population emerging through the bottleneck.

It is quite possible that dairy farming constituted its own niche, such that lactase-tolerant lineages emerged from bottlenecks as an increased proportion of the population. Isotopic studies of Neolithic skeletons are suggestive of different patrilineages that specialised in different forms of subsistence, such as livestock herding and cultivators (Bogucki 1993; Bentley *et al.* 2008). If we consider the factors of dairying possibly as hereditary specialisations, and the wealth associated with the livestock also as hereditary and possibly unequal, these bottlenecks may have served as very strong selection in favour of wealthy, lactase-persistent cattle-owning lineages.

The socioeconomic element of this hypothesized niche-construction process may help explain why LP did not flourish everywhere in the Neolithic world, such as China or Southeast Asia. In fact, recent studies have demonstrated that the rice-based Chinese Neolithic may have brought about different, more egalitarian and collective norms of food sharing (Talhelm *et al.* 2014) than the wheat-based European Neolithic. Hence, the socioeconomic niche in China co-evolved differently with agricultural practices there. The point is NCT allows us to consider all of these factors together in the evolution of LP, whereas standard evolutionary theory would focus on the nutritional aspects, which make it hard to explain why LP evolved only in particular Neolithic regional populations.

Conclusion

NCT offers conceptual tools not yet readily used within the human sciences, such as a variety of experimental and theoretical methods for establishing where niche construction is consequential and quantifying its impact (Odling-Smee *et al.* 2003; O'Brien and Laland 2012). It also offers theoretically and empirically derived insights into the dynamics of evolving systems, which add to the tools used by archaeologists, anthropologists and other social and behavioural scientists interested in understanding complex systems such as the European Neolithic dairying niche. NCT promotes a systems approach to exploring human evolution and ecology using standard methods regularly and successfully deployed by archaeologists, anthropologists, ecologists and evolutionary biologists.

What is different is the focus of investigation, which moves from the study of the ecological impact or evolutionary response in a single taxon to the investigation of human eco-evolutionary systems, pathways or networks. This requires that we move beyond normal practice and ask, 'what causes the selection pressures leading to a specific evolutionary response?' rather than treating those selection pressures as a starting point (Laland and O'Brien 2014). The key to progress is (1) to break down complicated pathways in networks into tractable component pieces – such as the role of storage in the evolution of the Neolithic dairying niche – (2) to subject each to analysis and (3) to reconstruct the network, including the strength of interactions and how they vary over time. Carrying out such a programme successfully has steep data requirements, and in the case of Neolithic dairying we have much better data than exists in most instances. Still, the effort is worth it in terms of what it will tell us about the ecological as well as evolutionary consequences of human behaviours such as food storage (Morgan 2012). Hopefully, the broad outline sketched here will attract the attention of others who are interested in understanding those consequences.

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References

Alcock, J. 1972. The evolution of the use of tools by feeding animals. *Evolution* **26**, 464–73.

Aoki, K. A. 1986. Stochastic model of gene–culture coevolution suggested by the 'culture historical hypothesis' for the evolution of adult lactose absorption in humans. *Proceedings of the National Academy of Sciences* **83**, 2929–33.

Audouze, F. and Buchsenschutz, O. 1992. *Towns, Villages and Countryside of Celtic Europe*. Bloomington: University of Indiana Press.

Balasse, M. and Tresset, A. 2002. Early weaning of Neolithic domestic cattle (Bercy, France) revealed by intra-tooth variation in nitrogen isotope ratios. *Journal of Archaeological Science* **29**, 853–9.

Balasse, M., Bocherens, H. and Mariotti, A. 1999. Intra-bone variability of collagen and apatite isotopic composition used as evidence of a change of diet. *Journal of Archaeological Science* **26**, 593–8.

Beja-Pereira, A., Luikart, G., England, P. R., Bradley, D. G., Jann, O. C., Bertorelle, G., Chamberlain, A. T., Nunes, T. P., Metodiev, S., Ferrand, N. and Erhardt, G. 2003. Gene–culture coevolution between cattle milk protein genes and human lactase genes. *Nature Genetics* **35**, 311–3.

Bender, B. 1978. Gatherer–hunter to farmer: a social perspective. *World Archaeology* **10**, 204–22.

Bentley, R. A., Lake, M. W. and Shennan, S. J. 2005. Specialisation and wealth inequality in a model of a clustered economic network. *Journal of Archaeological Science* **32**, 1346–56.

Bentley, R. A., Wahl, J., Price, T. D. and Atkinson, T. C. 2008. Isotopic signatures and hereditary traits: snapshot of a Neolithic community in Germany. *Antiquity* **82**, 290–304.

Bentley, R. A., Bickle, P., Fibiger, L., Nowell, G. M., Dale, C. W., Hedges, R. E. M., Hamilton, J., *et al.* 2012. Communty differentiation and kinship among Europe's first farmers. *Proceedings of the National Academy of Sciences* **109**, 9326–30.

Bersaglieri, T., Sabeti, P. C., Patterson, N., Vanderploeg, T., Schaffner, S. F., Drake, J. A., Rhodes, M., Reich, D. E. and Hirschhorn, J. N. 2004. Genetic signatures of strong recent positive selection at the lactase gene. *American Journal of Human Genetics* **74**, 1111–20.

Bettinger, R. L. 1999. What happened in the Medithermal, pp. 62–74 in Beck, C. (ed.), *Models for the Millennium*. Salt Lake City: University of Utah Press.

Bickle, P. and Whittle, A. 2013. *The First Farmers of Central Europe: Diversity in LBK Lifeways*. Oxford: Oxbow.

Bleed, P. 2006. Living in the human niche. *Evolutionary Anthropology* **15**, 8–10.

Bleed, P. and Matsui, A. 2010. Why didn't agriculture develop in Japan? A consideration of Jomon ecological style, niche construction, and the origins of domestication. *Journal of Archaeological Method and Theory* **17**, 356–70.

Bocquet-Appel, J. P. 2011. When the world's population took off: the springboard of the Neolithic demographic transition. *Science* **333**, 560–1.

Bogaard, A. 2005. 'Garden agriculture' and the nature of early farming in Europe and the Near East. *World Archaeology* **37**, 177–96.

Bogaard, A., Strien, H.-C. and Krause, R. 2011. Towards a social geography of cultivation and plant use in an early farming community: vaihingen an der Enz, south-west Germany. *Antiquity* **85**, 395–416.

Bogaard, A., Fraser, R., Heaton, T. H. E., Wallace, M., Vaiglova, P., Charles, M., Jones, G., *et al.* 2013. Crop manuring and intensive land management by Europe's first farmers. *Proceedings of the National Academy of Sciences* **110**, 12589–94.

Bogucki, P. 1984. Linear pottery ceramic sieves and their economic implications. *Oxford Journal of Archaeology* **3**, 15–30.

Bogucki, P. 1986. The antiquity of dairying in temperate Europe. *Expedition* **28**, 51–8.

Bogucki, P. 1988. *Forest Farmers and Stockherders*. Cambridge: Cambridge University Press.

Bogucki, P. 1993. Animal traction and household economies in Neolithic Europe. *Antiquity* **67**, 492–503.

Bramanti, B., Thomas, M. G., Haak, W., Unterlaender, M., Jores, P., Tambets, K., Antanaitis-Jacobs, I., *et al.* 2009. Genetic discontinuity between local hunter–gatherers and central Europe's first farmers. *Science* **326**, 137–40.

Broughton, J. M., Cannon, M. D. and Bartlelink, E. J. 2010. Evolutionary ecology, resource depression, and niche construction theory: applications to central California hunter–gatherers and Mimbres–Mogollon agriculturalists. *Journal of Archaeological Method and Theory* **17**, 371–421.

Buchanan, B., O'Brien, M. J. and Collard, M. 2011. The impact of niche construction on the structure of toolkits of hunter-gatherers and food producers. *Biological Theory* **6**, 251–9.

Burger, J., Kirchner, M., Bramanti, B., Haak, W. and Thomas, M. G. 2007. Absence of the lactase-persistence-associated allele in early Neolithic Europeans. *Proceedings of the National Academy of Sciences* **104**, 3736–41.

Cavalli-Sforza, L. L., Piazza, A. and Menozzi, P. 1994. *History and Geography of Human Genes*. Princeton, NJ: Princeton University Press.

Coelho, M., Luiselli, D., Bertorelle, G., Lopes, A. I., Seixas, S., Destro-Bisol, G. and Rocha, J. 2005. Microsatellite variation and evolution of human lactase persistence. *Human Genetics* **117**, 329–39.

Collard, M., Edinborough, K., Shennan, S. and Thomas, M. G. 2010. Radiocarbon evidence indicates that migrants introduced farming to Britain. *Journal of Archaeological Science* **37**, 866–70.

Collard, M., Buchanan, B. and O'Brien, M. J. 2013. Population size as an explanation for patterns in the Paleolithic archaeological record: caution is needed. *Current Anthropology* **54**, S388–96.

Colledge, S., Conolly, J. and Shennan, S. 2005. The evolution of Neolithic farming from SW Asian origins to NW European limits. *European Journal of Archaeology* **8**, 137–56.

Conolly, J., Colledge, S., Dobney, K., Vigne, J.-D., Peters, J., Stopp, B., Manning, K. and Shennan, S. 2011. Meta-analysis of zooarchaeological data from SW Asia and SE Europe provides insight into the origins and spread of animal husbandry. *Journal of Archaeological Science* **38**, 538–45.

Conolly, J., Manning, K., Colledge, S., Dobney, K. and Shennan, S. 2012. Species distribution modeling of ancient cattle from early Neolithic sites in SW Asia and Europe. *Holocene* **22**, 997–1010.

Copley, M. S., Berstan, R., Dudd, S. N., Docherty, G., Mukherjee, A. J., Straker, V., Payne, S. and Evershed, R. P. 2003. Direct chemical evidence for widespread dairying in prehistoric Britain. *Proceedings of the National Academy of Sciences* **100**, 1524–9.

Copley, M. S., Berstan, R., Dudd, S. N., Aillaud, S., Mukherjee, A. J., Straker, V., Payne, S. and Evershed, R. P. 2005. Processing of milk products in pottery vessels through British prehistory. *Antiquity* **79**, 895–908.

Coward, F., Shennan, S., Colledge, S., Conolly, J. and Collard, M. 2008. The spread of Neolithic plant economies from the Near

East to northwest Europe: a phylogenetic analysis. *Journal of Archaeological Science* **35**, 42–56.

Craig, O. E. 2011. The development of dairying in Europe: potential evidence from food residues on ceramics. *Documenta Praehistorica* **29**, 97–107.

Craig, O. E., Chapman, J., Heron, C., Willis, L. H., Bartosiewicz, L., Taylor, G., Whittle, A. and Collins, M. 2005a. Did the first farmers of central and eastern Europe produce dairy foods? *Antiquity* **79**, 882–94.

Craig, O. E., Taylor, G., Mulville, J., Collins, M. J. and Parker Pearson, M. 2005b. The identification of prehistoric dairying activities in the Western Isles of Scotland: an integrated biomolecular approach. *Journal of Archaeological Science* **32**, 91–103.

Cuddington, K. 2011. Legacy effects: the persistent impact of ecological interactions. *Biological Theory* **6**, 203–10.

Cuddington, K., Byers, J. E., Wilson, W. G. and Hastings, A. 2007. *Ecosystem Engineers (vol 4): Plants to Protists*. New York: Academic Press.

Dawkins, R. 1982. *The Extended Phenotype: The Long Reach of the Gene*. Oxford: Oxford University Press.

Diamond, J. 1997. *Guns, Germs and Steel: The Fates of Human Societies*. New York: Norton.

Divale, W. 1999. Climatic instability food storage, and the development of numerical counting: a cross-cultural study. *Cross Cultural Research* **33**, 341–68.

Dudd, S. N. and Evershed, R. P. 1998. Direct demonstration of milk as an element of archaeological economies. *Science* **282**, 1478–81.

Durham, W. H. 1991. *Coevolution: Genes, Culture and Human Diversity*. Stanford, CA: Stanford University Press.

Edwards, C. J., Bollongino, R., Scheu, A., Chamberlain, A., Tresset, A., Vigne, J. D. and Baird, J. F. 2007. Mitochondrial DNA analysis shows a Near Eastern Neolithic origin for domestic cattle and no indication of domestication of European aurochs. *Proceedings of the Royal Society B* **274**, 1377–85.

Ehrlich, P. R. 2000. *Human Natures: Genes, Cultures, and the Human Prospect*. Washington, DC: Island Press.

Enattah, N. S., Sahi, T., Savilahti, E., Terwilliger, J. D., Peltonen, L. and Järvelä, I. 2002. Identification of a variant associated with adult-type hypolactasia. *Nature Genetics* **30**, 233–7.

Enattah, N. S., Jensen, T. G. K., Nielsen, M., Lewinski, R., Kuokkanen, M., Rasinpera, H., El-Shanti, H., *et al.* 2008. Independent introduction of two lactase-persistence alleles into human populations reflects different history of adaptation to milk culture. *American Journal of Human Genetics* **82**, 57–72.

Evershed, R. P., Payne, S., Sherratt, A. G., Copley, M. S., Coolidge, J., Urem-Kotsu, D., Kotsakis, K., *et al.* 2008. Earliest date for milk use in the Near East and southeastern Europe linked to cattle herding. *Nature* **455**, 528–31.

FAOSTAT. 2010. Yield data 2010 – cow milk, whole, fresh. Rome: Food and Agriculture Organization of the United Nations. http://faostat.fao.org/site/569/DesktopDefault.aspx?PageID=569#ancor.

Feldman, M. W. and Cavalli-Sforza, L. L. 1989. On the theory of evolution under genetic and cultural transmission with application to the lactose absorption problem, pp. 145–73 in Feldman, M. W. (ed.), *Mathematical Evolutionary Theory*. Princeton, NJ: Princeton University Press.

Flannery, K. V. 1972. The origin of the village as a settlement type in Mesoamerica and the Near East: a comparative study, pp. 23–53 in Ucko, P. J., Tringham, R. and Dimbleby, G. W. (eds.), *Man, Settlement, and Urbanism*. London: Duckworth.

Fort, J., Jana, D. and Humet, J. 2004. Multidelayed random walks and application to the Neolithic transition in Europe. *Physical Review E* **70**, 031913-1–6.

Fortunato, L. 2011. Reconstructing the history of residence strategies in Indo-European–speaking societies: neo-, uxori-, and virilocality. *Human Biology* **83**, 107–28.

Geertz, C. 1963. *Agricultural Involution: The Processes of Ecological Change in Indonesia*. Berkeley: University of California Press.

Gerbault, P., Liebert, A., Itan, Y., Powell, A., Currat, M., Burger, J., Swallow, D. M. and Thomas, M. G. 2011. Evolution of lactase persistence: an example of human niche construction. *Philosophical Transactions of the Royal Society B* **366**, 863–77.

Giddens, A. 1984. *The Constitution of Society: Outline of the Theory of Structuration*. Cambridge: Polity.

Gregg, S. 1988. *Foragers and Farmers: Population Interaction and Agricultural Expansion in Prehistoric Europe*. Chicago: University of Chicago Press.

Haak, W., Brandt, G., de Jong, H. N., Meyer, C., Ganslmeier, R., Heyd, V., Hawkesworth, C., Pike, A. W. G., Meller, H. and Alt, K. W. 2008. Ancient DNA, strontium isotopes, and osteological analyses shed light on social and kinship organization of the later Stone Age. *Proceedings of the National Academy of Sciences* **105**, 18226–31.

Haak, W., Balanovsky, O., Sanchez, J. J., Koshel, S., Zaporozhchenko, V., *et al.* 2010. Ancient DNA from European early Neolithic farmers reveals their Near Eastern affinities. *PLoS Biology* **8**, 1–16.

Halstead, P. 1996. Pastoralism or household herding? Problems of scale and specialization in early Greek animal husbandry. *World Archaeology* **28**, 20–42.

Hansell, M. H. 1984. *Animal Architecture and Building Behaviour*. London: Longman.

Hardesty, D. L. 1972. The human ecological niche. *American Anthropologist* **74**, 458–66.

Hastings, A., Byers, J. E., Crooks, J. A., Cuddington, K., Jones, C. G., Lambrinos, J. G., Talley, T. S. and Wilson, W. G. 2007. Ecosystem engineering in space and time. *Ecological Letters* **10**, 153–64.

Hawks, J., Wang, E. T., Cochran, G. M., Harpending, H. C. and Mayzis, R. K. 2007. Recent acceleration of human adaptive evolution. *Proceedings of the National Academy of Sciences* **104**, 20753–8.

Hayden, B. 2001. The dynamics of wealth and poverty in the transegalitarian societies of Southeast Asia. *Antiquity* **75**, 571–81.

Helmer, D., Gourichon, L., Monchot, H., Peters, J. and Sana Segui, M. 2005. Identifying early domestic cattle from pre-pottery Neolithic sites on the Middle Euphrates using sexual dimorphism, pp. 86–95 in Vigne, J. D., Peters, J. and Helmer, D. (eds.), *The First Steps of Animal Domestication: New Archaeozoological Approaches*. Oxford: Oxbow.

Hendon, J. A. 2000. Having and holding: storage, memory, knowledge, and social relations. *American Anthropologist* **102**, 42–53.

Holden, C. and Mace, R. 1997. Phylogenetic analysis of the evolution of lactose digestion in adults. *Human Biology* **69**, 605–28.

Holden, C. J. and Mace, R. 2003. Spread of cattle led to the loss of matrilineal descent in Africa, a coevolutionary analysis. *Proceedings of the Royal Society B* **270**, 2425–33.

Husselman, E. M. 1952. The granaries of Karanis. *Transactions and Proceedings of the American Philological Association* **83**, 56–73.

Hüster-Plogmann, H. and Schibler, J. 1997. Archäozoologie, pp. 40–121 in Schibler, J., Hüster-Plogmann, H., Jacomet, S., Brombacher, C., Gross-Klee, E. and Rast-Eicher, A. (eds.), *Ökonomie und Ökologie neolithischer und bronzezeitlicher Ufersiedlungen am Zürichsee*. Zurich: Zürich and Egg.

Ihara, Y. 2011. Evolution of culture-dependent discriminate sociality: a gene–culture coevolutionary model. *Philosophical Transactions of the Royal Society B* **366**, 889–900.

Ingram, C. J. E., Elamin, M. F., Mulcare, C. A., Weale, M. E., Tarekegn, A., Oljira Raga, T., Bekele, E., *et al.* 2007. A novel polymorphism associated with lactose tolerance in Africa: multiple causes for lactase persistence? *Human Genetics* **120**, 779–88.

Ingram, C. J. E., Mulcare, C. A., Itan, Y., Thomas, M. G. and Swallow, D. M. 2009. Lactose digestion and the evolutionary genetics of lactase persistence. *Human Genetics* **124**, 579–91.

Itan, Y., Powell, A., Beaumont, M. A., Burger, J. and Thomas, M. G. 2009. The origins of lactase persistence in Europe. *PLoS Computational Biology* **5**(8), e1000491.

Itan, Y., Jones, B. L., Ingram, C. J., Swallow, D. M. and Thomas, M. G. 2010. A worldwide correlation of lactase persistence phenotype and genotypes. *BMC Evolutionary Biology* **10**, 36.

Jones, C. G. and Lawton, J. H. (eds.). 1995. *Linking Species and Ecosystems*. New York: Chapman and Hall.

Jones, C. G., Lawton, J. H. and Shachak, M. 1994. Organisms as ecosystem engineers. *Oikos* **69**, 373–86.

Jones, C. G., Lawton, J. H. and Shachak, M. 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* **78**, 1946–57.

Kendal, J. R., Tehrani, J. J. and Odling-Smee, F. J. 2011. Human niche construction in interdisciplinary focus. *Philosophical Transactions of the Royal Society B* **366**, 785–92.

Koenig, W. D. and Mumme, R. L. 1987. *Population Ecology of the Cooperatively Breeding Acorn Woodpecker*. Princeton, NJ: Princeton University Press.

Kuijt, I. and Finlayson, B. 2009. Evidence for food storage and predomestication granaries 11,000 years ago in the Jordan Valley. *Proceedings of the National Academy of Sciences* **106**, 10966–70.

Lacan, M., Keyser, C., Ricaut, F.-X., Brucato, N., Duranthon, F., Guilaine, J., Crubézy, E. and Ludes, B. 2011. Ancient DNA suggests the leading role played by men in the Neolithic dissemination. *Proceedings of the National Academy of Sciences USA* **108**, 18255–9.

Laland, K. N. and O'Brien, M. J. 2010. Niche construction theory and archaeology. *Journal of Archaeological Method Theory* **17**, 303–22.

Laland, K. N. and O'Brien, M. J. 2011. Cultural niche construction: an introduction. *Biological Theory* **6**, 191–202.

Laland, K. N. and O'Brien, M. J. 2014. Niche construction, in Scott, R. A. and Kosslyn, S. M. (eds.), *Emerging Trends in the Social and Behavioral Sciences*. New York: Wiley.

Laland, K. N. and Sterelny, K. 2006. Seven reasons (not) to neglect niche construction. *Evolution* **60**, 1751–62.

Laland, K. N., Odling-Smee, F. J. and Feldman, M. W. 2000. Niche construction, biological evolution, and cultural change. *Behavioral and Brain Sciences* **23**, 131–75.

Laland, K. N., Kendal, J. R. and Brown, G. R. 2007. The niche construction perspective: implications for evolution and human behaviour. *Journal of Evolutionary Psychology* **5**, 51–66.

Laland, K. N., Odling-Smee, F. J. and Myles, S. 2010. How culture has shaped the human genome: bringing genetics and the human sciences together. *Nature Reviews Genetics* **11**, 137–48.

Leonardi, M., Gerbault, P., Thomas, M. G. and Burger, J. 2012. The evolution of lactase persistence in Europe: a synthesis of archaeological and genetic evidence. *International Dairy Journal* **22**, 88–97.

Lewontin, R. C. 1983. Gene, organism, and environment, pp. 273–85 in Bendall, D. S. (ed.), *Evolution from Molecules to Men*. Cambridge: Cambridge University Press.

Lewontin, R. C. 2000. *The Triple Helix: Gene, Organism and Environment*. Cambridge, MA: Harvard University Press.

Lomer, M. C., Parkes, G. C. and Sanderson, J. D. 2008. Review article: lactose intolerance in clinical practice – myths and realities. *Alimentary Pharmacology and Therapeutics* **27**, 93–103.

Manning, K. M., Downey, S. S., Colledge, S., Conolly, J., Stopp, B., Dobney, K. and Shennan, S. 2014. The origins and spread of stock-keeping: the role of cultural and environmental influences on early Neolithic animal exploitation in Europe. *Antiquity* **87**, 1046–59.

Mayr, E. 1973. *Populations, Species, and Evolution*. Cambridge, MA: Harvard University Press.

McCormick, F. 1992. Early faunal evidence for dairying. *Oxford Journal of Archaeology* **11**, 159–62.

McCracken, R. D. 1971. Lactase deficiency: an example of dietary evolution. *Current Anthropology* **12**, 479–517.

Milisauskas, S. and Kruk, J. 2002. Middle Neolithic continuity, diversity, innovations, and greater complexity, 5500/5000–3500/3000 BC, pp. 193–246 in Milisauskas, S. (ed.), *European Prehistory: A Survey*. New York: Springer.

Morgan, C. 2012. Modeling modes of hunter–gatherer food storage. *American Antiquity* **77**, 714–36.

Mulcare, C. A., Weale, M. E., Jones, A. L., Connell, B., Zeitlyn, D., Tarekegn, A., Swallow, D. M., Bradman, N. and Thomas, M. G. 2004. The T allele of a single-nucleotide polymorphism 13·9 kb upstream of the lactase gene (*LCT*) (*C-13·9kbT*) does not predict or cause the lactase-persistence phenotype in Africans. *American Journal of Human Genetics* **74**, 1102–10.

Myles, S., Bouzekri, N., Haverfield, E., Cherkaoui, M., Dugoujon, J.-M. and Ward, R. 2005. Genetic evidence in support of a shared Eurasian–North African dairying origin. *Human Genetics* **117**, 34–42.

Nagy, D., Tömöry, G., Csányi, B., Bogácsi-Szabó, E., Czibula, Á., Priskin, K., Bede, O., *et al.* 2011. Comparison of lactase persistence polymorphism in ancient and present-day Hungarian populations. *American Journal of Physical Anthropology* **145**, 262–9.

Naiman, R. J., Johnston, C. A. and Kelley, J. C. 1988. Alterations of North American streams by beaver. *Bioscience* **38**, 753–62.

Nowak, R. 1991. *Walker's Mammals of the World*. Baltimore: Johns Hopkins University Press.

O'Brien, M. J. and Holland, T. D. 1992. The role of adaptation in archaeological explanation. *American Antiquity* **57**, 36–59.

O'Brien, M. J. and Holland, T. D. 1995. Behavioral archaeology and the extended phenotype, pp. 143–61 in Skibo, J. M., Walker, W. H. and Nielsen, A. E. (eds.), *Expanding Archaeology*. Salt Lake City: University of Utah Press.

O'Brien, M. J. and Laland, K. N. 2012. Genes, culture and agriculture: an example of human niche construction. *Current Anthropology* **53**, 434–70.

Odling-Smee, F. J. 1988. Niche-constructing phenotypes, pp. 73–132 in Plotkin, H. C. (ed.), *The Role of Behavior in Evolution*. Cambridge, MA: MIT Press.

Odling-Smee, F. J. 2007. Niche inheritance: a possible basis for classifying multiple inheritance systems. *Biological Theory* **2**, 276–89.

Odling-Smee, F. J. and Turner, J. S. 2011. Niche construction theory and human architecture. *Biological Theory* **6**, 283–9.

Odling-Smee, F. J., Laland, K. N. and Feldman, M. W. 2003. *Niche Construction: The Neglected Process in Evolution*. Princeton, NJ: Princeton University Press.

Pearson, R. 2006. Jomon hot spot: increasing sedentism in southwestern Japan in the Incipient Jomon (14,000–9250 cal. BC) and Earliest Jomon (9250–5300 cal. BC) periods. *World Archaeology* **38**, 239–58.

Peske, L. 1994. Contribution to the beginning of milking in prehistory. *Archeologishe Rozhledy* **46**, 97–104.

Peters, J., von den Dreisch, A. and Helmer, D. 2005. The Upper Euphrates–Tigris Basin: Cradle of agro-pastoralism? pp. 96–124 in Vigne, J. D., Peters, J. and Helmer, D. (eds.), *The First Steps of Animal Domestication: New Archaeozoological Approaches*. Oxford: Oxbow.

Pinhasi, R., Fort, J. and Ammerman, A. J. 2005. Tracing the origin and spread of agriculture in Europe. *PLoS Biology* **3**, 2220–8.

Price, T. D. and Brown, J. A. 1985. Aspects of hunter-gatherer complexity, pp. 3–20 in Price, T. D. and Brown, J. A. (eds.), *Prehistoric Hunter-Gatherers: The Emergence of Cultural Complexity*. Orlando, FL: Academic Press.

Rafferty, J. E. 1985. The archaeological record of sedentariness: recognition, development, and implications. *Advances in Archaeological Method and Theory* **8**, 113–56.

Rendell, L., Fogarty, L. and Laland, K. N. 2011. Runaway cultural niche construction. *Philosophical Transactions of the Royal Society of London B* **366**, 823–35.

Renfrew, C. 1987. *Archaeology and Language*. London: Cape.

Richerson, P. J. and Boyd, R. 2005. *Not by Genes Alone*. Chicago: University of Chicago Press.

Richerson, P. J., Boyd, R. and Henrich, J. 2010. Gene–culture coevolution in the age of genomics. *Proceedings of the National Academy of Sciences* **107**, 8985–92.

Ridgwell, J. and Ridgway, J. 1986. *Food around the World*. Oxford: Oxford University Press.

Riede, F., 2011. Adaptation and niche construction in human prehistory: a case study from the southern Scandinavian Late Glacial. *Philosophical Transactions of the Royal Society B* **366**, 793–808.

Riel-Salvatore, J. 2010. A niche construction perspective on the Middle–Upper Paleolithic transition in Italy. *Journal of Archaeological Method and Theory* **17**, 323–55.

Rowley-Conwy, P. 2004. How the West was lost: a reconsideration of agricultural origins in Britain, Ireland, and Southern Scandinavia. *Current Anthropology* **45**, S83–113.

Rowley-Conwy, P. and Layton, R. 2011. Foraging and farming as niche construction: stable and unstable adaptations. *Philosophical Transactions of the Royal Society B* **366**, 849–62.

Salque, M. 2010. Down on the farm, 10 000 years ago: an archaeologist investigates dairying. *Catalyst: GCSE Science Review* **21**(2), 17–9.

Salque, M. 2012. Was milk processed in these ceramic pots? pp. 127–41 in Fuelner, F., Gerbault, P., Gillis, R., *et al.* (eds.), *May Contain Traces of Milk: Investigating the Role of Dairy Farming and Milk Consumption in the European Neolithic*. Hesington, UK: University of York.

Salque, M., Bogucki, P., Pyzel, J., Sobkowiak-Tabaka, I., Grygiel, R., Szmyt, M. and Evershed, R. P. 2013. Earliest evidence for cheese making in the sixth millennium BC in northern Europe. *Nature* **493**, 522–5.

Scott-Phillips, T. C., Laland, K. N., Shuker, D. M., Dickins, T. E. and West, S. A. 2014. The niche construction perspective: a critical perspective. *Evolution* **68**, 1231–43.

Shennan, S. J. 2011. Property and wealth inequality as cultural niche construction. *Philosophical Transactions of the Royal Society B* **366**, 918–26.

Shennan, S. J., Downey, S. S., Timpson, A., Edinborough, K., Colledge, S., Kerig, T., Manning, K. and Thomas, M. G. 2013. Regional population collapse followed initial agriculture booms in mid-Holocene Europe. *Nature Communications* **4**, 2486.

Sherratt, A. 1981. Plough and pastoralism: aspects of the secondary products revolution, pp. 261–305 in Hodder, I., Isaac, G. and

Hammond, N. (eds.), *Pattern of the Past: Studies in Honour of David Clarke*. Cambridge: Cambridge University Press.

Sherratt, A. 1983. The secondary exploitation of animals in the Old World. *World Archaeology* **15**, 90–104.

Shumaker, R., Walkup, K. and Beck, B. 2011. *Animal Tool Behavior: The Use and Manufacture of Tools by Animals.* Baltimore: Johns Hopkins University Press.

Simoons, F. J. 1970. Primary adult lactose intolerance and the milking habit: a problem in biological and cultural interrelations. II. A culture historical hypothesis. *American Journal of Digestive Diseases* **15**, 695–710.

Simoons, F. J. 1981. Geographic patterns of lactose malabsorption: a further interpretation of evidence for the Old World, pp. 23–48 in Paige, D. M. and Bayless, T. M. (eds.), *Lactose Digestion: Clinical and Nutritional Consequences*. Baltimore: Johns Hopkins University Press.

Smith, B. D. 2007a. Niche construction and the behavioral context of plant and animal domestication. *Evolutionary Anthropology* **16**, 188–99.

Smith, B. D. 2007b. The ultimate ecosystem engineers. *Science* **315**, 1797–8.

Smith, B. D. 2009. Resource resilience, human niche construction, and the long-term sustainability of pre-Columbian subsistence economies in the Mississippi River valley corridor. *Journal of Ethnobiology* **29**, 167–83.

Smith, B. D. 2011. General patterns of niche construction and the management of 'wild' plant and animal resources by small-scale pre-industrial societies. *Philosophical Transactions of the Royal Society B* **366**, 836–48.

Šoberl, L., Žibrat Gašparič, A., Budja, M. and Evershed, R. P. 2008. Early herding practices revealed through organic residue analysis of pottery from the early Neolithic rock shelter of Mala Triglavca, Slovenia. *Documenta Praehistorica* **35**, 253–60.

St Amant, R. and Horton, T. E. 2008. Revisiting the definition of animal tool use. *Animal Behaviour* **75**, 1199–208.

Sterelny, K. 2009. Where does novelty come from? A hypothesis, pp. 93–109 in Barberousse, A., Morange, M. and Pradeau, T. (eds.), *Mapping the Future of Biology: Evolving Concepts and Theories.* New York: Springer.

Steward, J. H. 1955. *Theory of Culture Change: The Methodology of Multilinear Evolution*. Urbana: University of Illinois Press.

Talhelm, T., Zhang, X., Oishi, S., Shimin, C., Duan, D., Lan, X. and Kitayama, S. 2014. Large-scale psychological differences within China explained by rice versus wheat agriculture. *Science* **344**, 603–8.

Tegel, W., Elburg, R., Hakelberg, D., Stäube, H. and Büntgen, U. 2012. Early Neolithic water wells reveal the world's oldest wood architecture. *PLoS ONE* **7**(12), e51374.

Testart, A. 1982. The significance of food storage among hunter–-gatherers: residence patterns, population densities, and social inequities. *Current Anthropology* **23**, 523–37.

Tishkoff, S. A., Reed, F. A., Ranciaro, A., Voight, B. F., Babbitt, C. C., Silverman, J. S., Powell, K., *et al.* 2006. Convergent adaptation of human lactase persistence in Africa and Europe. *Nature Genetics* **39**, 31–40.

Tresset, A. 1996. *Le Rôle des Relations Homme/Animal dans l'Évolution Économique et Culturelle des Sociétés des V-IVe Millénaires en Bassin Parisien*. Paris: Thèse de Doctorat, Université Paris 1.

Tripković, B. 2011. Containers and grains: food storage and symbolism in the central Balkans (Vinča period). *Documenta Praehistorica* **38**, 159–72.

Troy, C. S., MacHugh, D. E., Bailey, J. F., Magee, D. A., Loftus, R. T., Cunningham, P., Chamberlain, A. T., Sykes, B. C. and Bradley, D. G. 2001. Genetic evidence for near-eastern origins of European cattle. *Nature* **410**, 1088–91.

Turner, J. S. 2000. *The Extended Organism: The Physiology of Animal-Built Structures.* Cambridge, MA: Harvard University Press.

Vander Wall, S. B. 1990. *Food Hoarding in Animals.* Chicago: University of Chicago Press.

Vayda, A. P. 1969. *Environment and Cultural Behavior*. Garden City, NY: Natural History Press.

Vigne, J.-D. and Helmer, D. 2007. Was milk a 'secondary product' in the Old World Neolithisation process? Its role in the domestication of cattle, sheep and goats. *Anthropozoologica* **42**, 9–40.

Wcislo, W. T. 1989. Behavioral environments and evolutionary change. *Annual Review of Ecology and Systematics* **20**, 137–69.

Weisdorf, J. L. 2005. From foraging to farming: explaining the Neolithic revolution. *Journal of Economic Surveys* **19**, 561–86.

Wesson, C. B. 1999. Chiefly power and food storage in southeastern North America. *World Archaeology* **31**, 145–64.

West, M. J., King, A. P. and Arberg, A. A. 1988. The inheritance of niches: the role of ecological legacies in ontogeny, pp. 41–62 in Blass, E. (ed.), *Handbook of Behavioral Neurobiology.* New York: Plenum.

Whittle, A. 1996. *Europe in the Neolithic: The Creation of New Worlds*. Cambridge: Cambridge University Press.

Williams, G. C. 1992. Gaia, nature worship, and biocentric fallacies. *Quarterly Review of Biology* **67**, 479–86.

Wollstonecroft, M. M. 2011. Investigating the role of food processing in human evolution: a niche construction approach. *Archaeological and Anthropological Sciences* **3**, 141–50.

Wood, J. 2000. Food and drink in European prehistory. *European Journal of Archaeology* **3**, 89–111.

Wooding, S. P. 2007. Following the herd. *Nature Genetics* **39**, 7–8.

Wright, J. P., Jones, C. G. and Flecker, A. S. 2002. An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia* **132**, 96–101.

Yoder, D. T. 2005. *Storage and Mobility among the Fremont: Changing Forms through Time*. Unpublished M.A. thesis, Department of Anthropology, Brigham Young University, Provo.

Zeder, M. A. 2012. The broad spectrum revolution at 40: resource diversity, intensification, and an alternative to optimal foraging explanations. *Journal of Anthropological Archaeology* **31**, 241–64.

Zeder, M. A. and Hesse, B. 2000. The initial domestication of goats (*Capra hircus*) in the Zagros Mountains 10,000 years ago. *Science* **287**, 2254–7.