The Extended Evolutionary Synthesis, Ethnography, and the Human Niche

Toward an Integrated Anthropology

by Agustin Fuentes

Seeing bodies and evolutionary histories as quantifiable features that can be measured separately from the human cultural experience is an erroneous approach. Seeing cultural perceptions and the human experience as disentangled from biological form and function and evolutionary history is equally misguided. An integrative anthropology moves past dichotomous perspectives and seeks to entangle the "inside" and "outside," methodologically and theoretically, to move beyond isolationist trends in understanding the human. In this paper I illustrate the underlying rationale for some anthropological lack of engagement with neo-Darwinian approaches and review contemporary evolutionary theory discussing how, in combination with a dynamic approach to human culture, it can facilitate integration in anthropology. Finally, I offer an overview of the human niche concept and propose a heuristic framework as a set of shared assumptions about human systems to help frame a sincerely anthropological and emphatically evolutionary approach to the human experience.

Providing Context

Despite recent movement reflecting cross-fertilization in the core areas of ethnography and evolutionary approaches (e.g., Andersson, Törnberg, and Törnberg 2014; Barnard 2012; Downey and Lende 2012; Hewlett and Lamb 2005; Ingold and Paalson 2013; Trevathan, Smith, and McKenna 2008; Wiessner 2014), the divisions that plague anthropology remain substantial. For anthropology to be most successful in its stated endeavor, the study of the human (writ large), we need a reintegration of diverse methodological and theoretical tool kits. Neither everyone working in anthropology nor all anthropological questions require such an integrated tool kit. However, the field on the whole severely needs such approaches as part of its normative practice if we are to be able to honestly assert that we are indeed different from other social sciences, to provide better and more holistic options than the biological sciences, and to live up to our ideals of equally valuing the humanistic and the scientific in the understanding of human being and becoming (e.g., Peregrine et al. 2012; Wolf 1964).

Key areas contributing to the lack of reintegration are the ways in which evolutionary and social anthropological approaches are conceptualized as antagonists and how this is applied in professional practice and the training of graduate students. Core elements facilitating this standoff are the ways in which evolutionary processes are (mis)understood by many sociocultural anthropologists as incompatible with humanistic and ethnographic approaches (e.g., Segal and Yanagisako 2005) and the (over)simplification of complex dynamic human systems by many evolutionary anthropologists as they attempt to fit their analyses of the human into neo-Darwinian models (e.g., Kaplan et al. 2000).

Many anthropologists underplay or ignore the fact that evolutionary processes are ongoing in human populations. This practice is due in part to the lack of easy fit between the kinds of data that emerge from deep ethnographic study and basal assumptions about evolutionary approaches (Schultz 2009) and a lack of actual familiarity with contemporary (post-1980s) evolutionary theory on the part of many anthropologists. However, there is validity to the assertion that in "evolutionary" approaches over the past 40 years, it is common to see, for practical reasons, a prioritization of a trait-based natural selection and the use of cost-benefit analyses in explaining human behavioral action (e.g., Alexander 1987; see also Smith 2000). For many social anthropologists there are simply too many reductive assumptions in such an approach relative to the observable complexity in human systems (Ingold 2007; Schultz 2009).

To get beyond this sticking point and move to a better anthropology, we need to dismantle the conceptualization of the biological and social as distinct domains in the human and see them as intertwined processes that are not wholly separable in our models and analyses. We need to adopt an integrative approach that has as its basal assumption a system of entangled

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agents and processes involved in the human experience (Ingold and Paalson 2013; Marks 2012, 2015; Schultz 2009).

Much of what I suggest in this paper is already extant in anthropological practice (Downey and Lende 2012; Goodman and Leatherman 1998; Hewlett and Lamb 2005; Ingold and Paalson 2013; Lipatov, Brown, and Feldman 2011; Wiessner 2014, and others). However, there is no standard theoretical tool kit for such endeavors, and the bulk of anthropological practitioners are not truly up to date with contemporary evolutionary theory (e.g., extended evolutionary synthesis [EES]; Laland et al. 2015). My goal in this essay is to contribute to the ongoing reintegration of ethnographic and evolutionary approaches in anthropology by blending the inside and outside views via fostering an enhanced engagement with contemporary evolutionary theory.

I will do this by first illustrating an underlying rationale for some anthropological lack of engagement with neo-Darwinian approaches. I will then review contemporary evolutionary theory and discuss how, in combination with a dynamic approach to human culture, it can facilitate integration. Finally, I offer an overview of the human niche concept and propose a heuristic framework as a set of shared assumptions about human systems to help frame a sincerely anthropological and emphatically evolutionary approach to the human experience.

Beyond Traditional Neo-Darwinian Assumptions

In any evolutionary analyses, organism-environment interactions are a central concern, and understanding the context in which natural selection and other evolutionary processes act is key to developing insight. However, many neo-Darwinian approaches assume that the individual and its relationship to the environment (assessed ultimately via genetic fitness tradeoffs)[1] is the most salient feature of a system (e.g., Hawkes et al. 1998; see Smith 2000). Even when there is explicit acknowledgment of a key role for social groups and institutions, the basal assumption is that evolutionarily relevant processes ultimately result from the competition for reproductive success between individuals (as mediated by their environment and social groups; e.g., Glowacki and Wrangham 2015; Macfarlan et al. 2014). This creates a theoretical context wherein the individual and its fitness-based relationship to a given (social/ecological) environment is the basal heuristic framework for evolutionary models. Or, in a minority of cases when group-level selection is introduced, the common tactic is to model groups as units (i.e., individuals) in competition with one another as affecting the reproductive success of the individual members constituting the competing groups (Choi and Bowles 2007).

In these approaches evolutionary pressures are modeled as potential effects on reproductive output, challenges to individuals' energy budgets (and associated health risks), and the variation in future potential fitness via individuals' actions in relation to other individuals and local environmental contexts (Smith 2000). Such approaches have provided significant contributions for the construction of models and theory (e.g., Flinn et al. 2007; Kaplan et al. 2000), but they remain incomplete. Evolutionary theory has come to a point that mandates a move away from focusing exclusively on natural selection, genetic-based fitness, and their relationships to individuals to a systems approach in analyses of evolutionary histories and processes (Bateson and Gluckman 2011; Hinde 1976; Laland et al. 2015; Lewontin 1983; Oyama, Griffiths, and Gray. 2001; Sterelny 2012).

Humans construct ecological, technical, and cultural niches that influence the structure of evolutionary landscapes.[2] Manipulation of plants and animals, developing tools and machines, construction of dwellings and alteration of landscapes, religious, legal, and familial institutions all affect the contexts and options available to humans (individually and communally) in regard to interactions with evolutionary processes: these structure and channel the strategies of human actors. Given the centrality of entangled physiological, social, semiotic, cognitive, historical, and institutional processes in the human niche, evolutionary approaches need to be better integrated with a broader anthropological context in order to best facilitate greater understanding of humans (Downey and Lende 2012; Goodman and Leatherman 1998; Ingold and Paalson 2013).

A core challenge to this integration is the development of a heuristic that includes an evolutionary framework that engages with cultural systems and processes including institutions and recognizes the fluid and entangled interfaces between individuals, groups, and community-level dynamics. To do this we need to take both biology and history into account. Instead of thinking of human biological and social processes as distinct, we need to see them as intertwined and integrated (and at multiple levels; Fausto-Sterling 2000; Marks 2015; Read 2012). This can be accomplished by integrating perspectives from contemporary evolutionary theory along with approaches in social anthropology. By doing so we can better equip ourselves to examine the patterns and processes that facilitated such complex creatures (us) who evolve(d) in mutually malleable relationships with their ecologies and each other and continue to do so at a rapid pace.

1. Here "fitness" is assumed to be lifetime reproductive output, or simply the number of times one gets one's genetic makeup successfully into the next generation. Even though many nongenetic elements can be used as proxies, the standard neo-Darwinian assumption is that the evolutionarily relevant inheritance unit is that of genetic material, so neo-Darwinian fitness equals the number of times an individual's DNA sequences are transmitted into subsequent generations relative to other individuals of the same species in the same population.

2. I am using the term "niche" in the contemporary ecological and evolutionary view: it is the dynamic *N*-dimensional space in which an organism exists—the totality of the biotic and abiotic factors that make up an organism's main context for the evolutionary dynamic (the interaction between organisms and evolutionary forces; e.g., Hutchinson 1957; Wake, Hadley, and Ackerly 2009).

Engaging the EES

"Organisms are constructed in development, not simply 'programmed' to develop by genes. Living things do not evolve to fit into preexisting environments, but co-construct and coevolve with their environments, in the process changing the structure of ecosystems" (Laland et al. 2014:162). Natural selection, a key process by which biological variants achieve differential representation in subsequent generations, is not the only salient evolutionary process. A neo-Darwinian theoretical orientation that places primacy on natural selection as the primary architect of evolutionary function inhibits enhanced integration (Andersson, Törnberg, and Törnberg 2014; Laland et al. 2014). Evolution is a synergy of multiple processes, and EES stresses that a range of drivers, including ones that cannot be reduced to genic levels, are relevant. Laland and colleagues (Laland et al. 2014:1) argue that "the 'extended evolutionary synthesis' (EES), retains the fundaments of evolutionary theory, but differs in its emphasis on the role of constructive processes in development and evolution, and reciprocal portrayals of causation. In the EES, developmental processes, operating through developmental bias, multiple modes of inheritance and niche construction, share responsibility for the direction and rate of evolution, the origin of character variation and organism-environment complementarity."

Our basic understanding of how biological evolution works in the early twenty-first century is as follows. Mutation introduces genetic variation that in interaction with epigenetic and developmental processes produces biological variation in organisms that may be passed from generation to generation. Natural selection is the shaping of this variation in response to specific constraints and pressures in the environment (sensu lato), and gene flow and genetic drift also contribute to changes (or lack thereof) in the topography of the landscape of variation from generation to generation. However, dynamic organism-environment interactions can result in niche construction that can change the patterns, foci, and intensity of natural selection and create modified ecologies that are inherited by subsequent generations. Niche construction is an organism(s)-environment relationship that is dynamic, bidirectional, and mutually malleable. Organisms responding to the ecological pressures on them can restructure the local ecology affecting the very patterns of pressures on them, creating suites of dynamic feedback relationships in evolutionary processes.[3]

Niche construction plays a key role in human evolutionary processes via our ability to modify our surroundings through behavioral means (e.g., O'Brien and Laland 2012). Laland, Kendall, and Brown (2007) suggest that niche construction theory (NCT) is especially important in the context of the dynamics of human cultural processes because NCT envisions the effects of cultural contexts and actions as a key part of the human niche. For humans, constructing and inheriting ecological contexts is often mediated via material culture (tools, clothes, buildings, towns, etc.), and the actions involved in developing and utilizing this material culture are rooted in the beliefs, institutions, histories, and practices of human groups. Human cultural processes can play central roles in niche construction and are thus active components in an evolutionary dynamic (Kendal 2012; Olding-Smee et al. 2003; Read 2012; Tooby and DeVore 1987).

O'Brien and Laland (2012) use the classic biological anthropological examples of dairying by Neolithic groups in Europe and Africa and the rise of the "sickle-cell allele" among certain agricultural groups in West Africa as concrete examples of niche construction processes in the evolutionarily recent past through today. They describe the shifting behavioral actions, cultural perceptions, and ecological conditions that mutually interacted to produce genetic and physiological changes that themselves resulted in further modification of behavior, physiology, and ecologies. For the example of the sickle-cell/malaria scenario, O'Brien and Laland (2012) illustrate that a by-product of human social-ecological patterns (crop planting) promotes the spread of malaria, which leads to selection for the sickle-cell allele and an increased incidence of sickle-cell disease. This, in some contexts, favors shifting the agricultural practice toward the planting of yams and other crops with medicinal benefits, which also enables further spread of the sickling allele. This eventually facilitates the development of medical treatments (social and physiological) for malaria and more recently pesticide treatments for mosquitoes, which then creates selection for resistance to pesticides in mosquitoes. And today this entanglement continues affecting bodies (not just human bodies), behavior, and institutions.

Historical and current social schemata and behavioral actions can affect genetic and other biological patterns and the process of natural selection, which in turn can affect developmental outcomes (e.g., Henrich 2011; Richerson and Boyd 2005), which can then feed back into the cultural processes and behavioral actions continuing the dynamic interface. The use of the examples of sickle-cell and dairying/lactase retention are not new to anthropological explanations of human evolution, but the application of NCT to the examples moves us away from seeing natural selection constructing evolutionary changes in a directional, and necessarily reductionist, manner to describing multifarious feedback webs and dynamic systems of mutual interface and malleability. Evolutionary change is neither unidirectional nor unimodal; natural selection is not the sole causal agent of relevant change or the sole architect of function. Even the patterns of inheritance that underlie natural selection—the transmission of variation across generations—are dynamic.

Jablonka and Lamb (2005) demonstrate that evolutionarily relevant information, the variation that is the fuel for evolu-

3. See http://lalandlab.st-andrews.ac.uk/ and Odling-Smee, Laland, and Feldman (2003) for basic overviews, O'Brien and Laland (2012) for applications to classic biological anthropological scenarios, and Fuentes, Wyczalkowski, and MacKinnon (2010) for integrations between basic population growth equations and the niche-construction equation applied to human evolutionary scenarios.

tionary change, is transferred from one generation to the next by many interacting inheritance systems: genetic, epigenetic, behavioral, and symbolic (see also Bonduriansky and Day 2009; Ledón-Rettig, Richards, and Martin 2012). Genetic inheritance, the system of primary interest for neo-Darwinian approaches, is the transmission of genetic material (including both DNA and various RNAs) from generation to generation. Epigenetic inheritance (EpgI) is the inheritance of molecular processes, enzymatic actions, protein activity, and/or developmental sequences that affect developmental and/or physiological processes but do not emerge as a result of causal action of specific DNA/RNA systems. EpgI gives rise to morphological, structural, and functional variations at multiple levels in the organism that do not stem from variations in DNA but are still transmitted to subsequent generations of organisms (Jablonka and Raz 2009; Lock 2015).

Behavioral inheritance involves the behavioral actions, patterns, or particulars that are transmitted horizontally (within generations) and vertically (across generations), and it is found in many organisms, with increasing presence and importance in highly social vertebrates. The fourth form of inheritance, symbolic inheritance (SI), is likely only found in humans. SI is the cross-generational acquisition of symbolic concepts, ideologies, and perceptions. This mode of inheritance can have substantive influence on human action, agency, and perception, feeding back into and shaping the other types of inheritance (Andersson, Törnberg, and Törnberg 2014; Kendall 2012; Read 2012). Jablonka and Lamb (2005) also remind us that variation is constructed. Whatever the origin of a variant (genetic, epigenetic, behavioral, or symbolic), the variants that are actually inherited and what final forms they assume depend on various filtering and editing processes that occur before and during transmission at all levels (see also Laland et al. 2014).

Related to the expansion in types and processes of evolutionarily relevant inheritance is the recognition that plasticity in development and behavior is widespread in organisms (West-Eberhardt 2003). Humans displayed substantial plasticity in behavior and physiology in response to evolutionary pressures across our evolutionary history (Aiello and Anton 2012; Kuzawa and Bragg 2012; Potts 2012; Wells 2012). This variation has increased in contemporary contexts (Marks 1995). From early in our history as a species (and genus), there is increasing evidence that morphological and physiological plasticity is accompanied, and even superseded, by behavioral and cognitive flexibility in response to ecological and social challenges (Andersson, Törnberg, and Törnberg 2014; Anton, Potts, and Aiello 2014; Fuentes 2015). It is likely that behavioral/cognitive plasticity facilitated the development of our modern capacity for extensive shared intentionality, metacoordination, and language, and this proclivity for cultural complexity is increasingly invoked as a key to evolutionary explanations of human behavior (Henrich 2011; Kendal, Tehrani, and Olding-Smee 2011; Marks 2015; Richerson and Boyd 2005; Sterelny 2012; Tomasello 2014).

"Cultural Complexity" and the Human Niche Approach

As Margaret Lock (2015) notes, "individual bodies are not mere containers stuffed with biological entities that age and die over a lifetime; rather, they are products of human evolution; the longue durée of history; environments expansive and local; the communities that people live in; the diets they eat; the toxins, insults, and abuses they are exposed to; and the good times too" (171–172).

The human capacity for and expression of culture,[4] however one defines it,[5] is a key element in the human niche, and in the context of EES, it is thus central to evolutionary processes in humans (Andersson, Törnberg, and Törnberg 2014; Deacon 2011; Dean et al. 2012; Read 2012). I expect that most anthropologists (if not all) agree with this assertion. However, this agreement rarely results in serious efforts to link the human cultural experience in all its complexity and dynamism to evolutionary models. Why is that? The lack of linkage is probably due to (*a*) the immense complexity of human systems, which makes them difficult to fit onto existing evolutionary models based on an individual-fitness-focused natural selection paradigm, and (*b*) the lack of concordance between the experiences and insights of ethnographers and many neo-Darwinian explanations for human action.

I have published elsewhere (Fuentes 2015) that if we are to take human cultural processes, in all their complexity, as part of our evolutionary approaches, we cannot treat them as a social, material, historical, and perceptual veneer laid over a basal set of physiological capabilities. In human evolution the biological and social cannot be seen as distinct entities (Marks 2015). Nor can we assume "culture" operates in an equivalent nature to the "genome" in regard to natural selection process (Charney 2012; Claidière, Scott-Phillips, and Sperber 2014). Human relationships to evolutionary processes cannot solely be understood via patterns of genetic or cultural fitness costs and benefits (regardless of the proxy or actual fitness measure used) constrained and afforded by behavior, material technologies, socioeconomic and behavioral contexts, and ecologies.

The webs of action and perception, memory and history, items and ideas that humans are entangled in is a dynamic

4. I am avoiding the "do animals have culture" debates here. Yes, there are substantial commonalities and shared patterns between humans and other animals, and many mammals (and birds) have social traditions and regional variants in their behavior and vary even in their perceptions of the environment. However, that particular assemblage of traits that characterize all human societies—language, institutions, moral codes, symbolic and existential belief processes, etc.—is a discontinuity with other forms of life and thus relatively distinctive of our species.

5. Anthropologists have been debating a specific definition for the entire history of our field (e.g., Kroeber and Kluckhon 1952). Here I use the term as shorthand for what anthropologists often study: the observable, inferable, or otherwise assessable ways in which humans engage with, perceive, construct, and generally participate in the world.

and fundamental constituent of a human niche that is simultaneously constructed by and constructing of this human experience and is thus highly evolutionarily relevant. This is not a novel concept; it is a central theme in any attempt at an integrated anthropology (see Andersson, Törnberg, and Törnberg 2014; Dean et al. 2012; Downey and Lende 2012; Fuentes 2009*a*, 2009*b*, 2015; Geertz 1973; Kendall 2012; Read 2012; Richerson et al. 2016), and it needs to be embedded as a basal component in evolutionary approaches to the human.

Taking the EES outlined above and the last century of ethnographic studies seriously mandates that we cannot see human "culture" as just a cluster of measurable traits or culture units/variants. Human cultures are more than perceptions, beliefs, and behaviors—they are also rules, organizations, and so forth, with concrete structures and specified consequences. Cultural systems are interlaced with patterns of social constraint and facilitation, and this is potentially an evolutionary force. A contemporary evolutionary approach has to treat what humans do and experience as a complex system that has specific histories, has inherited ecologies and institutions, and includes a myriad of categories of action and perception as they relate to the interactions between individuals, groups, and the communities in which they exist.

For example, a cultural element of "honor" (often used in gene-culture coevolution scenarios; see Cohen et al. 1996; Richerson and Boyd 2005) has particular histories, symbolic referents, experiential contexts and alterations, and may have varying implications and effects at the individual, group, and community levels. If we are interested in the institutions, processes, and behaviors related to "honor," we need a system that includes at least these aforementioned processes and variables. These varying implications and interpretations of the concept of "honor" (because it is a concept and not a discrete trait) can play out in different manners in regard to the way it is perceived and embodied and the potential actions it facilitates and influences. These actions might have different, even conflicting, effects on niche-constructive elements and thus evolutionary landscapes at the level of the individual, group, and community. We need to place all of these patterns into an interactive system and accept the complex problems that causes in establishing the origin, function, and role(s) of such cultural elements and practices. It may be that practices have clear functional effects at one level and either none or contradictory ones at other levels.[6] This kind of dynamism has to be taken into account if we are to create comprehensive and more accurate descriptions of evolutionary processes in humans (Claidière, Scott-Phillips, and Sperber 2014).

In developing an integrated framework for thinking about evolutionary processes in humans, we need to break down the assumptions about boundaries between physiology/morphology, biological development, behavior, perception and embodiment, cultural institutions and history, social experience, and symbolic life. We need to focus on the myriad processes that constitute the moving target that is human existence rather than on the state of being human or of having become human in any one isolated context or manner. Doing this requires some way to, at least conceptually, integrate neurological, behavioral, morphological, ecological, material, and ethnographic elements at multiple levels.

Toward an Integrated Conceptual Framework

Both theoretical and practical research strongly suggests that we need to develop a framework that includes substantive feedback components involving behavioral, cognitive, material, and ecological components when trying to conceptualize the patterns and processes of human evolution from at least the mid-Pleistocene though today (Aiello and Anton 2012; Andersson et al. 2014; Anton, Potts, and Aiello 2014; Coward and Gamble 2008; Coward and Grove 2011; Kendall 2012; Kuhn and Hovers 2013; Sterelny 2014; Tomasello 2014; Whiten and Erdal 2012). It is also increasingly accepted (at least theoretically) that multilevel selection is an actual pattern in evolutionary processes (Laland and Brown 2011; Laland et al. 2014; Wilson and Wilson 2007).[7] Thus, any basal framework should include the possibilities of evolutionary processes influencing the individual, the group, and even the regional population in similar or different ways and intensities (Andersson, Törnberg, and Törnberg 2014; Richerson et al. 2016; Smaldino 2014; Wilson and Wilson 2007). Therefore, contemporary evolutionary approaches to examining human variation and behavior should be increasingly interested in the role of kinship, economic, religious, and political groups and institutions as they construct and influence the social and perceptual processes and contexts that structure the patterns and strategies for human action.

Despite the emerging trends toward complex systems as core in evolutionary analyses, it remains common for evolutionary approaches to focus on the interconnection between a few specific traits and their interactions with one another. For example, in many evolutionary approaches to contemporary foragers and small-scale societies, it is common to examine the relationship between caloric energy balance, foraging patterns, and the distribution of foraged and hunted goods or to examine marriage patterns, reproductive cycling, and one or two markers of socioeconomic status. These assessments are often undertaken in the context of the traditional neo-Darwinian framework, which mandates connecting these elements to a model wherein the basal explanation for the patterns being observed is derived via the potential effects on individual fitness (e.g., Hawkes et al.

6. Here, as in most evolutionary approaches, "functional" implies that there are evolutionarily relevant outcomes from the focus of interest (the concept of "honor" and all that it entails in this example).

7. Natural selection, as a process, can be modeled as functioning at the genetic, individual, and group levels.

1998; McFarlan et al. 2014; Tooby and DeVore 1987). This can lead to insightful but highly incomplete explanations.

A more anthropological framework would enable the inclusion of some of the key social, historical, perceptual, and institutional variables in which these elements of focus are entangled as a relevant part of the system producing the outcomes, not simply as emergent from or irrelevant to the underlying patterns driven by natural selection (see Atran 2016; Bird et al. 2016; Downey 2016; Gettler 2016; Lipatov, Brown, and Feldman 2011; Wiessner 2016).

If we take this approach seriously, then the range of evolutionary processes in the EES become valuable tools as an expansion on the traditional neo-Darwinian individual fitness framework (Fuentes 2015; Kendall 2012; O'Brien and Laland 2012). The inclusion of multiple modes of inheritance (Boyd, Richerson, and Henrich 2011; Jablonka and Lamb 2005) and the possibilities of significant plasticity in response as process itself (Kuzawa and Bragg 2012; Wells and Stock 2007; West-Eberhardt 2003) become necessary. Trying to include such a diverse suite of inputs, interfaces, and feedback cycles, while potentially quite "messy," enables a more dynamic role for a broader interpretation of cultural behavior and perception: cultural processes (and institutions) must also be part of such a system (Henrich 2011; Kendal 2012; Read 2012).

The Human Niche

Drawing on Anderrson et al. (2014), Deacon (2011), Donald (1993), Flynn et al. (2013), Laland, Kendall, and Brown (2007, 2015), Marks (2012, 2015), Smaldino (2014), Sterelny (2012), Trevathen, Smith and McKenna (2008), Worthman (2010), my previous work (Fuentes 2009*a*, 2009*b*, 2014, 2015), and others, I propose a heuristic framework for what the human niche looks like as a way to help integrate evolutionary and anthropological approaches. The primary goal here is to provide a starting point that is more representative of human evolutionary systems than those assumed in most standard neo-Darwinian models.

This framework emphasizes the roles of mutual mutability between agents, collective action, social perceptions, and the roles of experiences and institutions in structuring human behavior as well as encompassing what we know about evolutionary processes (via EES). In envisioning such a context, I acknowledge the influence of Bourdieu's (1977, 1990) conceptualizations of habitus and the framing of "structured structures predisposed to function as structuring structures" (Bourdieu 1990:53; see also Fuentes 2009*a*, 2009*b*; Kendal 2012). However, the challenge in developing such a framework is that it has to be reductive enough to meet basal needs of evolutionary approaches (there must be quantifiable elements and predictable outcomes/patterns) but not so reductive that it can only engage with human cultural and cognitive complexity through the lens of individual fitness and natural selection.

"The selection of units for any particular analysis is, of course, only in part a function of the theory that informs it. It is also a function of the problem at hand, in both its details and its magnitude" (Rappaport 1984:371). The human niche framework I propose consists of three components (or nodes) that interface with evolutionary processes and that have mutual influence on one another: the individual, the group, and the community. These are "units" in the sense proposed by Rappaport (1984), designations useful for the purpose of this heuristic framework, and I direct the reader to his discussion of units and their implications for a robust explanation of this approach.[8] I fully acknowledge that the definition of a human individual (or person) is a multifarious, dynamic, cross-culturally complex, and often contentious topic (e.g., Strathern 1988). However, in the heuristic I am proposing, the "individual" component is literally a single human. In the same vein, the "group" component is explicitly the main social unit for that single human as defined by the questions being asked (extended family, peer group, primary social interactors, etc.). The "group" then is the collection of individuals that form the core social network for the individual in the system of interest. This usage reductively bypasses complexities in definitions of "self" and "individual" for practical modeling reasons, but because what constitutes the "group" is defined by what questions are being asked of the system, it highlights the critical need for ethnographic and/or sociohistorical baselines at the start of any evolutionary modeling.

The component "community" deserves a bit more clarification. Drawing on evolutionary approaches in Rodseth et al. (1991), Gamble, Gowlett, and Dunbar (2011), and Smaldino (2014; see also Deane-Drummond and Fuentes 2014; Fuentes 2014, 2015), I define "community" for the purposes proposed here as the spatial and social context that includes the majority of social partners and the primary settings and ecologies with/in which an individual interacts. It is a collection of individuals/groups with shared "kinship" and social and ecological histories, which is the primary source of shared knowledge, security, and development across an individual's life span. The community has fluid boundaries and multiple possible subgroupings across space and time, but all members share cognitive, social, and ecological bonds even in the absence of close spatial proximity. It is within the context of this "community" that humans interface, interact with, modify, and are modified by social and ecological worlds during the course of our evolution and through today. The community is more than the local group and may range from a small extended network of affiliated groups to a much larger regional entity dependent on the system of interest and the questions being asked (see Richerson et al. 2016; Smaldino 2014).

Each core component in the human niche has its own evolutionarily relevant internal feedback processes. Within the individual, this feedback is across the life span between morphology, development, and behavior. For the social group, it is the feedback created by social relationships between members

8. Also found in sec. 10 of the second edition.

of the group, sexual interactions, and behaviors that occur at the group level via the coordination and relationships of the members. For the community, it is the feedback processes inherent in the relations between demography, institutions, beliefs, norms, and shared knowledge characterizing the community of interest. All three of these aspects of the human niche are also simultaneously in interaction with one another in both directional and feedback relationships. All of the interfaces within and between the three core components are highly dynamic and malleable, and the human niche is indeed a moving assemblage.

To illustrate this framework and its potential to provide a basal context for linking EES processes and anthropological approaches, I will walk through a very brief example of "human sexual partnering." Usually termed "mating" in neo-Darwinian evolutionary approaches, I use the term "sexual partnering" because in humans, as in many other complex social animals (e.g., Bailey and Zuk 2009), sexual bonds and alliances are not always related to reproduction. Therefore, a focus solely on mating (sexual activity related to reproduction) overly limits the analysis and ignores abundant anthropological knowledge. Sexual partnering per se is neither a trait nor an independent system; rather, it is a pattern of relationships between individuals in groups and communities, a part of human sexuality, and evolutionarily relevant.

Sexual Partnering and the Human Niche Framework

The biologist Anne Fausto-Sterling (2000), in a broad overview of neurobiology, behavior, and physiology, asserts that sexuality is a somatic fact related by a cultural effect. She and many others (e.g., Tolman and Diamond 2001) demonstrate that understanding patterns of adult sexual behavior cannot be effectively detailed without acknowledging the extreme entanglements and mutual mutability between developing bodies of individuals; the social and ecological experiences they have in groups; the structure, beliefs, and sexualities present in the groups; and the historical, economic, and political ecologies of the larger communities that shape the patterns of those groups. This same outcome is seen in ethnographic and psychological approaches to sexuality wherein individuals' expression of sexuality and desire, experience, embodiment, and agency are entangled with elements of groups and larger communities (see Donnan and Magowan 2010; Nanda 1999).

Sexual partnering is a common focus of evolutionary questions about humans. It is something that is found in all human societies, and our understandings of biology and the ethnographic record leave no doubt about the thorough and intricate entanglement of biological, behavioral, economic, historical, symbolic, experiential, and perceptual constituents of the processes involved. So, when seeking to understand sexual partnering in a given group of humans, we need minimally to include the following: (1) patterns of choice of sexual partners; (2) the possibility that there is a history of sexual selection that has influenced the morphologies, behaviors, and sexual processes we are observing; (3) the structural constraints and facilitators provided by specific reproductive physiology in humans; (4) individual variation (behaviorally, experientially, physiologically); (5) local ecological contexts; (6) group and community demography; (7) individual and group perceptions and display of gender roles and sexual activity; and (8) institutions, traditions, and technologies that promulgate and limit gender roles and sexual activity (marriage, laws/morals, kinship associations/regulations, economic constraints, medical interventions, etc.).

All of these elements are interactive, mutually malleable (with varying degrees of plasticity), and have a history that is both structured by and structuring of the ways in which humans navigate and interact with each other and their niche(s)—they are part of an evolutionary dynamic.

Figure 1 shows the component "individual" with its internal feedback process and the external pressure of ecologically mediated selection. This, by itself, reflects the basic model used in most standard neo-Darwinian approaches. Within the individual, the feedback processes involve structural constraints and facilitators of reproductive physiology, individual variation (behaviorally, experientially, physiologically), and physical and social development, and all are shaped via interfacing with local ecological contexts. In the case of sexual partnering, physical development (growth and maturation) and its relationships to morphology and physiology is central in establishing the basal parameters and is contingent on external factors related to nutrition, disease ecology, and social cues. As the individual matures physiologically (i.e., passes through puberty/menarche), endocrinological shifts can combine with behavioral options and ecological inputs/challenges in feedback relationships to prime or suppress physiological and perceptual/cognitive options for attempts, failures, and success in sexual activity (see Gettler 2016).

Figure 2 illustrates the addition of the second core component, the social group, to the framework. The group is the core social context in which the individuals interact with one another. Thus, it affects the patterns of evolutionary forces (bio/ecological and social) on the individuals, and by their actions the individuals can influence the structure and intensity of processes on/in the group. The same ecological context placing pressure on the individuals is also placing pressures on the group. This stage of the framework is common in many descriptions of group-level selection dynamics and in many approaches in human behavioral ecology, particularly in the context of intragroup competition (Fuentes 2009*a*, 2009*b*; Laland and Brown 2011).

In the context of sexual partnering, the group is the core social structure that provides the context in which the individual experiences and responds to evolutionary pressures. The age/sex makeup (demography) and subgrouping patterns within the social group, the frequency and tenor of social interactions, and the structure of social bonds between individuals within the group provide the central landscape (the social ecology) in which the internal feedback processes of the individual play out. This landscape shapes variables such as

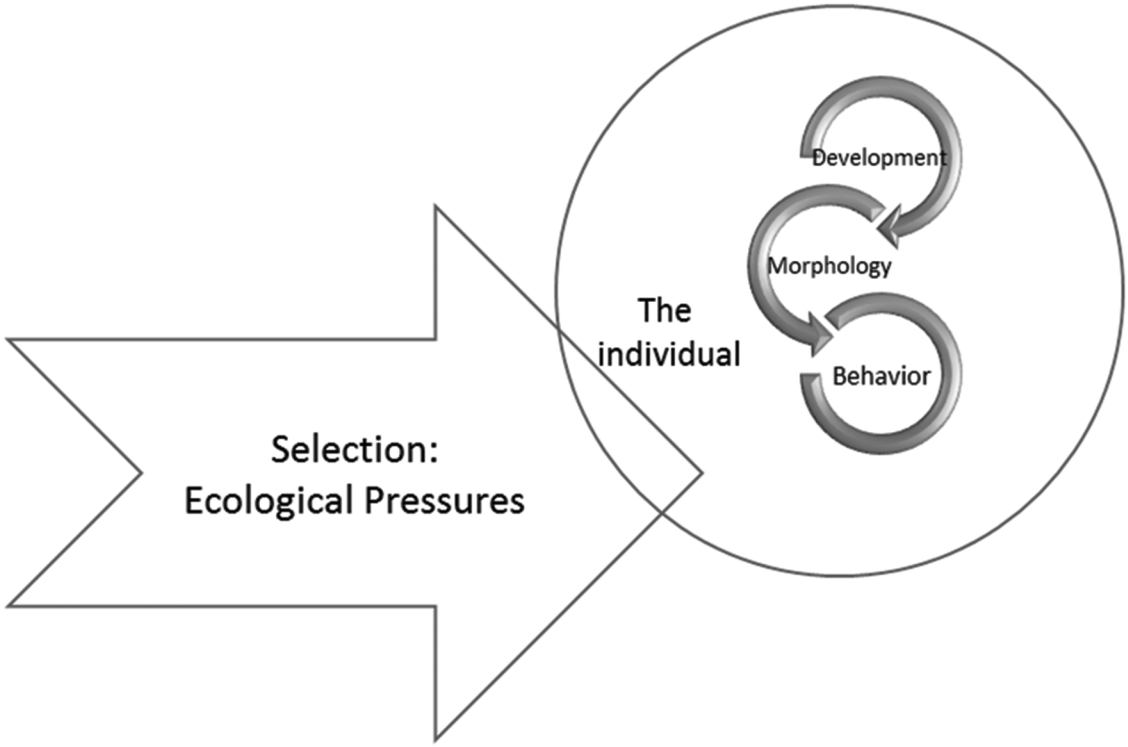

Figure 1. Component "individual" with its internal feedback process and the external pressure of ecologically mediated selection. A color version of this figure is available online.

opportunities for sexual activity, potential partners, and potential competitors for those partners. The social history of the group as it relates to sexual practices is a key inherited feature of the evolutionary landscape for individuals within the group.

While each individuals' trajectory in relation to sexual partnering is structured by the patterns present in the group, each individual also influences the very structures of the group that they are navigating. This is a dynamic process that has group-level outcomes shaped by the interfaces between individuals in the group, which can result in the first major aspect of niche construction in this framework.

Figure 3 includes the actions of individuals and collective action by the group as part of the processes that can modify both external ecological pressures and the internal feedback systems within the niche. Collective action by the group can alter the ecological pressures on the individuals, which can affect the feedback between their internal processes (development, morphology/physiology, and behavior), and the interactions between individuals potentially alter the internal feedback patterns at the group level (patterns of social bonds and sexual activity, group-level behavior). In humans, this pattern of interactive feedback in response to ecological pressures is particularly salient because it can be accomplished via a much wider array of elements and outcomes than in other animals: complex and multifaceted tool use, shared (collective) intentionality, and complex coordinated action between individuals resulting in large-scale modifications to local environments structured and facilitated by created/shared/inherited beliefs and perceptions, and so forth.

In the case of sexual partnering, group-level responses to external pressures can structure the kinds and intensities of basal pressures on individuals. For example, group-level actions in response to the ecological challenges of food availability and food collection and processing can affect energetic status of individuals influencing the internal feedback systems at the individual level and potentially patterns of physiology related to sexual activity—which in turn can alter the dynamic between individuals and the social group. Group-level landscape manipulation processes such as agriculture, food and livelihood procurement patterns, the structure and distribution of residences, and so forth can directly affect options for sexual behavior, access to potential partners, and energetic context for the individuals in the group. The choices and actions we observe in individuals are shaped via the group structuring of age and gender differences in daily activity patterns, social restriction of sexual activity, and gender role variation and the constraints on access to sexual partners that emerge from them.

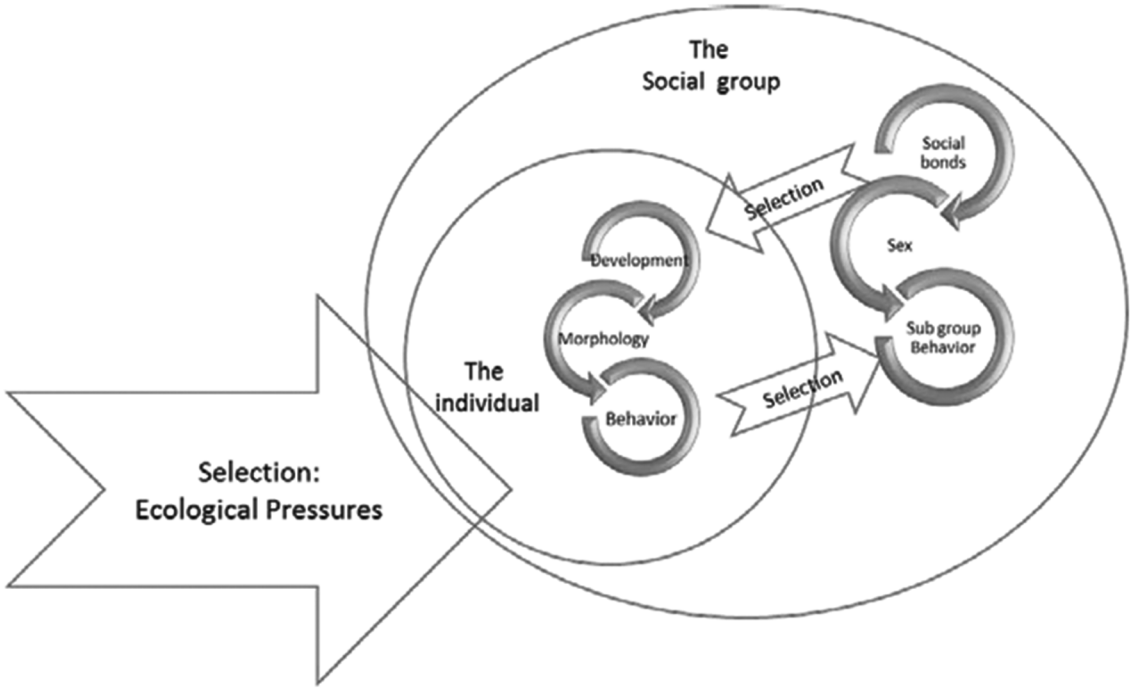

Figure 2. Social group. The social group is the core social context in which individuals interact with one another; thus, it affects the patterns of evolutionary forces (bio/ecological and social) on those individuals, and by their actions the individuals can influence the structure and intensity of processes on/in the group. The same ecological context placing pressure on individuals is also placing pressures on the group. A color version of this figure is available online.

If we add individuals' perceptions and display of gender roles and sexual activity to these structuring effects, one can see that just by thinking about the individual and the group as part of mutually interactive components in the niche, there is a dense entanglement of social and biological processes embedded in multiple feedback systems. Also, group-level processes in the form of traditions that may have been causally related to past ecological and/or social contexts can continue to structure elements of sexual behavior via shared histories and beliefs even in the absence of any of the original structuring contexts. The niche includes an inherited social ecology that can have very specific effects on future generations.

Figure 4 adds the final aspect of the framework, the community, and diagrams the internal and external feedback loops that complete this skeletal outline of the human niche. At the level of community, we add a potentially increased range and density of shared knowledge leading to an expanded, across-groups effect of shared intentionality and coordinated action. In the community, multigroup demographic patterns and processes come into play, and behavior that reflects multigroup, community-level actions can also play a role in the structuring processes of the niche.

Community-level effects on sexual partnering are obvious: the larger pool of potential partners creates a different set of options than we have at the group level. The spatial and social structuring of access to those partners shapes the patterns of action, and social relationships between groups can then shape the within-group dynamics that in turn affect individuals' behavior and their own internal feedback systems.

It is at the community level that the final niche-constructive element appears: joint feedback by the actions of individuals and groups at the level of the larger community that can modify the external ecological pressures on all three core components of the system. It is in this context that the distinctively human cultural processes of social, political, and economic institutions and large-scale intergroup behavior (such as warfare, extensive trade, market economies, religious organization, complex residential patterns and systems, coordinated landscape modification, marriage traditions, etc.) become especially salient. While it is easy to envision how the large-scale intergroup behavior plays a role in modifying ecological pressures and processes, these human institutions also directly affect perceptions, expectations, behavior, relationships, and thus physiologies of individuals resulting in concomitant feedback effects at the group and community levels. Community-level social processes (institutions) create social landscapes and contexts that become their own structured and structuring feedback systems, creating biological and social selective pressures and being reinforced or

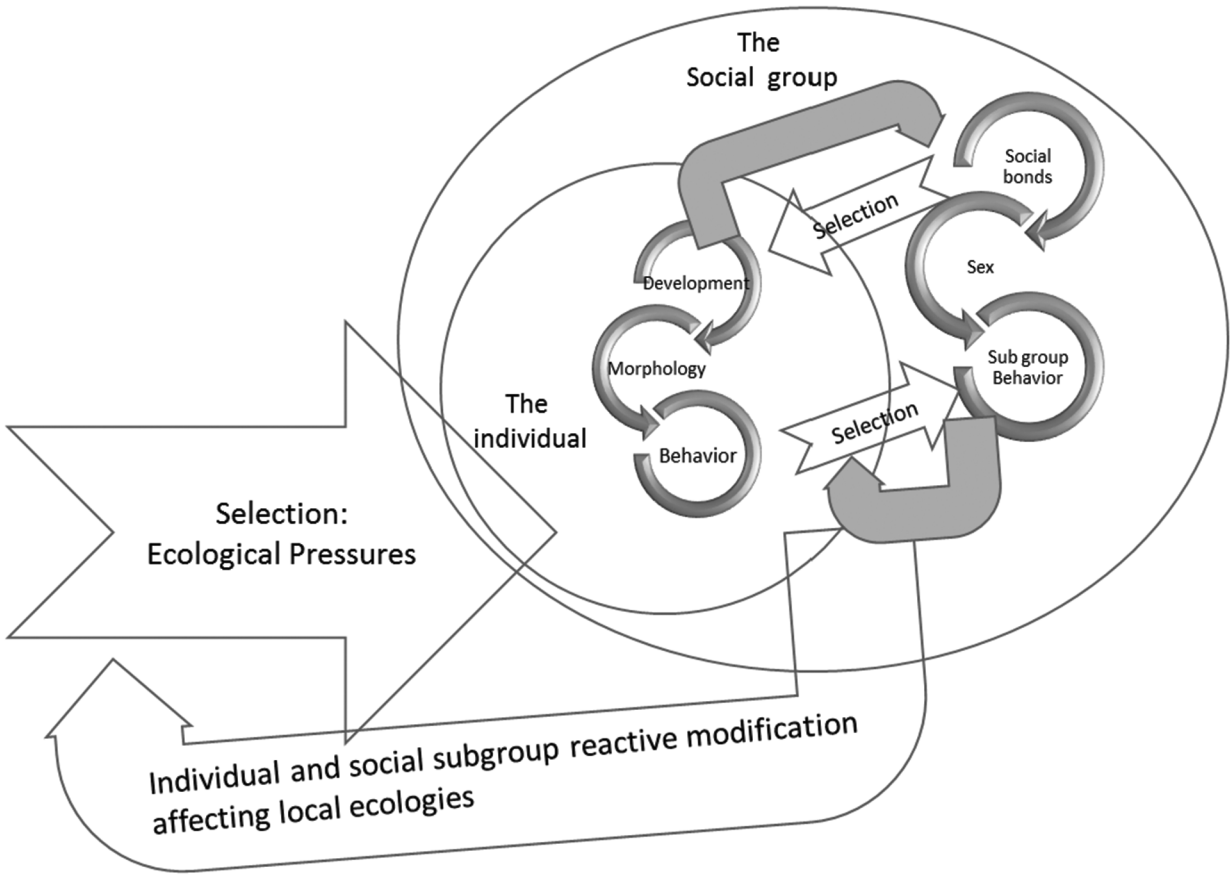

Figure 3. Actions of individuals and collective action by the group acting as part of the processes that can modify both external ecological pressures and the feedback systems within the individual and group levels. A color version of this figure is available online.

reshaped by the individual and group responses to those very pressures.

Aspects of This Conceptual Framework Are Already in Practice

The framework and the various factors in the human niche and the potential places and processes of interface between them enable anthropologists to take a multilevel view that inherently intertwines evolutionary and ethnographic approaches. Starting from the basal assumption that the human niche is the overarching system in which humans are evolving, one can then hone in on specific components (nodes), relationships, and feedback loops and conduct quantitative and qualitative assessments. Beginning with a framework of systemic complexity and dynamism, our baseline enables us to ask targeted questions about specific aspects of the human niche in order to develop more effective and integrated anthropological answers.

For example, Lee Gettler (2016) investigates socioendocrinological processes and patterns associated with male parenting. He and his colleagues' work with the men of Cebu demonstrates that "conceptualizing interplays and feedbacks between individual development (behavior-cognition-biology), family systems, and cultural institutions" is a valuable model for thinking about the niches occupied by these men. Further, he suggests that "we need to push the boundaries on our thinking in terms of how developmental experiences become embodied and the way in which those culturally constructed neurobiological-endocrine pathways enable individual behavior-cognition and social interactions, which are at least contributing factors to the emergent phenomenon of cultural complexity." Gettler and colleagues illustrate this by using long-term data to show that both psychosocial stressors and childhood nutritional status, via their effect on energetic constraints on the individual during development, influence entry into parenthood for men in the Cebu study and draw some causal inferences by connecting the feedback processes between individuals, their group (families), and community (urban Cebu; Gettler et al. 2015).

In a related vein, Doug Bird and colleagues (2016) demonstrate how landscape alteration and the use of fire by the Martu in Australia "operates as a form of dynamic cultural and eco-

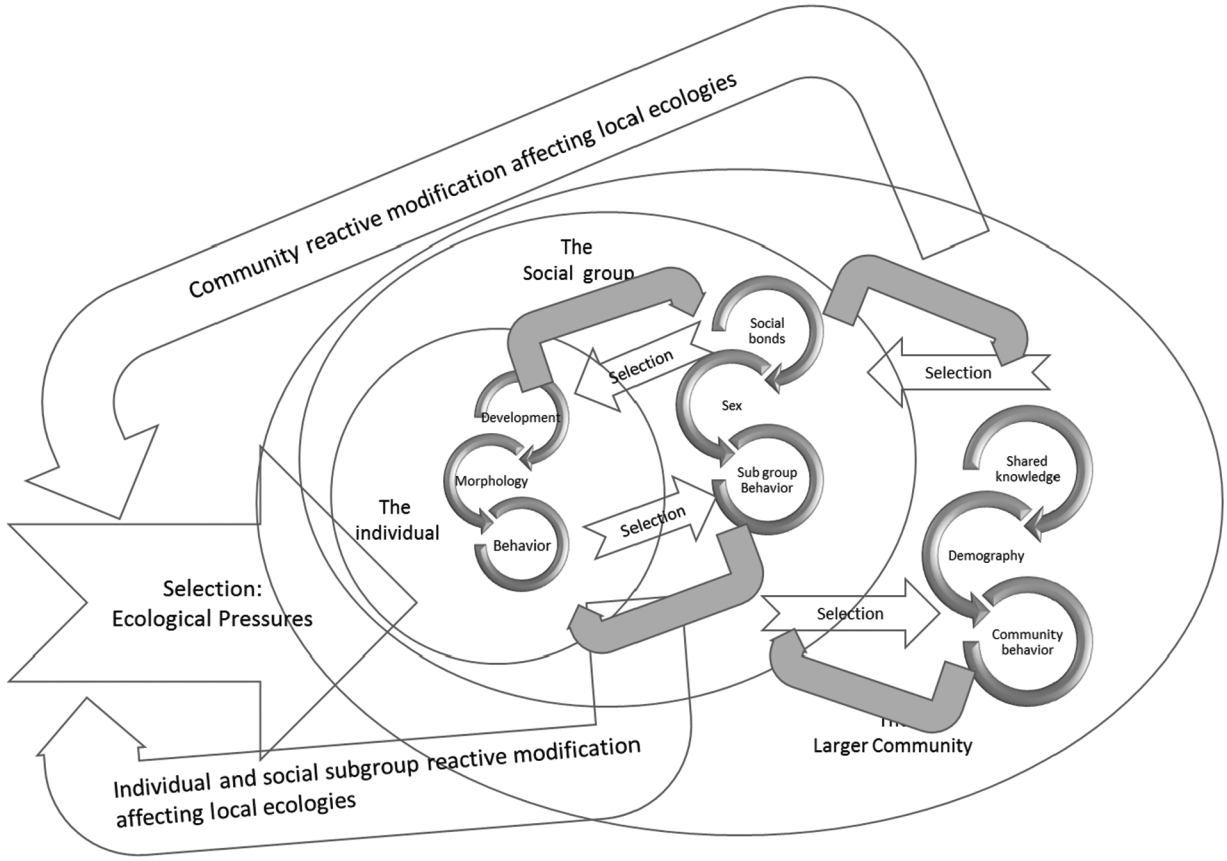

Figure 4. Community and internal and external feedback loops that complete the skeletal outline of the human niche. A color version of this figure is available online.

logical niche construction, shaping systems of sociality among people and their interactions with other species." In this system, individuals and social groups of Martu interface with their local environments, family members, the larger landscape, their social communities, and regional and local institutions in a suite of feedback relationships. These relationships are with landscapes, fire, bodies (Martu and their prey), history, and cultural traditions all interfacing with contemporary economic and political contexts. Bird and colleagues (2016) focus simultaneously on individuals, social groups and larger communities, and the interlacing of the physical, cultural, and ecological in order to work toward "explaining the processes of the social and material interdependencies that construct human niches" in the Martu.

Greg Downey (2016) integrates NCT, concepts of "enskillment" and "de-skillment," and ethnography of street children in Brazil to propose that we envision the urban niche as a behavioral-ecological-historical conjunction. Downey describes cities as a developmental niche where feedback between factors such as nutrition, locomotion, and activity patterns at the levels of individuals, youth peer groups, and the structures of the urban landscape are integral in the processes of shaping the human phenomenological experience (physically and perceptually). Downey proposes that the mutual mutability between bodies, behavior, and the urban landscape has created a distinctive urban phenotype, or a variety of urban phenotypes, as the result of these niche-constructive processes.

Parting Thoughts

The framework I present here is an oversimplification and provides only a basic skeleton of the dynamics of the human niche. Most of what I have argued is not new, and many of the elements are in practice, in one form or another, across multiple approaches in anthropology. However, they are rarely connected across subareas and theoretical divides.

We need an integrated anthropological framework for asking evolutionary questions about humanity—one that is inclusive of ethnographic and sociocultural theory and data as well as evolutionary approaches. I believe our challenge is to figure out how to effectively engage human cultural systems, individual actors, and group and community-level dynamics with biology, history, and human niche complexity. If we can do so, we will be better equipped to examine the patterns and processes at play in hu-

mans who evolved in, shaped, and are shaped by complex dynamic niches and who continue to do so at a rapid pace.

The human niche heuristic proposed here encompasses individual bodies, face to face interactions within social groups, interactions among social groups, and dynamics at the community levels as relevant in evolutionary inquiry. Selection exerts pressures at various nodes in the system, and responses to those pressures emerge at individual, group, and community levels. This pattern of reactive response to social and ecological pressures and contexts at various levels creates a local ecology of interactive material, social and cognitive aspects that are passed from one generation to the next; it creates an inherited ecology, a cultural context.

Using the human niche as a basal framework enables us to include the salient features, forces, and processes at multiple levels of feedback systems or at least be a part of an approach that acknowledges the interfaces across the levels as a core facet in the system of interest. It is a set of "structured structures predisposed to function as structuring structures" (Bourdieu 1990:53). In an evolutionary approach, this means adding social complexity and reducing reliance on simple or linear causality. Such a complex and dynamic approach requires a diverse anthropological tool kit, one that includes ethnography, social theory, and a serious engagement with human culture and human biology for effective inquiry. By explicitly joining contemporary evolutionary approaches (the EES) to an integrative basic framework for human evolutionary inquiry (the human niche heuristic), we are able to develop a more fertile and inclusive landscape for evolutionary approaches in an integrative anthropology.

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