

REVIEW ARTICLE

Human behavioral ecology and niche construction

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Abstract

We examine the relationship between niche construction theory (NCT) and human behavioral ecology (HBE), two branches of evolutionary science that are important sources of theory in archeology. We distinguish between formal models of niche construction as an evolutionary process, and uses of niche construction to refer to a kind of human behavior. Formal models from NCT examine how environmental modification can change the selection pressures that organisms face. In contrast, formal models from HBE predict behavior assuming people behave adaptively in their local setting, and can be used to predict when and why people engage in niche construction. We emphasize that HBE as a field is much broader than foraging theory and can incorporate social and cultural influences on decision-making. We demonstrate how these approaches can be formally incorporated in a multi-inheritance framework for evolutionary research, and argue that archeologists can best contribute to evolutionary theory by building and testing models that flexibly incorporate HBE and NCT elements.

KEYWORDS

archeology, extended evolutionary synthesis, foraging theory, human behavioral ecology, niche construction

1 | INTRODUCTION

Evolutionary theory is integral to explaining the origins of our species and appealing as a potentially unifying framework for understanding human behavior.¹ But the task of applying evolutionary theory in archeological contexts is non-trivial. Evolutionary biology is a highly-varied discipline with its own internal debates, in which much theoretical work is highly mathematical and focused on simplified hypothetical (e.g., single allele) systems. Understanding what theoretical concepts or approaches to choose—and how to operationalize them for human systems and for the available material record—can be a difficult task.

Here we review two bodies of theory that feature prominently in evolutionary anthropology and archeology: human behavioral ecology and niche construction theory. The relative merits of these two

approaches for understanding processes of change in human societies have been a subject of considerable debate within archeology. Our major aims are to clarify the relationship between these theoretical approaches, and to provide some guidance for how archeologists can fruitfully apply them in their work. To do so, we highlight some core differences in the content of these frameworks and some important nuances in how niche construction has been defined in archeology. We suggest that niche construction theory and human behavioral ecology can be viewed as having different, but complementary, sets of simplifying assumptions about the dynamics of evolutionary systems. By foregrounding these differences, some of the perceived conflicts between niche construction theory and human behavioral ecology fall away. We suggest that these approaches can be productively integrated by developing hypotheses based on the explicit specification of inheritance tracks (distinct systems that transmit information through time, such as genes or culture) and how these inheritance tracks impact behavior.

[Correction added on 19 February 2021, after first online publication: Projekt Deal funding statement has been added.]

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We begin by briefly introducing each of these frameworks and some of their main applications in archeology. While it is challenging to summarize these fields and related debates without losing important nuances, we hope this brief review will suffice as a general orientation to a complex topic. Other papers in this special issue (including articles by Murray, Benitez and O'Brien, O'Brien and Bentley, and Stiner) also provide relevant background to niche construction approaches in archeology.

2 | HUMAN BEHAVIORAL ECOLOGY

Human behavioral ecology (henceforth HBE) is a branch of evolutionary behavioral science that many archeologists have drawn upon as a source of theory to assist them in studying past behavior. HBE is a field that developed in anthropology starting in the 1970s, inspired by developments in the study of animal behavior in evolutionary ecology.² From its inception, HBE has deliberately focused on understanding how behavior (including cultural practices) might confer benefits to people that could enhance survival and reproduction within a specific cultural, social, and ecological context.³

HBE research generally begins by specifying a model of behavior that describes the problem faced by an organism (e.g., getting food to eat) and derives predictions for behavior by assuming that organisms should attempt to solve this problem as efficiently as possible given a defined set of available options and constraints. This method is called optimization analysis. The assumption that organisms should attempt to solve adaptive problems efficiently is justified on the grounds that organisms that do so will have greater fitness.^{4,5} Actual behavior can then be compared to the predictions of the model. Observed behavior usually does not match model predictions exactly, but these deviations yield important insights, for instance, revealing which of the model's assumptions are incorrect. What is tested in empirical studies is not the model itself (models are just a set of assumptions and math) but whether it leads to any useful insight about observed behavior.⁶

Historically, one of HBE's main areas of interest has been foraging behavior. Perhaps the most well-known model in the field is the diet breadth or prey choice model, which like many HBE models, originated in studies of animal behavior.⁷ The prey choice model predicts which of a set of possible food items (prey) a forager should choose to include in their diet. The efficient foraging strategy predicted by this model is that foragers should only take those food items that increase the energy acquired per time spent foraging. For example, a forager should not stop to take a rabbit if the forager can obtain more calories per unit time by ignoring the rabbit and searching instead for deer. This leads to the prediction that food items that provide a lower post-encounter return rate (calories per time spent processing the item) should only be added to the diet as higher-ranked prey items become less frequently encountered. Many of the earliest studies in HBE focused on applying the prey choice model to contemporary foraging populations. Early applications demonstrated basic agreement between model predictions and foraging behavior,^{8–11} while subsequent work paid closer attention

to the details of specific model violations, particularly relating to risk-sensitivity and gender differences in foraging.^{12–14}

Following on the success of the prey choice model in ethnographic research, archeologists have employed this model in diverse settings.^{15–18} Because the model predicts that diets will include a broader range of items when high-return prey become rare, archeologists have used the expansion and contraction of past diets, as reflected by the faunal/botanical record, as indicators of changing foraging efficiency over time. In many cases, changes in foraging efficiency are associated with technological or social change, such as the origins of agriculture and the emergence of social hierarchies.⁶

Although in archeology HBE is often strongly associated with foraging theory—specifically the prey choice model—we note that questions of economic production are only one branch of interest within a much larger field. Other foci of research within HBE include problems relating to resource distribution, such as food sharing, as well as reproductive decision-making, a broad topic including mating, fertility, and parental investment strategies.¹⁹ HBE is also not limited to studying foraging populations: over the past two decades the field has shifted away from its historical focus on foragers and expanded massively into industrialized contexts, reflecting a broader recognition and acceptance of the idea that simple models based in evolutionary theory make useful predictions about decision-making in all human societies.^{20,21} Despite these changes, most HBE research retains the field's distinctive research strategy. HBE's central tenet—the idea that organisms should attempt, however imperfectly, to behave in ways that maximize their fitness—continues to provide its practitioners with useful principles for establishing predictions about why people have certain kinds of preferences.

The HBE approach has also garnered much criticism within anthropology. Such critiques have been discussed in detail elsewhere.²² Here we briefly address two particularly common criticisms: (1) the approach is excessively reductionist, meaning it fails to accurately understand the relationship between variables because it ignores fundamental system components, and (2) the use of optimization models is problematic because organisms do not behave optimally.^{23,24} HBE is deliberately reductionist: it generally begins by focusing on one small component of a complex system and a restricted set of variables. However, the use of simple models does not imply that evolutionary explanations are assumed to be equally simple²⁵: models are not considered to provide complete explanations of human behavior.²⁶ Similarly, the use of optimization logic to generate predictions does not entail the assumption that organisms always behave optimally. The simplicity of HBE models means that they are “brittle”: they are expected to fail easily. When they fail they generally do so in interesting ways that uncover new insights and spur new research, allowing researchers to gradually build the complexity of hypotheses based on the results of previous empirical tests.

3 | NICHE CONSTRUCTION THEORY

In contrast to HBE, NCT is not (at least yet) a distinct research tradition or subfield within anthropology. Like the evolutionary models

that inspired HBE, NCT also originates in evolutionary biology. In their foundational text on the subject, Odling-Smee, Laland and Feldman define niche construction as “the process whereby organisms, through their metabolism, their activities, and their choices, modify their own and/or each other’s niches.”²⁷ They operationalize niche construction formally as any action by an organism that positively or negatively affects the availability of a resource in the environment, and use formal modeling to show that when environmental modifications are persistent across generations, niche construction can be a powerful force driving the trajectory of evolution. Odling-Smee and colleagues argue that classical population genetics focused excessively on the action of natural selection upon gene distributions occurring due to the response of organisms to their environments, while neglecting the fact that organisms also modify their environments. They suggest that incorporating niche construction as a first-order evolutionary phenomenon (on par with natural selection) remedies an asymmetry that otherwise exists in quantitative models of evolution. NCT is not primarily concerned with whether a behavior is adaptive or not—niche construction may negatively or positively impact fitness.²⁸ However, Odling-Smee and colleagues do suggest that organisms will generally attempt to behave in ways that promote their fitness, though these behaviors may have unintended negative consequences across generations.

NCT has occupied a prominent place in recent debates in evolutionary biology about whether standard evolutionary theory (also referred to as the modern synthesis), which is strongly rooted in classical population genetics, is adequate for describing the full range of processes involved in evolution. To summarize the debate extremely briefly, the primary (though not sole) justification for the new approach, called the extended evolutionary synthesis (EES), is as described above: advocates argue that standard evolutionary theory focuses on natural selection to the exclusion of other important evolutionary processes. These processes include niche construction as well as phenotypic plasticity (the idea that plasticity can produce new phenotypes, and this may later impact genes), inclusive inheritance (inheritance from non-genetic pathways), and developmental bias (phylogenetic or developmental sources of bias are considered to not only constrain but direct evolution).^{29–31} Proponents of the EES suggest that non-genetic inheritance pathways, not just genetic ones, must be considered to understand many evolutionary phenomena.^{27,29–31}

Detractors of the proposed EES generally make two main arguments: (1) the aforementioned processes are not ignored by and/or can be accommodated within standard evolutionary theory, and (2) the evidence for these processes is not sufficiently strong to warrant placing them on an equal footing with natural selection operating on genes.^{32,33} Another criticism is that these other processes often work through genetics (e.g., niche construction may impact future selection on genes), and so even if additional forms of inheritance are important, they represent a different level of explanation.³⁴

NCT has appealed to some researchers in archeology and biological anthropology as a potential way of better integrating non-genetic inheritance processes (notably, culture), as well as the interplay between genes and culture, into evolutionary approaches to the study

of the human and hominin past.^{23,24,35,36} Part of the appeal of NCT stems from how it is considered to foreground cultural and social factors that a long history of scholarship in archeology and anthropology have overwhelmingly shown to be important.^{22–24} Conversely, the factors emphasized in foraging theory, which has dominated applications of HBE in archeology, are usually demographic or environmental. NCT is thus viewed as a better alternative to HBE for investigating human-environmental relationships in the past. For example, Makarewicz writes that “NCT defies HBE concepts that construe human resource acquisition strategies as largely driven by resource scarcity and human modification of the environment as an adaptive response to environmental change.”³⁷

In the archeological literature, strong statements abound about what HBE and NCT should or should not do, or can or cannot do.^{22,37–42} For example, Smith suggests that “new perspectives [NCT and movement ecology] call into question the basic utility of HBE as a framework of understanding for complex human evolutionary processes,”⁴¹ while Gremillion and colleagues write “EE [Evolutionary Ecology, including HBE] is well-positioned to support and complement NCT.”⁴² In the following section, we examine differences in these approaches in more detail, and seek to clarify whether they are, or are not, incompatible.

4 | THE RELATIONSHIP BETWEEN HBE AND NCT

In order to answer questions about the purview and scope of HBE and NCT, and whether or not they are antithetical or complementary, it is useful to first consider the basic question of how scientific fields can be defined generally. Few authors make it explicitly clear how they answer this question, even when it is crucial to additional arguments. Here, we distill three common perspectives: topical, practice-based, and analytical. These are usually implicitly adopted and are not mutually exclusive. The topic-based perspective is perhaps clearest: What types of things does the field study? For example, “Physics studies the material world.” Such definitions are rarely perfect or exclusive. For instance, the topical foci of anthropology and sociology are highly overlapping. What really seems to distinguish these two fields is not their respective topics, but rather practice. By practice, we mean how a field goes about studying its topic(s): its methods, preoccupations, manners of discourse, and rules for resolving disagreements among practitioners. Finally, it is useful to separate out the analytical orientation of a field from its practice more generally. By analytical orientation, we mean that a set of well-specified phenomena, tied to models that characterize them, can be used to delineate a field’s purview more formally. This is especially common in the natural sciences; for example, special relativity addresses phenomena for objects moving close to the speed of light. We find that considering these distinctions between how fields are defined, and thus what may fall within their purview, is useful for framing the relationship between HBE and NCT.

We now relate the preceding concepts to the question of the relationship between NCT and HBE. We highlight three key points:

(1) the analytical foci of NCT (as formally defined in evolutionary biology) and HBE are different; (2) when niche construction is defined as the study of niche-constructing behavior (as opposed to as an evolutionary process), HBE provides an analytical framework that can contribute to this task; and (3) despite historical practice within the discipline, the analytical framework of behavioral ecology does not require excluding social or cultural influences on behavior.

4.1 | The analytical foci of HBE and NCT are different

HBE as a field of study is, at least historically, strongly linked to a specific analytic approach and set of models. Niche construction theory also has an analytical core, as an evolutionary process that stands symmetric to natural selection, linked to a set of formal mathematical and computational models that describe it.²⁷ For the main proponents of NCT in evolutionary biology, while the behavior of organisms can lead to niche construction, “formal theory explores the evolutionary consequences of niche construction,”⁴³ generally in mathematical systems with simple rules for inheritance of a trait. In fact, Odling-Smee and colleagues separate out niche constructing *behavior* from niche construction as a *process*: they “distinguish between two aspects of niche construction—environment alteration and subsequent evolution in response to constructed environments—equating the first of these with “ecosystem engineering.”⁴⁴ At its analytical core, then, NCT sets aside the specifics of what organisms do to focus on system dynamics.

In contrast, HBE is specifically focused on understanding why people make particular decisions given the socio-ecological choices and constraints they face. HBE generates predictions for behavior by considering the potential contribution of the behavior to fitness (or rather, potentially fitness-related outcomes such as economic or reproductive success). Indeed one could argue that, because of its

particular analytical stance, HBE is more like economics than it is like other branches of evolutionary biology²³: it is often only evolutionary in the sense that evolutionary theory is used to guide the choice of decisions to model, currencies to select, and utility function(s) to choose.

We further note that because of its topical focus on questions about the adaptive function of behavior (how a behavior may confer a selective advantage to an organism in the present),⁴⁵ HBE research has generally used a “snapshot,” or static, approach to examine what factors shape decision-making at a particular moment in time. This approach avoids having to model the temporal dynamics of environments, without, we believe, intending to deliberately dismiss their potential importance.⁵ However, we note that a current trend towards longitudinal research in HBE reflects an increased interest in how people's actions impact their future environments.²² The clearest example of such work comes from Bliege Bird and colleagues.^{46,47} Their research, grounded in a foraging theory approach to modeling hunting decisions, has shown how the burning practices of Martu hunters in the Western Desert of Australia create small-scale vegetational mosaics that improve future hunting return rates (see Figure 1).

4.2 | HBE can provide an analytical framework to study niche construction as a behavior

Earlier, we noted that NCT as framed in evolutionary biology is not a theory of behavior. However, some proponents of NCT in archeology have taken a different approach. In their work on plant and animal domestication, archeologists Bruce Smith and Melinda Zeder are interested in niche construction as an evolutionary process, but they further link niche construction processes to a theory of behavior which they call Cultural Niche Construction (CNC). This use of niche construction more closely echoes topical definitions of niche



FIGURE 1 Past behaviors can shape future behaviors by changing the local environment. Small fires lit by Martu hunters in Australia create a habitat mosaic that improves future return rates and may draw hunters back to previously used hunting areas⁴⁷ (left panel). In the Canadian Arctic, Inuit hunters actively modify their environment in many ways to improve safety, comfort, and access to resources. Hunting shacks such as the one pictured above are generally built in preferred hunting locations; once built they serve as anchor points for travel routes and hunting excursions. Several cabins will often be built in the same location; a phenomenon that appears to be related to a desire for safety and social opportunities as well as resource abundance. More experienced hunters will sometimes seek out less-crowded locations, such as this inland goose hunting camp (right panel). Photos by Elspeth Ready

construction as a type of behavior, also called ecosystem engineering,⁴⁸ and which is distinct from formal NCT. We note that this use of “Cultural Niche Construction” is also distinct from uses of this phrase by niche construction modelers in biology; in this case the phrase generally refers to models of niche construction as a process used in cases where the inheritance process for one or more traits is cultural.^{49–51}

Smith and Zeder place their theory of behavior in opposition to foraging theory,^{23,52,53} due to a concern that an over-reliance on the prey choice/diet breadth model among archeologists has led to a narrow focus on demography and resource depression as the main drivers of human niche construction behaviors.^{37,54,55} As mentioned earlier, archeological applications of the diet breadth model have commonly argued that novel social, technological, and cultural behaviors in human groups, such as the origins of agriculture, were stimulated by efforts to mitigate lowered foraging efficiency caused by resource depression (itself sometimes linked to population growth).⁶ Smith and Zeder instead prioritize stability and reliability as goals of human resource use strategies, and argue that humans actively modified environments to meet these objectives.^{55,56} For example, Smith writes that “NCT explanations of [the origins of agriculture] are based on a solid general theory for human behavior: that human societies actively modify their surrounding environment to increase the relative abundance and reliability of preferred wild species of plants and animals and that such efforts have the potential to provide individuals and populations with an evolutionary advantage.”⁵⁶

We think that framing this issue as one pitting niche construction against non-niche construction explanations misses the analytical distinction between formal theory in HBE and NCT. Following Odling-Smee and colleagues' definition of a niche-constructing behavior as any action that modifies the availability of a resource in the environment and impacts future selection pressures,²⁷ it does not matter whether humans modified their environments because of population pressure, resource depression, or other some other objective. In any of these cases, their response could modify selection pressures, and therefore set niche construction (the process which is the focus of formal theory in NCT) into motion. This is why practitioners of HBE in archeology, while generally not disputing the existence of niche construction as an evolutionary process, maintain that HBE models, including foraging theory, are well-suited to investigating when and why people engage in behaviors that lead to niche construction^{39,40,42,57–60}; because HBE and formal NCT are theories of different things. In fact, many HBE models are models of niche construction as a *behavior*: for instance, models of mobility and of investments in technology explicitly consider when and why people decide to modify their relationship to resources in their environment.³⁹

The debate over NCT approaches in archeology is therefore first and foremost a debate about what models of behavior are most appropriate for interpreting the archeological record. Further, we think the narrative model-building strategy adopted by Smith and Zeder masks underlying similarities of their theory of behavior with the more formal analytical approach of HBE. Their view that

human decisions are goal-oriented is consistent with the HBE view that people have the capacity to evaluate fitness trade-offs. Moreover, their argument that resource use practices may prioritize predictability and reliability over energy maximization is not new to HBE,⁶¹ and has been a focus of relatively recent work on human foraging strategies.^{62,63} Thus we agree that the idea that people seek predictability in foraging strategies is a reasonable starting point for developing hypotheses to explain major transitions in prehistory, one that is also well-grounded in anthropological and economic literature^{64–66} and that makes intuitive sense in view of the geometric nature of fitness (i.e., individuals should be very averse to events that wipe out their lineages).⁶⁷ For archeologists interested in the idea of risk-aversion as a driver of human niche construction behavior, HBE can provide a theoretical toolkit for building models and generating predictions.

4.3 | HBE does not require excluding social, political, or cultural drivers of human behavior

Finally, perhaps because of the strong focus on the diet breadth model in archeological applications of HBE, there is a perception that HBE approaches exclude the possibility of non-ecological determinants of human behavior. For example, the assumptions of some specific foraging models have sometimes been confounded with the assumptions of HBE generally.⁴¹ There has indeed been a strong focus on environmental variables within HBE. But despite these origins, human behavioral ecologist Eric Smith once observed that “beginning with a problem that seems to lack any profound social dimensions (e.g., prey-choice, birth spacing, or group size), behavioral ecologists pursue what they hope will be simple answers, only to find that all roads lead to complex social interactions.”²⁶ In this sense, HBE is a field in which empirical evidence has led to the expansion of practice within the discipline. Compared to early research in the field, recent research on kinship, social support, and intergenerational resource transfers in HBE reflects a much more expansive view of the relevant “environment” that factors into decision-making: one that includes existing cooperative ties, kinship systems and other social and cultural factors.^{68–74}

More generally, HBE can accommodate an inclusive view of inheritance because it is fundamentally agnostic with respect to how phenotypes are acquired. The HBE research strategy usually involves black-boxing the mechanisms through which phenotypes are acquired or produced (e.g., genetic inheritance, ontogeny, social learning) and studying phenotypes (often behavior) directly, since it is assumed that phenotype is what produces a selective advantage regardless of how it is acquired. This assumption is referred to as the phenotypic gambit. There exist a number of slightly incongruous definitions of the phenotypic gambit.^{75–79} A suitable definition for our purposes is that the phenotypic gambit posits that the detailed process whereby one or more of genes, culture, the environment, and other factors produce a phenotype can be ignored under the assumption that, regardless of

the process, it produces behavior likely to optimize some proximate currency that improves fitness.

However, there are important cases where the phenotypic gambit does not hold, for instance, if there is a heterozygote advantage, such as in sickle cell anemia.⁸⁰ In this case, balancing selection between the advantage of the heterozygote (sickle/non-sickle) and the disadvantage of the sickle/sickle homozygote maintains a portion of the population with a sub-optimal phenotype (sickle/sickle): the mechanism of genetic inheritance in this case constrains the population from moving towards the optimum. A researcher studying the dynamics of sickle-cell phenotypes without knowing about the inheritance mechanism could potentially draw the false conclusion that the different phenotypes had equal fitness.⁷⁵ The phenotypic gambit may also not hold in cases where learning strategies are themselves socially learned.⁸¹

The phenotypic gambit is particularly relevant in archeology, when the relative costs and benefits of phenotypes cannot be directly measured and often the goal is to infer them from changing distributions of material detritus through time. Because of the potential limitations of the phenotypic gambit, we think that HBE, and perhaps especially archeological applications of HBE, could benefit from a more explicit consideration of the set of inheritance tracks that shape the acquisition of behaviors.⁵⁷ HBE has traditionally left the study of how cultural information spreads to its adjacent discipline, cultural evolution.⁵ Critically, the study of cultural evolution processes is already theoretically integrated with the study of niche construction.⁵¹ Recent ethnographic research has begun to better integrate cultural evolution and HBE approaches, for example, by investigating how people learn skills that may have an adaptive function.^{82–85} This integration is something that has long been called for by researchers in both fields,^{86–88} and will hopefully help us better understand when, why, and how cultural learning and inheritance processes may lead to violations of the phenotypic gambit.

In summary, our view is that there is no inherent conflict between HBE and NCT. From an analytical perspective, NCT as defined in evolutionary biology focuses on the evolutionary dynamics of environmental modification, while HBE focuses on human decision-making. Though HBE has in the past placed the study of environmental feedback processes and inheritance tracks outside of its focus, recent research has begun to expand the scope of the discipline. In archeology, NCT has been extended to include a set of predictions about human cultural niche construction behaviors defined in opposition to foraging theory-based explanations. We do not think that foraging theory is incompatible with niche construction, but agree with proponents of niche construction in archeology that feedback processes resulting from past human behavior may impact the direction of future evolution and that risk-management is an important component of human resource use strategies. In the following section, we demonstrate the compatibility of these approaches further through an analytic delineation of the scope of HBE and NCT within a multi-inheritance framework for evolutionary research. This provides a basis for the practical suggestions we offer for future work.

5 | HBE AND NCT AS SPECIAL CASES OF MULTI-INHERITANCE

We suggest that an evolutionary framework that incorporates both HBE and NCT can be defined using an analytical treatment that systematically pays attention to inheritance tracks. An inheritance track is a distinct physical system that transmits information through time.⁸⁹ Crucially, if inheritance tracks are to be both useful and valid, they must contain heritable information or material that can in principle be described and measured: genetic information in DNA or RNA, for example, or, for culture, it could be neural patterns in the brain or (more archeologically relevant) persistent patterns in material artifacts. For application to particular problems the details of how the inheritance tracks evolve and influence behavior must be specified. In their foundational work on NCT, Odling Smee et al.²⁷ follow Lewontin^{90,91} in presenting two differential equations that conceptually illustrate the symmetry of natural selection and niche construction. We adopt a comparable approach here to illustrate how behavioral ecology can be part of this framework.

To proceed, let us restrict attention topically to human behavior, for which we have a set of time-dependent observations represented generically by $B(t)$, where B stands for behavior and t is time. Our goal is to explain these observations: why does behavior change with time (or not)? We begin by nominating three general examples of state variables that could influence behavior (and each other): the physical environment, $E(t)$; culture, $C(t)$; and genes, $G(t)$. We model the system dynamics using a governing equation

$$\frac{d\mathbf{S}}{dt} = \mathbf{h}(\mathbf{S}), \quad (1)$$

where $\mathbf{S}(t) = [E(t), C(t), G(t), B(t)]^T$ is a time-dependent system state vector and $\mathbf{h} = [h_E(\mathbf{S}), h_C(\mathbf{S}), h_G(\mathbf{S}), h_B(\mathbf{S})]^T$ is a vector function that specifies the time evolution (first derivative) of the system. Equation (1) is deliberately exceedingly general, so that we can gain analytical traction by considering simplifications of it. For example, not all the state variables may be pertinent to a given situation and we might assume, as in the examples we consider below, that the dynamics of a given variable depends on only a restricted subset of state variables. Further, the functions in \mathbf{h} are different for each special case, and may be simplified versions of the general form in Equation (1).

The HBE research strategy generally focuses on how B , behavior, can be predicted from a set of other state variables. For example, in most foraging models, the role of genes and culture, G and C , are not explicitly accounted for under the assumption that (1) the environment is independently evolving, $dE/dt = h_E(E(t))$, and (2) behavior depends directly (and only) on the environment:

$$B(t) = g_B(E(t)), \quad (2)$$

where behavior, B , optimizes some proximate currency given the current environment, E , and $g_B(\cdot)$ is the function that maps environment onto behavior. This notation highlights the reason that the HBE

approach is useful archeologically: it provides a means of inferring behavior from other state variables that can potentially be observed in the material record. The simple case shown above (Equation (2)), is perhaps too restrictive, however, as things other than the environment can influence an individual's behavior. For example, perhaps technology changes the productivity of a subsistence activity. We can represent this with a new cultural state variable, $C_T(t)$, and the model can be redefined as $B(t) = g_B(E(t), C_T(t))$.

The core relationship of interest in most HBE research is the function specifying $g_B(\cdot)$, but it is worth noting that the assumptions described above for Equation (2) imply a governing equation in the form of Equation (1) which, by the chain rule, is:

$$\frac{dS}{dt} = \begin{bmatrix} \frac{dE}{dt} \\ \frac{dB}{dt} \end{bmatrix} = \begin{bmatrix} h_E(E) \\ h_E(E)g'_B(E) \end{bmatrix}, \quad (3)$$

where g'_B is the derivative of g_B (Equation (3) assumes scalar state variables for simplicity, but the extension to multivariate state variables is straightforward). Equation (3) is in fact a representation of the simplifying assumptions of the prey choice model, in the case that all environmental change can be considered independent of human activity. We note, however, that many applications of the prey choice model in archeology actually seek to disprove the hypothesis that Equation (3) is true and instead suggest that some other variable related to human activity (e.g., population growth) is responsible for the change in environments that led to change in behavior.⁵⁷

As we described earlier, HBE is flexible in its ability to incorporate additional variables into g_B , the model of behavior. However, an expanded model of the system dynamics (compared to Equation (3)) is needed if inheritance tracks for additional variables must be accounted for, for instance if the phenotypic gambit is violated, or if parts of the system mutually influence each other over time, for instance if behavior also influences the change in the environment (Figure 1). These ideas can be analytically linked to niche construction (cf. Equations (4) and (5) with equations (1.3)–(1.4) in Odling-Smee et al.²⁷).

For example, imagine a behavioral model specified by $B(t) = g_B(E(t), G(t))$. This could be a model to explain investment in dairying, for instance: g_B would be a function predicting dairying as a function of the environment (e.g., suitability for raising cattle), and genetics (e.g., the frequency of lactase persistence in the population). Dynamics of the inheritance tracks for genes, $G(t)$, and the environment, $E(t)$, could be governed by:

$$\frac{dE}{dt} = h_E(E(t), G(t), g_B(E(t), G(t))) \quad (4)$$

and

$$\frac{dG}{dt} = h_G(E(t), G(t), g_B(E(t), G(t))). \quad (5)$$

Here, the dynamics of genes, h_G , represents natural selection: genes change as a result of current genes, the environment, and behavior. In the classical population genetics view, h_E (the dynamics of the environment) is a function of only E ; that is, genes and behavior do not impact the future environment.^{27,90,91} The addition of genes and behavior to h_E makes this a niche construction model: the environment is not simply an extrinsic factor, but is affected by the actions of organisms.^{27,92} What is important about Equation (4) in particular is that it contains both HBE and niche construction elements: a model of behavior, and a model of how variables respond to each other through time, as part of a simplification of the more general Equation (1). Quite a number of other simplifications are possible that nevertheless involve niche constructing behavior. For instance, in this model we might make the perhaps plausible assumption that genes do not directly influence the future environment, doing so only through behavior. Moreover, for many archeological and anthropological research questions, genes may not be a relevant state variable or inheritance track at all.

6 | WAYS FORWARD

In the preceding section we have shown how HBE and human-focused NCT can be seen, analytically, as sub-fields of a broader field of multi-inheritance theory concerned with human behavior. A graphical summary of our view of the relationship between HBE and NCT is provided in Figure 2. In this final section we attempt to provide some concrete suggestions for linking the two bodies of theory in future archeological research and consider an illustrating case: archeological site size distributions.

First, a summary of what we think are important takeaways from our review. Archeologists interested in niche construction should be reassured that they need not necessarily “choose a side” in the debate over the extended evolutionary synthesis and standard evolutionary theory. Even critics of the EES^{28,32} agree that behavior can modify environments and influence future natural selection—the opposing camps within evolutionary biology disagree largely on whether niche construction deserves equal footing with natural selection as an evolutionary process. Regardless of these debates in biology, then, the best way for archeologists and anthropologists to contribute to the development of evolutionary theory is not with rhetorical claims, grand statements, or imprecise narrative models. Rather, we should lay our assumptions bare using formal analytical models and subject the predictions of such models to empirical testing. This will help us learn more about how niche construction works, and move us beyond simple assertions that niche construction exists and could have played a role in human evolution. As we detail below, we think this goal can be best accomplished through careful comparison of alternative hypotheses that do or do not include various inheritance tracks.

We have also noted distinctions between niche construction as a complementary process to natural selection, and niche construction as a kind of behavior, which require different kinds of analytical models. Finally, we hope to have clarified some persistent confusions

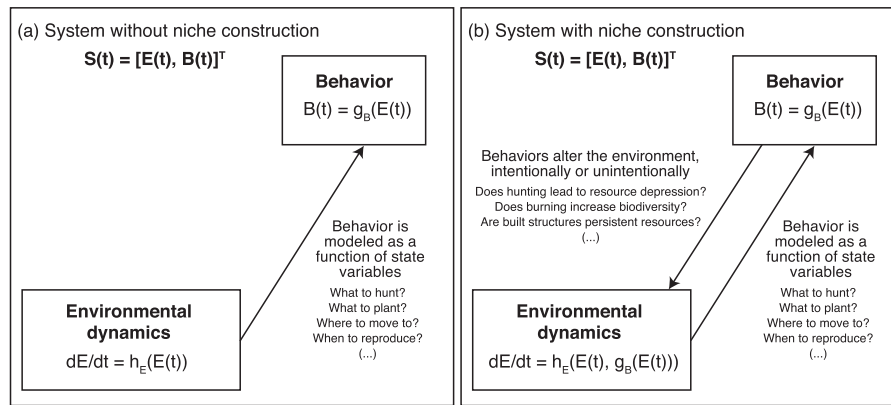


FIGURE 2 Schematic of a simple evolutionary system, S , with two state variables (B , behavior, and E , environment). HBE models, represented by the function g_B in the “behavior” component, focus on predicting behavior using a limited set of variables; for instance, based on the current environment, represented by an arrow from environment to behavior in the diagram. Change in the environment through time (dE/dt) is represented by the function h_E , which can also take a variety of inputs. For instance, in panel (a), representing a non-niche construction model, the impact of the organism on the environment is considered negligible. In (b), change in the environment is also influenced by the action of the organism on the environment, producing a niche construction model with an embedded HBE component

around HBE, some of which stem from a relatively narrow application of HBE theory within archeology. In particular, we have sought to clarify the misconception that using HBE models commits a researcher to a “gene-centric” view of evolution, or to an assumption that people do not actively modify their environments. HBE contains a much broader range of models than just the diet breadth model, and while retaining its focus on behavior, recent research in the field increasingly incorporates a broader range of social and cultural variables as factors in decision-making. In sum, like other proponents of HBE in archeology,^{39,40,42,57–60} we do not view HBE and NCT as competing bodies of theory but instead as complementary sets of concepts and tools: the first (HBE) focused on generating models of how people will act in view of a certain set of goals and constraints, and the second (NCT) focused on feedbacks of that behavior onto future conditions of the system.

To illustrate the complementarity of HBE and NCT, in the previous section we detailed a simple analytical framework for evolutionary systems that recovers each approach as a special case. We now draw on this framework to offer some practical advice that we hope will help archeologists navigate the development of a research project that engages with niche construction processes. This is by no means a comprehensive guide to archeological research design, but rather focuses on two steps that we think allow archeological research to narrow-in empirically on why and when different inheritance tracks and their dynamics constitute essential components of evolutionary explanations for human behavior. These are: (1) explicitly identifying the set of state variables and inheritance tracks under consideration and (2) collapsing (or expanding) the set of state variables and inheritance tracks included in a step-by-step manner. To highlight how these suggestions can be applied, we use a recent example that, to us, represents a well-thought through application of an NCT approach in archeology: Haas and Kuhn's examination of

Late Archaic Period hunter-gatherer settlement systems in the Lake Titicaca Basin, Peru.⁹³

We assume that the researcher has in mind already a research question or topic of interest relevant to evolutionary anthropology: for instance, why did domestication take place in one region at a given time but not in an adjacent area? In the case of Haas and Kuhn, their basic question is: what explains hunter-gatherer settlement strategies? In particular, they are interested in explaining variation in site size: why are a few hunter-gatherer sites extremely large, and many of them very small?

At this stage it is useful to consider what behaviors underlie the events, patterns, or processes related to the research problem. Is it decisions about mobility? About resource procurement? Adopting new technologies (or not)? Considering the behaviors involved can help with our first suggestion for implementing NCT archeologically, which is: determine which state variables you consider to be necessary for an adequate answer to the research question. Put another way, what are the relevant factors that condition the behaviors involved in the evolutionary process that interests you? Are environmental factors sufficient? Do you need to account for some important genetic or cultural factors or constraints, or do you think can they be safely ignored? This may seem difficult, but in practice this choice will often be guided by literature review. For instance, you may think past research has focused on the wrong set of variables, or has omitted an important one. Reading through existing literature and writing out the models within it as simple equations, such as those in the previous section, may be a helpful exercise.

We illustrate how this can be done with Haas and Kuhn's example, which shows clearly how to link a model of behavior with a model of process using an inheritance track. The behavior they are modeling is one related to mobility: which location should a forager choose to occupy? They suggest that the existing literature considers site choice

behavior simply as a function of resources in the “natural” environment, things such as water and food, that are in this case considered to be independent of human behavior. Using our earlier notation, we could represent this as: $B(t) = g_B(E_N(t))$: behavior is a direct function of E_N (the “natural” environment) at time t . They contend, however, that resources contained in existing sites, such as discarded raw material, may be an important additional factor motivating site choice. Consequently, they suggest an alternative model that includes cultural modifications to the site environment, which we label E_C , that is independent of other environmental resources: $B(t) = g_B(E_N(t), E_C(t))$. If all sites are identical in terms of available natural resources (meaning E_N is a constant), we can leave the dependence on E_N implicit, yielding $B(t) = g_B(E_C(t))$. Haas and Kuhn argue that, for their study region, this assumption holds.

Having specified the behavior(s) and state variable(s) that are relevant can then guide the choice (or creation) of a behavioral model to help derive predictions. Foraging theory is one potential option in some cases, but there is a much broader range of HBE and non-HBE models to choose from—the main difficulty in model specification is likely to be finding a model that generate predictions with potential archeological correlates. In Haas and Kuhn's case, they suggest that foragers should have a preference for sites that have existing available “cultural” resources. Consequently, they use a non-deterministic preferential attachment model to map between environment and behavior (g_B): foragers have a higher probability of choosing sites with more resources, but also sometimes choose other sites, for reasons that are not modeled.

The next step is to consider whether the dynamics of the state variables, that is, their inheritance tracks, need to be included, and if so, how they should be modeled. If one of the inheritance tracks represents environmental change, then paleoenvironmental evidence can potentially be used to represent it, as in many archeological applications of foraging theory. If environmental change is assumed to be independent (not influenced by past behavior), its dynamics may not need to be explicitly modeled but instead just treated as a factor in a decision-making model—this is typically how tests of diet breadth have operated. Other inheritance tracks will likely require modeling to understand how they may change through time. In Haas and Kuhn's case, change in the culturally-modified environment is influenced by the past environment and by past behavior. The function h_{E_C} in this case simply specifies that whenever foragers occupy a site they enrich it, leaving behind “resources” there that are attractive to potential future occupants. The preferential attachment model for site choice behavior means that previously occupied sites exert a greater pull on foragers in the future. Haas and Kuhn generate predictions what for distributions of archeological sites generated by this process should look like using a very simple agent-based model.

We note that using our previous notation, the two differential equations specifying the system evolution in this case are

$$\frac{dE_C}{dt} = h_{E_C}(E_C, B) = h_{E_C}(E_C, g_B(E_C)) \quad (6)$$

and

$$\frac{dB}{dt} = h_{E_C}(E_C, B)g'_B(E_C) = h_{E_C}(E_C, g_B(E_C))g'_B(E_C). \quad (7)$$

Equation (6) shows clearly the embedding of a behavioral model within the model of temporal change.

Once a model of behavior and relevant dynamics has been defined, the process can be repeated with an alternative hypothesis. In Haas and Kuhn's study the alternative hypothesis is not explicitly modeled: they argue that, in their case study, environments are relatively stable across the landscape and through time, and therefore the hypothesis that the formation of large sites is driven only by availability of “natural” resources is disproven a priori. Their preferential attachment model provides a possible mechanism for the creation of large sites in the absence of environmental variability.

The value of including different state variables and their inheritance tracks can then be evaluated by comparing the available archeological evidence to the predictions of models that do or do not include them. We suggest approaching this problem by starting with the simplest possible model and gradually relaxing the assumption that various variables and their inheritance tracks can be ignored. The key is to determine whether more complex models explain added features of the data that cannot be explained by simpler versions, or whether the differences between the models simply cannot be discerned with the available evidence (see Box 1). Whether or not more complex models are helpful for answering different research questions is a matter for empirical investigation.

We note four ways that one might alter a joint behavioral-niche construction model: by proposing (1) a different behavioral model for the same set of predictor variables (e.g., changing the objective function of a foraging model); (2) a behavioral model that uses a different set of state variables (e.g., adding another variable into the decision model); (3) a different specification for the dynamics of the same inheritance tracks; or (4) a different set of inheritance tracks. For example, a logical next step to build on Haas and Kuhn's work would be to test the preferential attachment model in a case where there is also heterogeneity in site quality; that is, where both the “natural” and “cultural” environmental states inform decision-making. This would require modifying the behavioral model to incorporate the role of variation in access to natural resources (perhaps water) in site selection; and could require tracking changes in quality across sites through time, for instance, if water availability changed significantly through time in the study region. Alternatively, one might propose a model that instead focuses on social interaction as a factor in site choice behavior. Many models may result in similar or even identical archeological predictions (Box 1), but this does not obviate the potential value of this approach for helping us discover new patterns in the archeological record, disproving alternative hypotheses, or uncovering the range of scenarios plausibly compatible with the archeological record.

BOX Equifinality

Equifinality occurs when two or more distinct processes lead to identical or similar outcomes that cannot be distinguished given available data and statistical methods.^{96,97} For instance, perhaps the proportion of small-bodied animals changes through time in a site's faunal assemblage. One explanation could be that preferences for what type of animal to eat changed over time. Alternatively, perhaps taste has not changed but the relative abundance of animals has changed, due to over-hunting or climate change. Without additional evidence for one of these hypotheses, we cannot know what explains the shift.

The example we describe in the text also has issues with equifinality. Haas and Kuhn suggest that site areas should be distributed log-normally. However, many sets of objects that “grow” over time (for whatever reason) might be expected to have a log-normal distribution of sizes, so it is unlikely that this characteristic of site distributions can be uniquely linked to the preferential attachment model. Thus, despite a well-thought through theoretical approach, the empirical predictions made by Haas and Kuhn still have considerable limitations. This is not a critique of their approach but rather intended to highlight a general problem in archeology. The predictions are still helpful, as they could be disproven, but they are potentially compatible with multiple hypotheses.

Broadly, there are two means to deal with equifinality. The first involves using additional types of data to resolve the equifinality by demonstrating that one or more possible explanations (e.g., climate change not caused by human activity) can be ruled out. This is the most commonly-used approach in archeology today. An alternative approach to dealing with equifinality is adopting statistical methods that can accommodate it. For example, with a Bayesian approach, one can assign different prior probabilities to alternative explanations, and update these prior probabilities using the available data to yield the best posterior assessments of alternative hypotheses.⁹⁸ Since a range of useful data—such as evidence for what has occurred in other regions—can inform the priors (and the models), one can effectively accommodate the ambiguity imposed by equifinality in a statistically rigorous way. Nevertheless, some hypotheses may be truly indistinguishable on the basis of archeological evidence.⁹⁶

7 | CONCLUSION

In conclusion, we note some important potential implications of the research strategy we outline above. First, the call to consider multiple inheritance tracks means that research will more often have to be coordinated across sub-specialties that still often work somewhat independently (e.g., zooarcheology, lithic analysis, and bioarcheology). Second, deriving archeological predictions that account for the inheritance tracks is not something that can easily be done intuitively. Thus, to better engage with NCT, archeologists will have to overcome a common aversion towards math and computer programming. Agent-based models are the most commonly-used and most accessible tools for this task.⁹⁴

The latter point is also related to the need for archeologists to move beyond a correlational approach and to focus on identifying causal mechanisms that can connect different features of the archeological record. Marean and colleagues have called for more paleoenvironmental research to address this problem,⁹⁵ and to this we add the need for more ethnoarcheological research that can help us better understand how cultural inheritance tracks shape the material record. Finally, even with better theory and data, the archeological record will still often continue to present problems of equifinality, which means that alternative hypotheses may still not be distinguishable on the basis of the available evidence.

In summary, we argue that NCT and HBE are not only compatible but complementary: HBE can provide a lens into past human behavior, and NCT into the impacts of that behavior on the environment (broadly defined). Further, HBE provides a modeling

strategy that can be used to generate new models for why and when people engage in niche-constructing behaviors. The HBE approach is not limited to using only energy maximization as the goal of resource-use behavior, nor is it incompatible with cultural and social influences on that behavior. We suggest that by clearly specifying which state variables and inheritance tracks are essential components of a hypothesis, archeologists can be guided in the design and/or selection of behavioral models and in the choice of how (and if) to model the feedbacks between behavior and environmental states. Nevertheless, regardless of the theoretical approach taken, the empirical challenges of archeology persist. NCT, HBE, or any other theory does not allow us to escape the ever-present specter of equifinality.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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