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# Operationalizing niche construction theory with stone tools

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## Abstract

One of the greatest difficulties with evolutionary approaches in the study of stone tools (lithics) has been finding a mechanism for tying culture and biology in a way that preserves human agency and operates at scales that are visible in the archaeological record. The concept of niche construction, whereby organisms actively construct their environments and change the conditions for selection, could provide a solution to this problem. In this review, we evaluate the utility of niche construction theory (NCT) for stone tool archaeology. We apply NCT to lithics both as part of the "extended phenotype" and as residuals or precipitates of other niche-constructing activities, suggesting ways in which archaeologists can employ niche construction feedbacks to generate testable hypotheses about stone tool use. Finally, we conclude that, as far as its applicability to lithic archaeology, NCT compares favorably to other prominent evolutionary approaches, such as human behavioral ecology and dual-inheritance theory.

KEYWORDS
cultural evolution, lithics, niche construction

## 1 | INTRODUCTION: THE NCT PROMISE FOR ARCHAEOLOGY

In the last few decades, evolutionary biologists and social scientists have reached a consensus that an adequate understanding of human evolution cannot ignore culture as an active influence on evolutionary trajectories. Overtures made to one another resulted in various schools of thought on how best to integrate biology and culture, such as human behavioral ecology (HBE),[1] gene-culture co-evolution (or dual inheritance theory, DIT),[2] and evolutionary archaeology.[3] The extended evolutionary synthesis (EES), the most recent addition to this list, adds a constructivist, and internalist perspective that archeologists, and social scientists in general, find intuitively appealing. It introduces the process of niche construction,[4] which refers to organisms actively modifying their surroundings, and therefore, the conditions for future selective pressures on themselves and their descendants.[5] This process extends similar concepts from evolutionary biology, such as ecosystem engineering,[6] to include socially learned and transmitted behaviors, including culture. Although niche construction theory (NCT) states that all organisms engage in niche construction, humans immediately stand out as the most capable regional or even global scale environmental engineers.[7] Moreover, because the study of human evolution is often plagued by the difficulty of studying the historical process of becoming human while avoiding circular arguments surrounding the definition of humanity itself, it is exactly its applicability to human and animal alike that makes NCT attractive. To date, most NCT discussions center on the origins of food production,[8] which are the most obvious examples of early human ecosystem engineering on a large scale. Although hunter-gatherers clearly also construct their environments,[9] this leaves subtler material traces, with lithic use in hunter-gatherer niche construction only rarely considered.[10–12] Here, we review the ways NCT serves as an explanatory framework in stone artifact archaeology and generates testable hypotheses, while also comparing it to other commonly employed frameworks. We conclude with possible contributions for refining aspects of NCT and suggestions for future research.

## 2 | NCT AS AN EXPLANATORY FRAMEWORK IN ARCHAEOLOGY

NCT combines most theoretical strands of archaeology via three major concepts. First is the concept of triple inheritance, which adds an ecological inheritance[13] to the genetic and cultural information that humans inherit as posited by dual-inheritance theory (DIT). Thus, cultural artifacts with longer temporalities, such as domestic spaces,[14] monuments, or even constructed landscapes, become part the ecological inheritance passed on to future generations.[15] This allows us to think of human artifacts having evolutionary significance despite their apparent lack of immediate selective advantages. Second, NCT integrates human agency into evolutionary thinking. As organisms can actively modify their environments by perturbation (physically changing them) or relocation (moving to a location where conditions are different), and because this modification can be inceptive (initiated by themselves),[4] this framework allows consideration of human agency in causal arguments about behavioral adaptation. This is in contrast to classic evolutionary approaches in archaeology, where nearly all material culture could ex post facto be considered adaptive.[16] Third, NCT provides a method for hypothesis testing, which involves seeking closed feedback loops among the three inheritance systems. The greatest difficulty lies in establishing in which of the three inheritance systems a particular cycle began (a problem for the directionality of causation). Yet, with the focus on chronological controls and the long time spans captured by our datasets, archaeology is already well set up for answering this type of question.

Despite the advantages, NCT applications in archaeology face two major challenges,[17] which have kept them largely restricted to the Holocene (but see below for Pleistocene examples). First, for hunter-gatherer and highly mobile societies, the scale of visible human impact is small compared with the large-scale transformations witnessed during the process of early food production or indeed the Industrial Revolution.[18] This lack of visibility is unfortunate, as the part of the archeological community that is most likely to adopt evolutionary theory usually studies material from earlier time periods (e.g., Plio-Pleistocene). However, NCT includes a broader set of actions by which organisms modify their environments, including relocation, which, as we discuss below, is key to understanding the older part of the record.

Second, establishing reciprocal causation feedback among the cultural, ecological, and biological inheritance systems becomes more difficult as one reaches further back in time. The link between cereal agriculture and the evolution of the gene for amylase[19] provides a neat example of a cultural practice affecting the gene pool. However, we are only just beginning to probe functional variation in archaic genomes. The hypoxia pathway gene, for instance, is an altitude adaptation present in Tibetans but not in neighboring Han populations, suggesting a Denisovan introgression.[20] The latter's extremely early occupation of high-altitude areas of Asia (a possible example of inceptive relocation), was recently confirmed by archeological discovery.[21] These few examples suggest possible ways in which hypotheses could be set up to search for evidence of niche construction in the deeper past.

## 3 | LITHICS AND NICHE CONSTRUCTION

As lithics are generally well-preserved, they serve as a proxy for cultural behaviors that persisted for an extended period of time allowing integration with ecological evidence and behavior linked to skeletal biological changes (i.e. genetic changes) in the hominin lineage. Stone artifacts thus form one of the backbones for the application of the triple inheritance theory.

### 3.1 | Lithics as an "extended phenotype"

Fundamentally, a sharp stone flake ("sharp") extends the body (sensu Dawkins[22]). It functions by concentrating the force applied by the forelimb onto a small point or line, thereby cutting or slicing food items, or non-food items that expand foraging capabilities

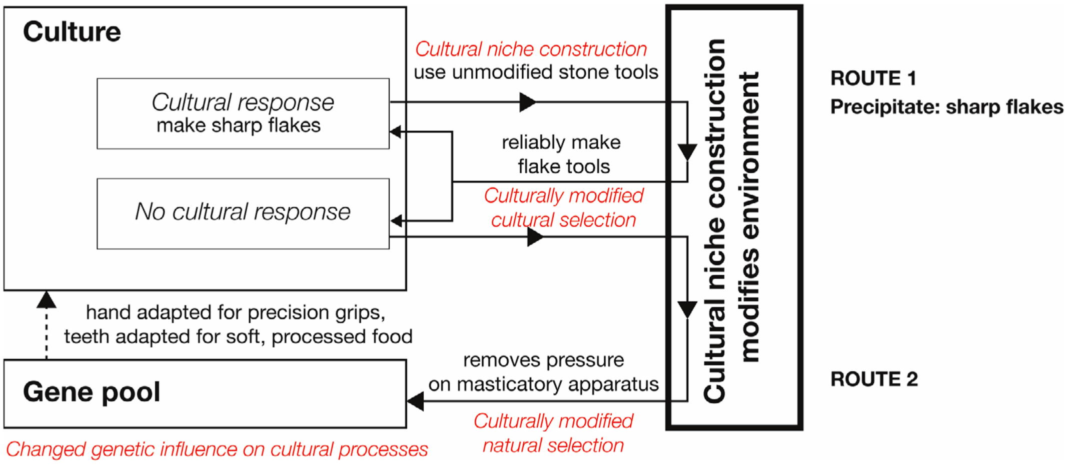


**FIGURE 1** Niche construction feedback loops related to the appearance of the first stone tools. Adapted from Odling-Smee et al[4]

(e.g., digging sticks). An NCT perspective sees the first stone tools as part of a process of externalizing food ingestion from the mouth to the hands.[23] Experiments show that using a stone tool to slice meat reduces the force for chewing and the size of the resulting bolus.[24] Moreover, the first routine, or "obligate"[23] use of flake tools[25] has relative contemporaneity with a reduction in chewing musculature[24] possibly preceded by the use of minimally modified stones focused on fat extraction from marrow.[26] Here, the niche-constructing trait, use of unmodified stone artifacts, produces a biological response (reduced cheek teeth), influencing further selection for the ability to make flakes (Figure 1). It is possible that the use of stone artifacts to process food resources, either plants or animal tissues[27] results in an adaptive release on brain size. Similarly, the potential reduction in the hominin digestive tract (relative to a presumed last common ancestor) may be explained by increased use of stone artifacts to modify food resources outside of the body as posited by the "expensive tissue hypothesis".[28]

## 3.2 | Lithics as niche construction residuals and precipitates

Several studies investigate properties of early stone artifacts as parts of the extended phenotype. For example, the calculation of the force required to hold,[29] make,[30] and use[31,32] stone tools show potential feedback loops between biological constraints and prehistoric gestures. Connecting these studies to hominin fossil changes provides a rare opportunity for interdisciplinary hypothesis-testing. However, other studies suggest a change in perspective, away from the notion that lithics themselves are part of the extended phenotype. First, in many contexts, stone artifacts were only *part of* more complex tools and technologies, often involving handles, shafts, glues, poisons, and other materials. Lack of preservation of such technologies leads to their absence referred to as "the missing majority".[33] Second, lithics have use-lives in excess of human generations, meaning their utility and contribution to fitness can transcend initial use. Here, NCT again provides a useful framework for thinking about long-term stone use and reuse. One might go a step further and propose that lithics can be thought of as "residuals" or "precipitates" of a process of niche construction scaled variously in time and space. This process involves ranges of activities conducted across past landscapes, forming a complex web of relationships with other objects of the physical world and with other humans and animals. This view keeps the fundamental structure of NCT reasoning without forcing a reification of culture *as* lithics. Below we give some examples using four categories of niche construction as broadly defined by Odling-Smee.[4] As mentioned above (see Section 2), he classifies NCT as being either inceptive (initiated by the organism) or counteractive (responding to a prior environmental change), and as consisting either of a perturbation (changing of the environment) or relocation (movement into a new environment).

### 3.2.1 | Lithics as residuals of counteractive perturbation

The most obvious example of an early technological response to environmental change is the development of clothing,[34] a modification of the organism's immediate environment to regulate temperature and moisture countering a prior change in climate. Given that humans evolved in the tropical Africa, and were likely naked before their first expansion,[35] the *prior* change in the environment likely involved an *inceptive relocation* (movement into the temperate zones of Eurasia). Clothes generally do not preserve, so the best early evidence for their use comes indirectly, from hide processing. This use leaves characteristic traces on stone tools.[23,34] Moreover, traces of hide scraping tend to be found on tools with an identifiable morphology—scrapers.[36] Some have repeatedly referred to various other technologies (e.g., Shea modes D1 and G2,[23] Levallois flakes, or prismatic blades[34]) as particularly well suited to cutting and possibly tailoring leather. However, the link between morphology and

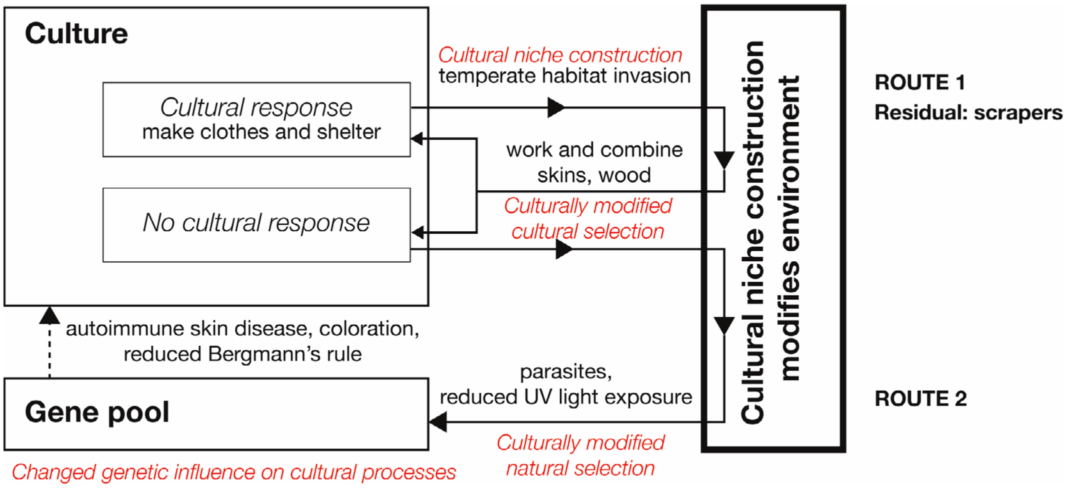


**FIGURE 2** Niche construction feedback loops related to the production of clothing. Adapted from Odling-Smee et al[4]

function is weaker in these than for scrapers.[37] The need for more efficient clothes created a selection for the ability to work and shape skins, but also bone and ivory for creating smoothers, needles, and awls for sewing and piercing hides. This cultural feedback loop (Figure 2) likely existed among Neanderthals[38] and accelerated during the early Upper Paleolithic settlement of the higher latitudes in European Russia and Siberia.

#### 3.2.2 | Lithics as residuals of inceptive perturbation

One of the classic cases of inceptive perturbation in hunter-gatherer societies is the controlled use of fire. Paleolithic archaeology examples often involve hearths, with examination of hearth-centered life emerging during the Middle Pleistocene.[39] But recent studies consider patch burning as ecosystem engineering among Australian hunter-gatherers who use it to increase their hunting returns for sand monitor lizards (varanids[40]). Suggestions that the behavior occurred at various times in the Pleistocene[41] highlight the social and ecological ramifications of fire regime management. Yet still little is known about the control and habitual use of fire in the earlier parts of human evolution, probably due to difficulties identifying intentional fires, especially in ephemeral situations[42] leading some to question its relationship to temperature regulation and cooking.[43] Yet fire-making may leave durable traces in the lithic record, in the form of use-wear traces on stone artifacts that were probably used as strike-a-lights[44] or as heat-fractured lithics[45] and heat retainers in some situations.[46] The very existence of these artifacts of human behavior is a sign of the changed selection pressures. Prior to these changes, hominins could not modify landscapes in such a dramatic way. Once hominins were able to make fire *anywhere*, through controlled, or even opportunistic production and use, landscape modification was likely inevitable.[47] Should these traces begin to be recognized more widely, the record of fire use could be better understood, despite patchy charcoal records.[48]

Inuit hunting weapons provide a more direct example of a lithic residual of inceptive perturbation. Friesen[49] describes caribou dispatched using either lances or bow-shot arrows. This, in turn, provided selective criteria for the different construction of game drives (narrow vs. wide openings). The much longer temporality of the constructed drives, now part of the ecological inheritance of both predator and prey, further reinforced the hunters' technological choice. Here, historical analysis reveals that the weapon technology (with a lithic residual) was invented first, and is thus the niche-constructing trait. However, the whole process occurs in the archeological record via the visibility of drive architecture.

An even more direct example involves the provisioning of places with re-usable stone artifacts[50] documented in parts of semi-arid western New South Wales Australia.[51] Here, people carrying cobbles used as cores, anvils, and even as grinding stones effectively made a lasting change to the environment of future generations. The conditions for selection of mobility and foraging strategies in these stone-poor, sandy landscapes were altered. The macro-scale patterns that emerge from the re-use of available stone on the landscape constitute a major determinant in the character of the lithic archeological record.[12,52,53] Here the stones are both the precipitate of the cultural niche construction *and* part of the ecological inheritance passed on to the offspring.

#### 3.2.3 | Lithics as residuals of counteractive relocation

Like many animals, humans relocate to avoid transitory environmental states to which they are poorly adapted.[4:65] Examples include summer and winter camps used for only parts of the year. Ethnoarchaeological studies describe changes in material culture that correlate with seasonal shifts in settlement pattern.[54] The key in archeological studies involves analyses that actually document movement rather than hypothetical expectations of mobility patterns. The most direct indicator is through raw material sourcing and artifact refitting.[55] Yet, while these difficult and labor-intensive approaches can unequivocally demonstrate the translocation of objects from Point A to Point B,[56] it remains challenging to evaluate the nature of human movement behind the transport events. Alternatively, an analytical methodology known as the cortex ratio[57,58] provides an objective measure for detecting and comparing past movement. A case study drawn from two different environments illustrates how people in the past practiced different forms of counteractive relocation.[59] Australian Aboriginal people faced environments with unpredictable resources reflecting a variable rainfall and low environmental nutrients. These communities adapted to a flora and fauna evolved to deal with unpredictable environmental changes. This adaptation operated at a variety of temporal and spatial scales in a topographically undifferentiated landscape characterized by high local heterogeneity but little systematic, regionally predictable patterning. Analysis of stone artifacts indicates frequent movement over considerable distances. This contrasts with the US Great Plains, a region of "islands" within a grassland "sea".[60] Similar to the Australian example, people here also transported stone artifacts. However, in Australia, artifact diversity is present only at the smallest, local level. Expanded to the scale of an entire drainage system, there is no association between landform pattern and the patterns of tool use. In contrast, within relatively circumscribed areas of the Great Plains, differences in raw materials, in artifact size, and in degree of retouch are apparent. In this region there are distinct, highly redundant, sets of stone artifacts indicating similar behavior within unique topographic and ecological contexts. In the Great Plains, places were used in similar ways throughout history but differently to other places in that landscape. In Australia, different places were used in largely similar ways reflecting a lack of fixity in landscape elements. This example demonstrates the excellent potential of lithics to illustrate different scenarios of counteractive relocation, particularly at a landscape scale, within and among regions of different environment and land-use history.

#### 3.2.4 | Lithics as residuals of inceptive relocation

Dispersal and habitat invasion, which are types of inceptive relocation, are frequently studied in human evolution. Most animal dispersals are dictated by ecological factors, such as resource depletion or the expansion of underlying sources of food (plants or other animals). For the earliest dispersals, the residual we seek is obvious: any simple presence of stone tools will do. The fact that subsequent human expansions out of Africa involved the invasion of the niches of archaic hominins[61] makes this exercise more difficult, because we are seeking, to a certain degree, the signature of culture contact. Initially, archeologists believed the newcomers had prior superior technologies, which would have made their adaptation to the new environments and/or outcompeting previous populations easier, while the local populations attempted to copy them.[62] However, the existence of documented successful dispersals or local populations' cultural adaptations without these technologies calls into question this argument. Modern humans most likely started to expand into southwest Asia after MIS 6[63] using lithic technologies that are essentially indistinguishable from those of the local Neanderthals.[64] Archeologists initially believed that these were unsuccessful dispersals, and that moderns were essentially unable to outcompete Neanderthals. A similar case can be seen on the island of Flores where the lithic technology of *Homo floresiensis* showed few differences to that associated with modern humans who arrived on the island later around 46 ka.[65] This is thanks to our inability to track people without a strong culture-historical signal at this time and to the discrepancy between the expectations generated by ecological models and the patterns observed in the archeological record. Seeing expansion (especially into another hominin-occupied territory) as niche construction provides a model for understanding what the lithic record might show. African hominins did not simply bring their technology with them, but they also received an ecological inheritance created by established patterns of predation and patch exploitation of local populations, in addition to site use and re-use, and so on. The record should, therefore, reflect the interaction of both.[53] The challenge is how to study this interaction.

#### 3.2.5 | Lithics as residuals of the cultural niche

The importance of the very process of creating the human cultural niche to begin with, touted as "the secret of our success"[66] is not lost on archeologists. Some[67] have argued that culturally-mediated behavioral plasticity itself is our species' fundamental niche. There is a general consensus among behavioral scientists that humans possess a capacity for learning different in kind, not only degree, from that in any other animal, and set apart by its cumulative character, achieved through a ratcheting effect of high-fidelity copying and imitation.[68] Sterelny[69] argues that the construction of the developmental niche made this possible, facilitated by copying cultural behaviors and products beyond the level of spontaneous discovery. Although leading to runaway complexity in cultural niche construction (Odling-Smee's Route 1, see Figures 1 and 2), the feedbacks to the genetic system were significant. The cognitive capacities involved in sustained social learning rest upon an anatomical architecture that had to evolve over time and includes not only a bigger brain and a vocal tract adapted for producing language, but also an increasingly honed set of fine motor skills. Although some believe there is no particular moment in time when humans became behaviorally "modern",[70,71] it should be possible to figure out when we surpassed the primate baseline, and lithics might be able to answer this. One possibility is to set the null hypothesis at low-fidelity copying behaviors and "latent solutions" that are easily re-discovered by individuals[72] investigating deviations in high-fidelity copying required for cumulative culture. In this view, Oldowan[73] and possibly Acheulian,[72,74] tools appear unchanged for millions of years because they are easy- to- reinvent "latent solutions". However, critics[75] claim this null hypothesis is difficult to falsify and thus rejects cultural transmission in too many cases.

## 4 | HOW LITHICS CAN INFORM NCT

As some[23,76] have recently remarked, archaeology in general, and especially lithic archaeology has largely functioned as a receptacle for theory imported from other sciences. And yet, given our discipline's unique focus on the long-term perspective on human history, and given the immense record of stone tools that we possess, we believe there are important contributions to be made. In particular, it is important to know if the uniqueness of human niche construction manifested itself from the very beginning of human evolution and how this might have differed from the obvious transformations of the planet we know from later periods.

### 4.1 | Lithics, culture history, and cultural evolution

Few archeologists would disagree that it is important to know when fire, projectile weapons, boats, and domestic structures were first invented, and if any of these were subsequently lost. From the perspective of niche construction, the day to day business of recording when a particular type of material culture appeared and how it developed is crucial for establishing which traits can be considered as "recipient" and which as "niche-constructing".[4,17] For instance, it makes a huge difference if hominins expanded from Africa naked or clothed, and even more so if there were differences in that respect between the early expansions and the later ones. It also makes a huge difference if the precision grip developed before or after the beginning of stone-knapping, and the same holds for high-fidelity copying. Many such examples exist and all come under the category of "big" culture history, the history of technological development or evolution writ large. Unfortunately, the value of what might be termed "little" culture history, the tracking of particular "traditions," "archeological cultures," and technocomplexes through space and time, is not so apparent. Largely abandoned in anglophone academic archaeology following the processualist critique, this version of culture-history has made a comeback, through renewed interest in applying evolutionary theory to archaeology generally.[77] At issue is whether culture is fundamentally adaptive or neutral. HBE approaches tend toward the former, but some comparative anthropological work has shown that cultural history often supersedes ecology with respect to cultural trait expression.[78,79] This is often used as a justification to focus on modeling the transmission of cultural traits as if they were neutral,[80] with copy-error mechanisms generating variation.[81] But, as Laland and Brown[82] explain, there could be several behavioral patterns that are (near-)optimally adaptive, and cultural history merely determines which of these is chosen in a particular group or situation. Historical contingency may be as important as the adaptive context for some cultural variants. Moreover, time-budgeting may actually affect copy error rates, thus affecting the strength of evolutionary change.[83] If this leads to traits becoming fixed very fast, we may not be able to "see" a group in the process of adapting, but only the complete, well-adjusted variant.

Since in some sense, copy-error occurs in any cultural context, and since it can in theory be measured from artifact morphology, there are calls to focus on tracking cultural phylogenies of artifacts[84] as a way to describe macroevolutionary processes. Others have focused on rates of change[85] and defining[86,87] and measuring the complexity of lithic technology[88] so that it can be studied at the millennial scale and beyond. The search for macro-scale patterns in cultural evolution has also brought about a discussion about how innovations can change the tempo and mode of cultural evolution,[89] and how these, in turn, can be lost again.[90,91] However, these studies face a range of issues, from the determination of finished products from which deviations might occur and the determination of particular artifact forms or sets having specific culture-historic significance through to the determination of what constitutes a group in culture-historical terms.[52]

NCT approaches may help to bridge "big" and "little" culture history approaches since multiple data sets are correlated. In the Inuit example above,[49] cultural history (tradition) determined which kind of weapon was used by the different groups (spear or bow and arrow), and that in turn created the conditions of selection for the kind of caribou drive built. While not stated in these terms, the construction of drives permanently affects the landscape and becomes part of the ecological inheritance. Riel-Salvatore[10] incorporates hunting pressure on small animals into a discussion of niche construction at the Middle to Upper Paleolithic transition. Riede[92] also uses phylogenies of lithic projectile points to explain different pathways in niche construction related to reindeer economies and dog use during the Postglacial.

But, as we showed above, lithics themselves are not culture, they are simply residuals/precipitates of cultural niche construction. Even if culture history is informative at a basic level to the overall Extended Evolutionary Synthesis, it does not give the entire picture. To complete it, we can turn to the study of human (and hominin) practice with material objects, in this case specifically, with stone tools.

### 4.2 | A hidden contribution: Lithics as residuals of human practice

Most of the evolutionary approaches to lithics privilege some types of information, such as manufacturing and form, over others, such as tool use or landscape-scale movement. Using the techno-morphology of stone artifacts and assemblages as the main focus of analysis raises a series of challenges.[93,94] First, the scale of inference is often mismatched to the scale of observation[76] because the relationship between individual decision-making and the operational sequences involved in stone tool production are not the only forces that shape the lithic record.[52,55] Instead, what we measure are the properties emerging from recursive actions involving selection, movement, modification, use, and discard, as well as contextual processes such as sedimentation, and erosion.[95] Second, focusing on techno-morphology privileges information coming from sites and regions where these attributes are visible, numerous, and variable enough for analysis. This creates a bias against studying records where the majority of artifacts are unretouched[96,97] or tiny[98] flakes, or those where artifact densities are low,[99,100] or where surface archives dominate.[52,101–104]

Evolutionary studies using such archives sometimes focus on why those places lack the "complexity" of others with more apparent variability of techno-morphological attributes. Others, however, show that, while the stone artifacts may be morphologically simple, the behavior they index was far from it. Furthermore, patterns of selection and transport suggest that the most important parts of stone-artifact use were happening off-"site" at locations away from the densities archeologists usually study.[105–107] Still other studies[108] demonstrate the hidden complexity of some "expedient" technologies in terms of the multitude of materials processed with them and their use within composite tools.

Moreover, assemblages, sites, and settlement patterns are themselves constituted by the interaction between landscapes and people, including the archeologists who define them.[95] Some of the geomorphic effects on the visibility of the archeological record, such as the dependence of perceived cultural rates of change on the age of the deposit and its degree of time-averaging[85,109] can be generalized more than others that are region- and topography-specific. For example, the existence and availability of caves and rockshelters[110] will create entirely different records than those seen in loess plains and deflated or accreted stony deserts. This has a double meaning: hominins choose to return to sites they previously occupied, partly in order to use tools left there,[111,112] and these choices are both influenced by their own perception and cultural categorization of the environment, impacting at the same time the strength of the signal that is later picked up by archeologists. Moreover, by repeatedly occupying only a subset of all possible locations, they also modify their surroundings and affect their ecological inheritance, and hence, the conditions for further selection.

Because hominins are such proficient niche constructors and because of our behavioral plasticity, we should expect behavioral responses to selective pressures, both natural and cultural, to be complex. This means that even if technology is generally an important adaptive domain, it forms only a part, and sometimes only a small one, of behavioral adaptation, even if it leaves the most durable trace.[113] Cultural evolution theory correctly emphasizes the importance of historical contingency in cultural pathways. But artifact production is not the locus of all cultural activity involving material objects—quite the contrary, people make and maintain artifacts to *use* them. And it is sometimes the cultural performance[114] rather than repertoire of items that contains the behavioral complexity. The case of the alleged Tasmanian "cultural decline" illustrates this perfectly. The low number of formal (retouched or shaped) tools was first thought to stem from a loss of cultural knowledge caused by demographic factors,[91] but a more careful assessment of both the archeological and ethnographic record revealed that the Tasmanians' behavior, using supposedly simple tools, was as complex as that of their mainland neighbors.[90,114]

Finally, material objects have different temporalities, and their meanings can shift as a function of their relationships to one another, their "entanglements".[115] A biface can also be a strike-a-light,[44] or a discoid core,[116] perhaps 200 years later, perhaps at the same time. Accumulations of grinding stones can be "site furniture"[52] or focal landscape points for mobile hunter-gatherers fixed on returning—or more simply the co–/re-occurrence of grinding behaviors over the long-term in places where grasses for seed grinding are present.[105] Recognizing the ubiquity of these entanglements requires a nuanced view of the lithic record, one incompatible with simply measuring techno-morphological attributes. However, there are also tangible benefits to this approach in studying long-term patterns, namely that cumulative culture juxtaposes and combines the temporalities of different cultural products, sometimes significantly as we saw with the appearance complex clothing. There is some evidence that the earliest musical instruments, like bows and percussion instruments, but also flutes, may have been adapted hunting implements.[117]

Thus, it may well be that the archaeology of the *practice of stone use*[95] may produce more reliable and more complete approximation of the history of human cultural niche construction than the traditional approaches based exclusively on manufacture and techno-morphological attributes. This contribution is also one that only archaeology can make within itself as a field, because the ethnographic record, as useful as it is, cannot contain the full diversity of past ways of life.[118]

## 5 | DISCUSSION

NCT provides several useful concepts for lithic archeologists, which, in our view, give it an advantage over other evolutionary approaches in archaeology (Table 1). First, the feedback loop allows for strong hypotheses, with rigorous chronologies distinguishing the niche constructing from the recipient traits. Second, the triple inheritance system, well suited to the lithic record because of its multiple temporalities, allows for the inclusion of inferred aspects of this record into the ecological inheritance. And finally, it allows the investigation of phenomena at the scale that is more appropriate to the data we can collect.

The scale problem is a serious one. By far the most influential current approach in evolutionary studies of lithic technology is HBE, as exhibited primarily by the technological organization school (see Shott[119] for a review). Stiner and Kuhn[39] argue that HBE and NCT could be used complementarily to generate hypotheses at different scales. In theory, this makes sense, because even when hunter-gatherers actively construct their environments, such as by burning landscapes, they usually intend to maximize immediate returns in hunting, rather than planning to alter long-term species abundance and diversity.[9] Yet it is clear that at the temporal resolution afforded by the lithic archeological record, HBE hypotheses are severely underdetermined.[76] Moreover, not only is the scale of individual human decisions inaccessible to the analyst, but even the basis for assuming optimally rational behavior may be culturally-dependent in an equally inaccessible way.[120] The solution proposed by DIT is to focus exclusively on identifying the type of transmission mechanism. Mathematical models provide a solid linkage between long-term patterns and micro-scale transmission processes, but in practice, choosing the relevant type of transmission still requires knowledge about how ancient societies functioned at a temporal scale for which the archeological

**TABLE 1** Comparison of the most commonly encountered evolutionary approaches in lithic archaeology. HBE—Human behavioral ecology; Evol. arch.—evolutionary archaeology; DIT—dual-inheritance theory; NCT—niche construction theory. Adapted from Laland and Brown,[82] table 8.1

| | *HBE* | *Evol. Arch.* | *DIT* | *NCT* |
|---|---|---|---|---|
| Scale of process | Micro | Macro | Micro/macro | Macro |
| Model generation | Optimal foraging models (mathematical) | Selectionist argument | Mathematical transmission models | Selectionist feedback arguments |
| Is culture adaptive? | Yes, always | Yes, always | Neutral | Usually yes, but it changes conditions for selection |
| Culture-biology relationship | Technology used to optimize foraging | Artifacts are part of the phenotype | Culture functions *like* biology, but separately | Each changes selective pressure on the other and on itself |
| Relevance to lithics? | Time and economic constraints on toolkit | Artifact form as evidence of selection | Artifact form as evidence of transmission | Artifacts as residuals of cultural practice/part of ecological inheritance |

record is too coarse. Moreover, anthropologists have critiqued DIT for having an overly simplistic view of cultural transmission biases, and for viewing culture as "packages" to be handed down.[115] As the Tasmanian example shows, there are many domains of cultural knowledge whose transmission is much more difficult to quantify, including much of the ecological knowledge about managing animals, weather patterns, landscape locations, etc.

This reinforces a point that may be uncomfortable for lithic specialists to accept: that lithics, beyond that early period when stone artifacts first became part of the standard hominin behavioral repertoire, may, in large part, be peripheral to cultural evolution. The logic of NCT impels archeologists to think of them only as "residuals" of other culturally-mediated activities and as parts of the ecological inheritance.

Although we see a lot of potential in NCT for extracting evolutionary meaning from the lithic record, it is not without some philosophical issues. First, it is unclear whether NCT as a scientific theory actually *explains* anything rather than just describing processes.[121] More specifically, one of the strongest critiques leveled at NCT is that it is too vague and general, allowing almost anything an organism does to qualify as niche construction.[121] Moreover, the four categories are perhaps too permeable, something that NCT theorists also admit.[122] But from a philosophical perspective, Godfrey-Smith[123] makes the argument that we can be inclusive in terms of what we accept as niche construction, as long as we are mainly interested in shifting perspectives. In his view, constructivist ideas in biology can be viewed as either having a philosophical quality, relating to how we should think about causation and explanation, or a scientific one, rooted in empirical causation. Godfrey-Smith recommends that scientifically-oriented accounts of niche construction focus on ways in which organisms actually modify their physical environment, rather than how they choose or define it. As we have discussed, with examples from lithic studies, selectively occupying the same places in a landscape leaves important physical traces that definitely pass on into the ecological inheritance, thus physically modifying it. In that sense, because of the delayed physical effect of many cultural-cultural selection (Route 1) loops, documenting such instances of defining and selecting our niche may in the end constitute archaeology's main contribution to the EES. For this reason, recommendations that we focus on documenting the variation of cultural types as a function of external factors and processes, such as geography and climate[76] may be too limiting. Internal processes *can* be studied given the right parameters and scale, and NCT could be the solution that allows us to do just that.

## 6 | CONCLUSION

We have made a case, using niche construction theory, that the Extended Evolutionary Synthesis may be a good theoretical home for the study of stone tools. NCT can accommodate both the strict, "extended phenotype" view of lithics as having a direct fitness effect, and the broader and more indirect view of them as "residuals" of other niche constructing activities. Through a few examples, we have shown that evolutionary arguments about lithics can be structured in terms of Odling-Smee's two interacting feedback loops, and that this brings several conceptual advantages to the praxis of studying lithics in comparison with the other commonly encountered approaches. The greatest difficulty consists of determining the place and importance of lithics within the niche-constructing activities hominins engaged in, and we concur with others,[23] that this is best done by shifting the focus away from the stone artifacts themselves and toward the processes that leave them behind. Following Lewontin,[5] we think a philosophical reorientation toward a "dialectical causation" in bio-cultural evolution, rather than a complete revolution, is necessary.

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## 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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