RESEARCH ARTICLE

Integrative Anthropology and the Human Niche: Toward a Contemporary Approach to Human Evolution

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ABSTRACT A niche is the structural, temporal, and social context in which a species exists. Over the last two million years, the human lineage underwent clear morphological changes alongside less easily measurable, but significant, behavioral and cognitive shifts as it forged, and was shaped by, new niches. During this time period, core human patterns emerged, including the following: hypercooperation; lengthy childhood and complex parenting; intricate and diverse foraging and hunting patterns; novel and dynamic material and symbolic cultures; and complex communication and information sharing, eventually resulting in language. Approaches to human evolution grounded in paleoanthropology and archaeology offer fundamental insights into our past, and traditional evolutionary theory offers a strong grounding for explaining them. However, given the centrality of distinctive physiological, social, semiotic, and cognitive processes in human evolutionary histories, a broader anthropological approach can facilitate additional understanding of the human story. An integrative anthropology, reaching across subfields and foci, combined with contemporary evolutionary theory is an approach that can enhance our abilities to model and understand human evolution. [*integrative anthropology, niche construction, evolution, extended evolutionary synthesis*, Homo, *semiosis, Pleistocene*]

RESUMEN Un nicho es el contexto estructural, temporal y social en el que una especie existe. Durante los últimos 2 millones de años, el linaje humano pasó por claros cambios morfológicos junto a cambios conductuales y cognitivos menos fácilmente medibles, pero significativos, en la medida, que forjó, y fue moldeado por, nuevos nichos. Durante este período de tiempo, patrones humanos centrales emergieron incluyendo los siguientes: hiper-cooperación; prolongada niñez y crianza compleja; patrones de caza y recolección intrincados y diversos; culturas simbólicas y materiales novedosas y dinámicas, y el compartir complejo de información y comunicación que finalmente resultó en lenguaje. Aproximaciones a la evolución humana basadas en paleo-antropología y arqueología ofrecen conocimiento fundamental de nuestro pasado, y la teoría evolucionaria tradicional ofrece un conocimiento básico sólido para explicarlo. Sin embargo, dada la centralidad de procesos fisiológicos, sociales, semióticos, y cognitivos distintivos en historias evolucionarias humanas, una aproximación antropológica más amplia puede facilitar un entendimiento adicional de la historia humana. Una antropología integrativa, extendiéndose a través de sub-campos y focos, combinada con teoría evolucionaria contemporánea es una aproximación que puede enriquecer nuestras habilidades para modelar y entender la evolución humana. [*antropología integrativa, construcción de nichos, evolución, síntesis evolucionaria extendida,* Homo, *semiosis, Pleistoceno*]

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> The environment man makes for himself is created through his symbol using ability, his capacity for abstraction. The symbols, the ideas, are created in the mind . . . but the human animal learns not only to create them, but to project them onto the external world, and there transform them into reality.
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> –Ashley Montagu, *The Human Revolution* [1965:2–3]

This quote from 50 years ago is as central today to the puzzle of human evolution as it was then (but now we would switch "human" for "man," and I am sure Montagu would agree). We know that bodies, behavior, and minds of the genus *Homo* changed over time as humanity came to construct, and be constructed by, a novel suite of niches. However, the models for understanding and explaining the diverse range of social, material, cognitive, ecological, and symbolic processes that characterize our lineage suffer from a lack of integrative anthropological attention. We are in a data- and theory-rich time period with regard to the evolution of bodies and behavior in the genus *Homo* (Aiello and Antón 2012; Gamble et al. 2011; Tattersall 2012). We need an expanded toolkit to develop a richer, and more nuanced, understanding of the cognitively sophisticated genus *Homo* and the diverse sorts of niches created and occupied by hominins across the Pleistocene (Kuhn and Hovers 2013; Sterelny and Hiscock 2014). A "big tent" anthropology with a strong linkage to contemporary evolutionary theory (Calcagno 2003; Fuentes 2009, 2012; Meggers 1959; Schultz 2009; Tax 1964; Washburn 1961) is a core context in which to address such needs.

Bio- and paleoanthropological and archaeological approaches rightfully dominate the inquiry into human evolution. These approaches generally take the form of morphological, ecological, and archaeological analyses that describe the compositions and context of the fossils, materials, and ecological characteristics at sites and make inferences from those details: this is the core mode of study into human evolution (e.g., Blumenschine et al. 2012; McHenry and Coffing 2000; Potts 2012). There is a range of interpretive approaches that interface with the fossil and archaeological data, most of which rely exclusively on standard neo-Darwinian perspectives with natural selection as the main architect of function. These include the following: ecological–economic approaches based on behavioral ecology and related to morphological and behavioral constraints on form and function and ecological modeling; physiological–cognition approaches, using assumptions about cognitive capacities or energetics as models, often also incorporating elements of human biology or behavioral ecology; and comparative primatological approaches, using other primates, traditionally apes (mainly chimpanzees) and baboons, as possible models for assessing hominin behavior and ecology (for overview, see Andersson et al. 2014, Fuentes 2009; for examples of these approaches, see Flinn et al. 2007, Kaplan et al. 2000, Klein 2000, Stanford 2001, Wrangham and Carmody 2010). An integrated or "big tent" anthropological approach is absent in these endeavors, and even when some attempt to include "culture" is made, it is focused on the functional aspects of material elements (primarily stone tools) in the archaeological record (e.g., Foley and Lahr 2003).

However, the emerging recognition that social interactions, symbolic and semiotic landscapes, and complex information sharing are central in human evolution suggests that sociocultural, linguistic, and other anthropologies should also be at the table when thinking about the human past, particularly in the genus *Homo*. The recent dynamism (or better put "revolution"; see Laland et al. 2014) in contemporary evolutionary theory also provides an enhanced lens for exploring and modeling our evolutionary histories (Flynn et al. 2013; Laland et al. 2007). While there is a recent trend in examining human evolution to connect various lines of inquiry, moving beyond the reliance on the approaches outlined above and attempting to connect more fully with contemporary evolutionary theory and some insights from social anthropology (e.g., Andersson et al. 2014; Barnard 2011; Gamble et al. 2011; Kendal et al. 2011; Kuhn and Hovers 2013; Read 2011; Sterelny 2012), the incorporation of a fuller range of anthropological and contemporary evolutionary theory remains underrepresented in analyses of the human evolutionary record.

I suggest that a reintegration of anthropological approaches, with an eye toward niche construction and other processes in the extended evolutionary synthesis (Laland et al. 2014), can facilitate richer understanding of the human niche(s), enabling more effective exploration of human evolution. To illustrate this, I start with an appraisal of contemporary evolutionary approaches, with an emphasis on niche construction, and a suggestion of how we might deploy these to help conceptualize the human niche. Then I revisit the central role of human culture in a broader anthropological approach to human evolution, followed by a précis of the evolutionary record of the genus *Homo* in the Pleistocene. I end with a specific example in which the integration I propose could be beneficial: stone tools, semiosis, and teaching and learning as a locale for integrating elements of the neurological, behavioral, morphological, archaeological, ecological, material, and ethnographic in a human niche approach.

TOWARD A CONTEMPORARY EVOLUTIONARY APPROACH

Humans do not live as individuals outside of social groups (at least not for long or typically). We are always interacting with multiple others in temporally and spatially dynamic social relationships as we interface with an ecology that is also partially socially mediated. Although we may use individual humans as the core unit for modeling evolutionary processes, changes, and responses, actual people almost never engage with evolutionarily relevant challenges (be they nutritional, social, ecological, economic, political, etc.) by themselves, outside of a social (cultural) network, or even outside of spatial proximity, or without reference, to other humans. Human action is contingent on a variety

of preexisting social relationships and a complex of shared knowledge directly connected the dynamic of the larger social group. Approaches to modeling the evolution of our genus need to take these features as their starting point and central theme but often do not.

Frequently evolutionary approaches focus on models of access to food, mates, and reproductive opportunities as presented from the perspective of individuals interacting with various environmental and social challenges. These approaches rely heavily on traditional neo-Darwinian selection models with assumed patterns of energetic trade offs for individuals and specific behavioral traits as the primary forces at play (e.g., embodied capital, grandmothering, provisioning, pair bonding, cooking, cooperative breeding, etc.; Burkart et al. 2009; Chapais 2008; Hawkes et al. 2003; Kaplan et al. 2000; Lovejoy 2009; Wrangham and Carmody 2010). When analytical models are introduced, they are often modeled as a single individual interacting in a landscape populated by other single individuals or as groups competing with other groups, with the dyadic encounter (between individuals or between groups) as the core pattern of interface between them (e.g., Choi and Bowles 2007). But heightened social and behavioral density and concomitant social complexity is a widespread, and potentially ancient, primate pattern, and the social networks of many primates are multidimensional and not best modeled as sequences of dyadic exchanges at either the individual or group level (Barrett et al. 2012; Strum 2012; see also Hinde 1976). So in thinking about human evolution, social and behavioral complexity and multifaceted interactions, not single trait or dyadic encounter foci, should be the baseline.

Scenarios that focus on assumptions about evolutionary costs and benefits can provide a positive heuristic tool and have moved analyses of human evolution forward; however, they seldom accurately capture the range of relevant dynamics in human evolutionary processes and histories. Such approaches (e.g., grandmothering, provisioning, pair bonding, cooking, cooperative breeding, etc.) are especially susceptible to oversimplification of systems due to their tightly constrained focus on the potential adaptiveness of a specific trait, mediated via the action of natural selection, as the core salient variable in its display and maintenance. Evolutionary biology and evolutionary theory are currently at a point at which many practitioners argue for a move beyond a focus on dyadic encounter simulations, individual traits, and standard cost–benefit selection models. They propose we move toward a systems approach, involving plasticity, complex inheritance patterns, and multilevel selection, in the analyses of evolutionary histories and processes (Bateson and Gluckman 2011; Hinde 1976; Laland et al. 2014; Oyama et al. 2001; Sterelny 2012).

Plasticity in the development and expression of bodies and behavior is more widespread in organisms than previously thought (West-Eberhard 2003), and complex social mammals, especially primates, reflect very high degrees of this plasticity (Campbell et al. 2011). This resonates particularly well with what we know about of members of the genus *Homo* across the last two million years: they display substantial plasticity in body shape and size, physiological function, and behavior in response to evolutionary pressures (Kuzawa and Bragg 2012; Wells 2012).

Over a half-century of debate about the targets and levels of natural selection has produced a robust recognition that selection likely acts on multiple levels (e.g., genomic, individual, group) in social organisms (Laland and Brown 2011; Wilson and Wilson 2007). This implies that collaborative and cooperative behaviors can be significant factors in evolutionary processes, just as are factors tied directly to individuals' potential reproductive success (the key indicator in natural selection; see Nowak and Highfield 2011; Sober and Wilson 1998).

Behavioral and social inheritances play particularly salient roles in evolutionary patterns for many primate species (Campbell et al. 2011; Strum 2012), especially members of the genus *Homo* (Andersson et al. 2014; Henrich 2011; Kendal 2012). In this light it is important to incorporate multiple evolutionarily relevant processes of inheritance (not just genetic but also epigenetic, behavioral, and symbolic–cultural) into evolutionary models (Bonduriansky and Day 2009; Jablonka and Lamb 2005; Ledón-Rettig et al. 2012). Recognition of multiple modes of inheritance and a feedback dynamic between organisms and their ecologies should be a central tool in integrating behavioral, biological, and ecological factors in modeling human evolution (Flynn et al. 2013; O'Brien and Laland 2012).

Claes Andersson and colleagues (2014) recently noted, "Darwinian forces are seen as necessary but not sufficient for explaining observed evolutionary patterns" in humans, and Dwight Read (2011) suggests that the modern extended evolutionary synthesis (Laland et al. 2014) is amenable to the inclusion of aspects of social–cultural systems as components of evolutionary processes. I suggest that, as anthropologists, we should use contemporary evolutionary theory in the analyses of human evolution via an approach that sees the emergence of novel niches, and the characteristics of the Pleistocene *Homo* communities that construct and are constructed by them, as the zone of focus when examining evolutionarily relevant actions and histories in our lineage.

HUMAN NICHES AND HUMAN EVOLUTION

In the context of contemporary evolutionary approaches, a *niche* is the structural, temporal, and social context in which a species exists. It includes space, structure, climate, nutrients, and other physical and social factors as they are experienced, and restructured, by organisms and via the presence of competitors, collaborators, and other agents in a shared environment (e.g., Wake et al. 2009).

Niche construction is the building and reshaping of niches by organisms and the mutually mutable interactions between organisms and environments (Odling-Smee et al. 2003). Niche construction reflects organism–environment feedback systems with organisms modifying

their niche and thus the evolutionary pressures acting on them, on their descendants, and on unrelated populations sharing the same landscape. The process of niche construction affects energy flows in ecosystems and creates an ecological inheritance that, like natural selection, contributes to changes over time in populations and environments.

Niche-construction theory forces us to consider the human niche in an evolutionary context as a synthesis of ecological, biological, and social landscapes rather than treating them as discrete spheres (e.g., Dean et al. 2012; Fuentes 2013; Fuentes et al. 2010; Kendal et al. 2011; Laland et al. 2007; O'Brien and Laland 2012). Human niche construction can emerge from, and feedback into, ecological systems, genetic processes, physiological processes, developmental processes, and cultural processes (Kendal 2012; Laland et al. 2010). In fact, "much of human niche construction is guided by socially learned knowledge and cultural inheritance" (Odling-Smee et al. 2003:260).

Susan Antón and Josh Snodgrass (2012:S492) recently proposed a model wherein the origin of the genus *Homo* (and its subsequent evolution) is characterized by a "positive feedback loop that drove life history evolution and contributed to cultural change." They describe a form of niche-construction—an iterative processes whereby increasing cognition, dietary quality, and cooperative behavior results in lowered extrinsic mortality risk and is connected to changes in brain size, body composition, life-history parameters, and behavioral and communicative complexity (Antón and Snodgrass 2012; see also Aiello and Antón 2012; Antón et al. 2014; Kaplan et al. 2000). This is a basal description of the patterns by which the genus *Homo* shapes and is shaped by niches across the much of the Pleistocene (Andersson et al. 2014; Antón et al. 2014). Other recent approaches to human evolution are using niche-construction theory and models as a tool in attempts to move past more static assumptions and simplistic feedback scenarios in human evolutionary systems, particularly in the contexts of tool construction and use, butchering and hunting practices, predator avoidance, changes in population sizes and resources use (Collard et al. 2012; Fuentes et al. 2010; Hiscock 2014; Kuhn and Hovers 2013; Riel-Salvatore 2010).

Human niche construction takes place in the spatial and social sphere that includes the social partners, perceptual contexts, and ecologies of human individuals and communities (and the many other species sympatric with humans). These human niches are the context for the lived experience of earlier humans and their communities, where they shared "kinship" (e.g., Sahlins 2013) and social and ecological histories, as well as where they created and participated in shared knowledge, social and structural security, and development across the lifespan.

Clive Gamble and colleagues (2011:115) argue that the "Paleolithic is best conceived as a gradient of change rather than a set of step-like revolutions in society and culture" (see also Kuhn and Hovers 2013; Shea 2011; Sterelny and Hiscock 2014). Robert Foley and Gamble (2009) refer to the human community as the basic building block for human society and the locus for this gradient of change (see also Rodseth et al. 1991). They define the human community as a group with shared dialects, kin bonds, cultural consonance and symbolic beliefs, and political organization, and with members having the capacity to maintain these common elements in the absence of close spatial proximity and during long periods when there is no contact (a definition that resonates well with much in social anthropology).

It is within the context of these communities that members of the genus *Homo* interacted with, modified, and were modified by social and ecological worlds: these communities are the core demographic unit for the human niche. Describing these human niches and the niche-constructive processes within them requires being able to integrate investigations on bodies, communities, created and modified materials, and local ecologies, with extrapolations and interpretations about behavior, social networks, and the possible meanings infused in all of these variables. This calls for an integrated anthropological toolkit.

Gamble and colleagues (2011) argue that we need an interdisciplinary framework to understand the process of amplification and coevolution of social and technological behavior in the evolution of our genus (see also Kuhn and Hovers 2013; Sterelny and Hiscock 2014). Some current approaches are engaging aspects of this perspective (e.g., Andersson et al. 2014; Dunbar et al. 2010; Sterelny and Hiscock 2014); however, the application of most of these integrations rarely extends deep into the history of the genus *Homo*.

One might argue that this absence is due to the fact that the further one goes back in time, the less material with which we have to work, and thus assessment of behavior, as well as cultural processes and practices, is near impossible. This is true to an extent but is not a fatal blow for this endeavor. Dietrich Stout and Thierry Chaminade (2012), Peter Hiscock (2014), and others demonstrate that there is a rich body of social, physiological, and ecological information to be extracted from even early Olduwan tools (ca. two million years ago), and others show that changes in fossil and material evidence of patterns of predation and resource exploitation might also offer clues to reconstructing human niches and modeling the processes within communities of early *Homo* (Fuentes et al. 2010; Morgan et al. 2015; Sterelny 2014).

An integrated niche-construction approach encompasses dynamic feedback systems at multiple levels; incorporates social, material, and demographic processes; and provides a locus to integrate investigation into the evolution of the genus *Homo* with theoretical and methodological perspectives in cultural and linguistic anthropologies (see Coward and Gamble 2008; Descola 2013; Downey and Lende 2012; Foley and Gamble 2009; Sterelny 2012). Such an approach has the basal assumption of a human niche that

encompasses face-to-face interactions within social groups, interactions among social groups, and complex social dynamics at both group and larger community levels as relevant in evolutionary processes. It also recognizes that feedback systems (ecological, physiological, and behavioral) affecting, and being affected by, evolutionary processes are characteristics of the individual over the lifespan, of social groups, and of the larger community. Evolutionary processes (including selection, drift, and gene flow) and the various inheritance mechanisms (genetic, epigenetic, behavioral, and symbolic) can affect all levels in the system, and responses to these evolutionary processes can emerge at individual, group, and community levels—which can feedback and affect the very evolutionary processes to which the responses are reacting. This pattern of reactive response to social and ecological pressures and contexts at various levels (individual, group, community) creates a local ecology of interactive material, social, and cognitive aspects that is passed from one generation to the next; it creates an inherited social and material ecology as part of a dynamic human niche; in other words, culture matters.

NICHES ARE ALSO CULTURAL

> The most significant paradox in the study of human evolution is that human evolution over the last few million years has been biocultural evolution, and it is thus perversely unscientific to try and imagine it as simply a succession of biological processes and effects. Without confronting the cultural aspects of human evolution, one cannot approximate the reality of human origins or human nature.
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> –Jonathan Marks, "The Biological Myth of Human Evolution" [2012:139]

A key element in the constitution and functioning of the current human niche is what we often term *culture* (Andersson et al. 2014; Dean et al. 2012; Foley and Gamble 2009; Read 2011). However, culture is not a social, material, historical, and perceptual veneer laid over a basal set of physiological capabilities. The range of action and perception, memory and history, items and ideas that we call "human culture" is a dynamic and fundamental constituent of the human niche that is simultaneously constructed by, and constructing of, the human experience and thus evolutionarily relevant (Dean et al. 2012; Downey and Lende 2012; Fuentes 2009; Kendal 2012; Read 2011).

The definition, use, and analysis of the term *culture* have a very long and complex history inside, and out, of anthropology since our early stages as a discipline (Kroeber and Kluckhohn 1952). However, regardless of how we label them, the myriad actions, symbols, meanings, histories, and ideas that are implicated in human culture—and how people actually create, navigate, and perceive these elements—is central to any robust exploration of human evolution.

In an evolutionary approach, we cannot fall back on a treatment of culture as primarily understandable and measurable via constituent "variants" or other heritable particles characteristic of many gene–culture coevolution approaches. Such approaches see cultural evolution as fundamentally Darwinian in its basic structure, with genes and culture variants being the key targets of selection (Richerson and Boyd 2005). While offering important options for modeling cultural change, such a perspective remains wed to a dual-inheritance context in which genes and culture variants are "obligate mutualists" and are seen as two side-by-side yet interfacing systems being driven by natural selection.

Nor can we deploy *culture* simply as a gloss that reflects adaptive behavioral patterns emerging from human evolutionary histories; we need a toolkit that enables a better understanding of the human experience in the past (Marks 2012). So, to better assess and understand patterns and processes of social complexity in human evolution, we should engage the various perspectives and treatments of the human experience that emerge from work by anthropological practitioners who focus intensively on what, how, why, and where humans think, act, and express themselves as they do. Human evolutionary studies can benefit from increased interaction with aspects of ethnographic approaches and elements of broader theory in social anthropology (e.g., Geertz 1973; Ingold and Vergunst 2008; Kohn 2013; Luhrmann 2012; Turner 1969).

This is not an argument that we should model the evolution of "protoculture" in earlier members of the genus *Homo* based on observations of ape "culture" or ethnography of modern-day foraging peoples. There is increasing evidence that other apes, such as chimpanzees, are not particularly good models for understanding the particulars of the evolution of the genus *Homo* (Marks 2002; Sayers et al. 2012; Sterelny and Hiscock 2014), and as such looking at ape "culture" or other animals' "cultures" as models for early human behavior and perception can only take us so far. In fact, it may end up inhibiting and misdirecting our analyses by modeling culture in earlier human niches simply as social traditions or patterns of intraspecific variation in social behavior and tool use. In the same vein, looking to modern forager populations to provide insights into past lifeways can be highly problematic and misleading. All humans alive today are fully cognitively and socially modern regardless of their group structures, technologies, political, and economic systems. Thus, while a focus on these small-scale societies can provide insight into human small-group dynamics and aspects of engagement with specific ecologies, technologies, and social processes (e.g., Wiessner 2014), such an approach does not give us access to a past in which our ancestors were not who we are today (Wobst 1978).

Culture is not a simple "thing" or an easily disentangled cluster of traits, so we need to bring appropriate tools to bear when attempting to describe and analyze this distinctive aspect of human niches. When I propose increased interaction with a broader anthropology, I am arguing for selective interfaces with interpretive and theoretical toolkits and models used and developed in social, linguistic, and other anthropologies, not with the actual methodologies of ethnographers or with facile comparisons

between past members of our genus and modern foraging peoples.

When thinking about evolution in the context of human niches, cultural processes are central components in niche construction at individual, group, and community levels across time. An integrated anthropological toolkit that brings diverse approaches to the understanding of human cultural processes, meanings, and embodiment (Downey and Lende 2012) is necessary when we are asking questions about how and why the genus *Homo* evolved as it did.

THE PLEISTOCENE BASELINE: WHAT ARE WE TRYING TO UNDERSTAND?

> Individuals did not face the ecological filters in their environment alone, but with others, and with the technology, information, and misinformation that their social world provides. Ecological and social complexity became fused, as the ecological problem of extracting resources as individuals from a world we did not make became the economic problem of extracting resources collectively from and in a human world.
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> –Kim Sterelny, "Social Intelligence, Human Intelligence and Niche Construction" [2007:728]

To best envision how we might engage the past with an integrated anthropological and contemporary evolutionary approach, we need to establish a baseline for what we know about a specifically human evolutionary history and what it is that we are trying to understand, explain, and connect to the present via evolutionary processes.

The ancestral lineage of humans diverged from those of the African apes approximately eight million years ago, and we refer to the members of the lineage as hominins. There are many overviews of the patterns and processes in hominin evolution from six to two million years ago (e.g., Wood 2010), so I will not review them here. The specifically human history starts in the most recent third of hominin history with the genus *Homo*. It is most likely that the genus *Homo* evolved from one of the multiple australopithecine hominin lineages in eastern or southern Africa between about three and two million years ago, and then it subsequently spread across Africa, into Eurasia, and eventually across the globe (Antón et al. 2014; Hawks et al. 2000; Lordkipanidze et al. 2013; Wolpoff et al. 2000; Wood and Leakey 2012).

Being specifically interested in human evolution, it is the distinctions between the genus *Homo* and other hominin lineages, and the niches within the genus *Homo* (Kuhn and Hovers 2013), on which we need to focus. So our explanations should be developed for the derived or modified patterns of the human lineage relative to other hominins rather than re-explaining, at a basal level, many of the evolutionary continuities we share with other hominins and even the hominoids (apes) (Wells and Stock 2007).

We know the hominoid and hominin evolutionary baselines—the set of morphologies, behavioral patterns, and adaptations that characterize the lineages from which the genus *Homo* arose. Anthropoids (monkeys, apes, and humans) exhibit a complex sociality that would have been present in multiple branches of the hominoids from which our earliest lineages diverged and, thus, in the hominins. We are not tasked with explaining why humans live in highly social groups with complex social relationships and networks that cut across biological kinship with relatively high levels of cooperation because this is a pattern found in the extant hominoids and is evolutionarily basal for humans and all hominins (MacKinnon and Fuentes 2011; Malone et al. 2012). This baseline includes the following: dynamic multiadult social organization (with possibility of fission-fusion communities), increased social cognition relative to other primates, high social reciprocity, local social tradition and innovation, and simple tool manufacture and use (Flinn et al. 2007; Foley and Gamble 2009; MacKinnon and Fuentes 2011; Malone et al. 2012; Pradhan et al. 2012). These are ancestral, not derived, traits: they are part of our baseline, just like grasping hands; forward-facing, overlapping eyes; a 360-degree-rotating arm-shoulder joint; a morphology enabling bipedal locomotion; and a relatively large brain- to body-size ratio.

Recent contributions (see Aiello and Antón 2012; Antón et al. 2014; Kuhn and Hovers 2013; Sterelny and Hiscock 2014) provide an up-to-date review of the fossil data and some associated physiological and behavioral correlates for Pleistocene *Homo* (circa two million to ten thousand years ago). Between two and approximately .3 million years ago, members of the genus *Homo* are characterized by increasing brain size and, in most fossil examples assumed to be in our direct lineage, decreasing robusticity and what appears to be an extension in the duration of childhood (juvenile development). Over this same time period, there are trends of decreasing relative tooth size in many of the fossils, and the morphology related to walking and running converges fully with our modern form (Antón and Snodgrass 2012; Potts 2012; Wells and Stock 2007). Stone tools associated with our genus slowly become more complex, with increasing diversity of patterns and materials most rapidly occurring over approximately the last three to four hundred-thousand years (Sahle et al. 2013; Wadley 2013). Antón and Snodgrass (2012) also suggest that members of the genus *Homo* were able to reduce the severity of extrinsic mortality (death caused by factors external to the individuals of interest, such as predation or ecological stress) substantially over the Pleistocene. By the last two to three hundred-thousand years, there is evidence of increasing range expansion, increasing population densities, and increasing rates of innovation in material cultures, as well as for the beginning of symbolic representation (McBrearty 2012; Powell et al. 2009; Wadley 2013). The emergence of distinctively human niches is spread over our evolutionary history and is not a single or short transitional event firmly associated with fossils of anatomically "modern" *Homo sapiens* (Andersson et al. 2014; Foley and Gamble 2009; Shea 2011; Sterelny 2014).

The archaeological, morphological, and inferred behavioral patterns noted above are those that emerge from traditional approaches extracting information from the fossil and archaeological record. There is also a set of distinctive sociobehavioral processes characterizing our species today that likely emerged during our Pleistocene evolutionary history. These are not traditionally, or easily, extrapolated from the fossil–archaeological record but are equally relevant in the context of contemporary evolutionary theory and especially indicative of the importance for an integrative anthropological approach to human evolution. These processes include the following: cultural innovation and accumulation via an autocatalytic process involving feedback between creativity and transmission and a coevolutionary interdependence among ecological, cognitive, and neural systems.

Today humans, unlike other tool-using animals, have rapid cultural innovation and accumulation via an autocatalytic process that involves feedback between creativity (the development of ideas and new modes) and transmission (the passing along of information about the construction and use of the new ideas or modes) (Donald 1993; Enquist et al. 2008; Montagu 1965; Ogburn 1950; Richerson and Boyd 2005; Tomasello 1999). This is a dynamic system wherein innovations (e.g., ideas and behaviors) and elements (e.g., material components and their use) can be gained and lost depending on innovation opportunities, social densities, and transmission fidelity. Novel innovation is often generated by combining existing technologies, elements, and perspectives. Social and material innovation can emerge individually or via cooperation, with accuracy of transmission between individuals and across generations acting to increase resilience of innovations. The actual number of innovations per generation–time period will grow with increases in the density of technologies, elements, and perspectives (i.e., the "raw materials" of innovation) and possibly with increases in population density (due to a higher likelihood of innovation transmission both laterally and vertically, Powell et al. 2009).

This process is well documented in modern humans (Enquist et al. 2008) but not for pre-*Homo* hominins or living apes. Thus, this process likely has its origins in the genus *Homo* during the last two million years. For example, later Pleistocene (the last two to three hundred-thousand years) stone tool technologies show rapid and broad diversification relative to the previous approximately 1.7 million years of human evolution. This may relate to the interface of cognitive, communicative, and cooperative patterns in populations of *Homo*, with slight increases in population densities and between-group social interactions, such that instances of innovation and the chances of such innovation being maintained and shared increased while the likelihood of new innovation extinction decreased (Gamble et al. 2011; Sterelny 2012).

Andrew Whiten and David Erdal (2012) argue for the recognition of a distinctive sociocognitive component to the human niche(s) that includes the dense conception and transmission of innovation and information alongside substantive neurological and behavioral plasticity. This human pattern of sociocognitive niche construction reflects a cognitive and behavioral configuration that is derived relative to the sociobehavioral contexts of previous hominins and all hominoids. Today this niche includes hypercooperation, shared intentionality, cultural transmission and innovation, teaching, and language (Donald 1993; Sterelny 2012; Whiten and Erdal 2012). This modern human niche is characterized by a rapidly increasing rate and density of innovations and concomitant ratcheting shifts in the pace and content of cultural and behavioral change and complexity, resulting in new and more effective ways of engaging and changing local ecologies (Kendal et al. 2011; Sterelny 2012; Tomasello 1999, 2014; Whiten and Erdal 2012).

A central aspect of this human sociocognitive niche is an increasingly dynamic feedback and interdependence among ecological, cognitive, and neural processes (Iriki and Taoka 2012). Humans use material tools, such as modified stone and wood, to extend our motor capabilities, enhancing our ability to interact with and modify our ecologies. Humans also use "sensory tools" to extend or externalize our existing sensory organs, enhancing our sight or hearing beyond the immediate somatic potential of our eyes and ears. We also use "symbolic tools" in much the same way, externalizing and sharing memories, placing symbolic meanings on the landscape, and imbuing material items with social meaning. These capabilities arose at some point during the last two million years (Coward and Gamble 2008; Grove and Coward 2008). It is likely that increases in brain size–neural connectivity and cognitive complexity, the extended childhood period, enhanced communication capabilities, and the plasticity of brain development set a niche-constructive context via feedback systems among neurobiology, innovation, instruction–learning, and increased and diversified "tool" use in our genus (Iriki and Taoka 2012; Stout and Chaminade 2012).

By at least 80 thousand years ago, the fossil and material record indicates that humans have a full-blown complex of behavioral–cultural adaptations involving our distinctive sociocognitive niche and a cumulative and ratcheting culture likely affecting neural architecture. The processes by which this emerges are strong candidates for the integration I am proposing.

A VERY BRIEF ILLUSTRATION: LEARNING AND SEMIOSIS IN EARLY TOOL MAKING

> The origin and operation of symbolically rich, complexly signaling human social systems was the consequence of the long-term evolution of multiple components of perceiving and negotiating social interactions, a contingent outcome of myriad adaptive shifts rather than a single event.
>
> –Kim Sterelny and Peter Hiscock, "Symbols, Signals, and the Archaeological Record" [2014:3]

Thinking about tools and tool making during the Pleistocene is a cornerstone of human evolutionary studies. But it also

provides a good example of why an integrated anthropology combined with a niche-construction approach can be beneficial. After all, "stone tools were material symbols long before the ochre and jewelry of behavioral modernity" (Sterelny and Hiscock 2014:2).

Hiscock (2014:27) notes that "most discussions of the role of lithic artifacts in the human niche treat these objects principally or exclusively as tools, and hence the role of lithic production is typically limited to the context of tool use, with little regard for the context of production." He argues that the early hominin niche of lithic production involved the development of highly scaffolded learning environment(s) that had substantive social, material, and ecological feedback loops that facilitated the creation and transmission of increasingly complex stone-manipulation processes. It is this context of production (social, material, and ecological) and the niche-constructive feedback relationships at multiple levels that constitute a core early component of the human niche, and examining such a system is best tackled via an integrated anthropological approach (see also Morgan et al. 2015).

The social anthropologist Eduardo Kohn (2013), following the biological anthropologist Terrance Deacon (1997), suggests that we should understand the human niche as a world that is permeated and constituted by semiosis (the creation and interpretation of signs). Given what we know, and assume, about the fossil record of our genus and the role of human cognition and behavior in our evolution, it is clear that learning and teaching are central facets in the evolution of the genus *Homo*. These arenas—semiosis, teaching, and learning—are exemplary foci for integrating elements of the neurological, behavioral, morphological, archaeological, ecological, material, and ethnographic in a human niche approach. I sketch an outline of this here.

Based on years of ethnography and engagement with Pierceian philosophy, and via the work of Deacon (1997), Kohn (2013) lays out a scenario wherein many species, not just humans, are navigating and co-creating semiotic niches. For other animals, indexical signs (correlated with or otherwise affected by what they represent, e.g., dark clouds indicating rain) and iconic signs (sharing a likeness with what they represent, e.g., a macaque monkey's open-mouth threat and an aggressive bite) permeate the world, and as humans, we add symbolic signs. For us, the emergent properties of symbolic representation enable a system wherein symbols can maintain stability and meaning even in the absence of their objects of reference. A key to understanding the human is to recognize that our symbolic mode of existence is emergent. That is to say, it arises from the interactions of many elements (bodies, brains, senses, perceptions, experiences, etc.), but none of these have in themselves the specific property of symbolic experience: it emerges from the interrelationships of these components (e.g., Deacon 1997; Kohn 2013).

One way to access this process in the evolutionary record is though the material remains of items constructed and used by past humans. It is likely that neural mechanisms—particularly bimodal, canonical, and mirror neurons and the late mylenation (the insulation of neural connections) of fundamental brain areas associated with symbol and language—are involved in the physical, sensory, and symbolic actions of making material items ("tools" of stone, bone, and wood; Gallese and Lakoff 2005). It is possible that material, neurological, and social processes interacted with other developmental and learning mechanisms as aspects in the niche-construction process in the genus *Homo* from the point of early tool use over two million years ago though to the development of the complex social contexts of today (Downey and Lende 2012; Grove and Coward 2008; Hiscock 2014; Stout and Chaminade 2012).

Innovation in, and accumulation of, material culture is a central component of the human niche as it is evidenced in the archaeological record. To construct, participate in, and be shaped by such a niche involves the following: the interaction between creation and use of material items (physically functional or symbolically functional); the interface between individuals with, and without, particular skillsets; and an ability to convey shared meaning and implication. This process involves feedback between visual and manual neurological systems (hands, eyes, cognition), in addition to social communication (gestural, vocal) and the sharing of knowledge and perceptions (using indexical, iconic, and symbolic signs). It requires an intensity and range of information transfer that is rare, if present at all, in other organisms, even earlier hominins and other primates (or other tool-using animals) (Boyd et al. 2011; Grove and Coward 2008; Iriki and Taoka 2012; Morgan et al. 2015; Stout and Chaminade 2012).

While some crows use rocks and chimpanzees use hammer stones (and can be taught by humans to create flakes), making even simple stone tools, using them for various purposes, and learning to repeat the process requires a particular processing and transmission of information, a pattern that appears to be common only among humans (and those on our lineage) (Sterelny and Hiscock 2014; Stout 2012). From at least the latest Olduwan and earliest Acheulean toolkits (processes that emerge circa 1.5–1.75 million years ago) onward, acquisition and reliable replication of a given tool requires understanding the final shape and use of an item that is not clearly indicated by its current form, observation of skilled tool makers, access to full and partial templates, and some form of complex information transfer (Hiscock 2014; Sterelny 2012, 2014; Stout and Chaminade 2012). Stout (2012) and Naama Goren-Inbar (2012) note that there is a need to develop a synthesis in our understanding of technical abilities, social structure, and subsistence strategies as we try to model our ancestors' individual capacities for hierarchical information processing as well as the social mechanisms of skill acquisition.

Kim Sterelny (2012) proposes a particular mode of learning, the apprentice model, as an element of a distinctively human niche that develops during approximately the past 1.5 million years. In the apprentice process, central social and material skills are acquired by combining information from the social world and the material world. Early humans learned by doing in an environment seeded with

informational resources (indexical, iconic, and eventually symbolic) without what we would term explicit instruction and without formalized institutions (e.g., a tool-making guild). In this model, incremental construction, emulation, and passive and active information transfer occurred in the context of a highly social, cooperative community of cognitively complex early humans who were capable of shared intentionality (Sterelny 2012, 2014; Tomasello 2014). Members of the genus *Homo* integrated diverse semiotic elements in their collaborative efforts to interact with, and modify, their local physical and social ecologies, which in turn altered those ecologies and created new potential for evolutionary dynamics: this is niche construction. Such a system, although not formal instruction, results in relatively high-fidelity replication of the target material culture (as evidenced by the increasing presence and spread of material "tool" types across the Pleistocene). This element in the human niche involves feedback systems at individual, group, and community levels; it left a pattern in the archaeological record; and it affected the social landscape and neurobiology of the genus *Homo* (Hiscock 2014; Morgan et al. 2015; Stout and Chaminade 2012).

This description of a system of interactive patterned transmission of skill via learning, doing, and constructing shared meaning seems particularly applicable to what we know about the middle and later Pleistocene *Homo* tool-making record (Grove and Coward 2008; Morgan et al. 2015; Pradhan et al. 2012; Shultz et al. 2012; Sterelny 2012; Stout 2011; Stout and Chaminade 2012). Such a system is also amenable to enhanced understanding via what social anthropologists such as Tim Ingold (2000) describe as a core human process: enskillment. In fact, in developing the apprentice-learning model, Sterelny (a philosopher of biology) integrated evolutionary theory, paleoanthropological and archaeological evidence, ethnographic examples of apprentice-style skill acquisition, and a broad understanding of the processes and limitations of tool making in other animals. Adding approaches that include the perceptual–experiential context of semiosis promoted by Kohn and Deacon and the cultural and experiential elements of enskillment as developed by Ingold expands our description, and interpretation, of the core elements at play acting to both shape and be shaped by dynamic niches in earlier humans.

The archaeological record is becoming denser with specific examples of entire stone tool-making events (dating back to more than two million years ago), enabling reverse reconstruction of the flaking trajectories and the shape and pattern of the creation of the tool (e.g., Delagnes and Roche 2005). This enables us to think of an "ecology of materials that focuses on [the materials'] enrollment in form-making processes" (Ingold 2012:427). This enables us to assess elements of cognitive, experiential, and semiotic complexity in earlier *Homo's* imagining of the end products of tool manufacture and the social dynamic of communication involved in this highly cooperative, social, interactive, and hands-on niche-construction process (Hiscock 2014; Nonaka et al. 2010; Sterelny 2012). We can extend our understanding of this early tool making by integrating insights on process and patterns from ethnographies of apprentice learning, theoretical approaches via the concepts of enskillment and embodiment, and a focus on the interface of the semiotic, the biological (neurological), and the paleoanthropological (see Gallese and Lakoff 2005; Iriki and Taoka 2012; Lave 2011; Lende and Downey 2012; Morgan et al. 2015).

MOVING FORWARD

Antón and Snodgrass (2012) stress the role of positive feedback on *Homo* life history, noting that multisystem evaluations of the behavior, physiology, and anatomy are necessary. Fiona Coward and Clive Gamble (2008:1971) tell us that finding the core patterns in human evolution means realizing that they are "underpinned by changing social relationships between hominins—and, crucially, between hominins and the material world—building on a basic hominid cognitive repertoire expanded during hominin evolution through the spinning of networks of social relationships that link us over increasing distances through space and time." Greg Downey and Daniel Lende (2012) remind us that humans exist in a cultural niche that is simultaneously selection pressure and adaptive response, and Richard Potts (2012) demonstrates that ecological adaptability and physiological plasticity alongside behavioral complexity (situated on an ever-changing, and at times quickly changing, environmental landscape) played a central role in the evolution of Pleistocene *Homo*.

Using the concept of the human niche(s) and thinking about the dynamics of human communities across our evolutionary history in the context of the extended evolutionary synthesis force us to prioritize the integration of individuals, materials, social networks, communities, and local ecologies. This enables a kind of anthropology in which attention is paid to the dynamic feedback loops between ecological innovation, social complexity, symbols and interpretation, and cultural transmission. Such an approach forces us to incorporate the material with the cognitive and the behavioral with the morphological as key elements in evolutionary processes. To do this well requires drawing insights from ethnography, broader sociocultural theory, and the extended evolutionary synthesis, alongside the traditional approaches in paleoanthropology, archaeology, and human evolutionary studies.

Obviously, a primary focus for any investigation into human evolution must reside in the archaeological and paleoanthropological datasets. But given what we now know about human bodies, minds, experiences, and landscapes, we should recognize that we need models for human evolution that explicitly interlace diverse anthropological and evolutionary perspectives to best address the puzzles we encounter. Interaction and mutual engagement across multiple anthropologies and contemporary evolutionary perspectives, especially niche construction, can get us closer to better answers.

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NOTES

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