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Identifying Mechanisms behind Middle Paleolithic and Middle Stone Age Cultural Trajectories

by Francesco d'Errico and William E. Banks

A critical analysis of the debate that has surrounded the emergence of “modern behavior” during the last two decades and new ways to study material culture and human-environment relationships allow us to design a novel approach with which we can understand the mechanisms that have led human populations to develop the variety of cultures that we recognize today. We propose a methodological framework that moves away from narrative explanations for the origin of “behavioral modernity” and instead focuses on the interplay between cultural adaptation and environmental change. We argue that by applying this approach to the many different instances of cultural change as well as stasis that characterized the last 300 kyr of human societies we may identify the mechanisms that have led us to become what we are and, if any, the underlying trends that guided this process.

Introduction

Twenty years ago, the path followed by humans to attain “behavioral modernity” appeared evident to most archaeologists and paleoanthropologists. Best exemplified by the publication of *The Human Revolution* monograph (Mellars and Stringer 1989), this path was short, abrupt, exclusively associated with anatomically modern humans (AMHs), and best reflected in the European Upper Paleolithic archaeological record. However, apart from a possible neurological switch (Klein 2000, 2009), no solid cause was proposed that could explain why this should have happened where it did and in such an instantaneous way. Subsequently, the discovery that AMHs originated in Africa (Henn et al. 2011; Trinkaus 2005; Weaver and Roseman 2008) along with a growing body of archaeological evidence supporting the emergence of key cultural innovations in that continent before the purported European “revolution” ca. 40 ka gave rise to a different explanatory model: “modern behavior” must have developed gradually in Africa as a consequence of the origin of our species there and would have been expressed by a process of gradual accretion of innovations observed in the African ar-

chaeological records over the past 300 kyr (Marean et al. 2007; McBrearty and Brooks 2000). The idea that the emergence of cultures such as ours was abrupt nevertheless remained in play, and some viewed innovations occurring in southern Africa ca. 70 ka as the factor that allowed cognitively modern AMHs to qualitatively change their adaptive abilities and rapidly expand out of that continent ca. 60 ka (Mellars 2006). In parallel, other researchers proposed that “modern” cognition was associated with various members of our lineage, not just AMHs, and that social and demographic factors, arguably triggered by climate change, could explain the asynchronous emergence, disappearance, and reemergence of key cultural innovations among both African Middle Stone Age and Eurasian Middle Paleolithic populations (Conard 2008; d'Errico 2003; d'Errico and Stringer 2011; Hovers and Belfer-Cohen 2006; Langley, Clarkson, and Ulm 2008; Nowell 2010; Zilhão 2001, 2007). The partisans of this model relied on cultural innovations found in the Neanderthal archaeological record (burials, use of pigments, complex lithic and hafting technologies, and personal ornamentation at the end of the Neanderthal evolutionary trajectory) to counter the idea that behavioral modernity is unique to our species. The recent finding that significant interbreeding occurred between Neanderthals, Denisovan, and modern populations originating in Africa (Green et al. 2010; Meyer et al. 2012; Reich et al. 2010) is used to support such a scenario because it blurs previously accepted taxonomic boundaries between Upper Pleistocene hominins. In parallel with these scenarios, which are in one way or another anchored in the archaeological and genetic records, some researchers have proposed that the evolution of inherent components of present-day modern cog-

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nition may have played a key role in reaching the cognitive capacity expressed in our species and the ensuing “complexification” of material culture. Altruism (Bowles 2009), enhanced memory (Wynn and Coolidge 2010), complex language (Dunbar 2003), increased capacity for social learning (Mesoudi, Whiten, and Laland 2006; Richerson, Boyd, and Bettinger 2009; Tomasello 1994), creation of adapted learning environments (Sterelny 2011), hierarchical mental constructions (Gibson 2007), and acquisition of syntactical language (Bickerton 1990) have each been proposed as the prime mover that allowed AMHs to cross the threshold of behavioral modernity. It has been argued, though, that the capacity for “modernity” resulting from a speciation event is a necessary but not sufficient condition for the development of modern cultural traits. In this vein, a number of scholars have explored the roles played by population pressure (Compton 2011) as well as demography and cultural transmission (Henrich 2004; Powell, Shennan, and Thomas 2009; Shennan 2001) in the spread and maintenance of cultural innovations. By applying modeling techniques, these latter authors argue that population size, density, rates of reproduction, and networks of information exchange determine whether or not cultural innovations can be diffused, maintained, and in some cases lost. The interest of their results is that they account for such events without invoking speciation as a prime mover and that their expectation better fits the archaeological record than models predicting abrupt or incremental changes in behavior. However, it has been argued that while demography may be key to the diffusion and maintenance of innovative behaviors, it does not necessarily favor their emergence and acceptance. Each society has its own way of regulating the acceptance of deviations from a behavioral norm, which produces different postures toward innovation even when potentially advantageous (Bar-Yosef and Belfer-Cohen 2011). The spread of innovations is also dependent on a society’s ability to create settings of high-fidelity learning: even with sufficient population size, if such settings are absent, innovations may not be maintained (Sterelny 2011). Another shortcoming, as pointed out by d’Errico and Stringer (2011), is that Powell, Shennan, and Thomas (2009) signal climate change as a generic factor behind the increase or fragmentation of populations in their demographic-based “mechanism,” but they offer no means of testing this, especially when considering that specific climate changes had very different effects in various regions of the world. Implicit in their (Powell, Shennan, and Thomas 2009) contention that favors demography is the assumption that in order to produce the spread and maintenance of innovations, this demographic-based mechanism is only relevant to AMH populations. It has been noticed that contrary to their assumption, such a mechanism is equally applicable to archaic hominins and that differences between cultural trajectories of Neanderthals and AMHs may have been dependent on group size and rates of cultural exchange rather than on built-in differences in cognition (d’Errico and Henshilwood 2011). These criticisms serve to show that de-

mography is important but that it is only one factor in the spread and maintenance of innovations, not the prime mover nor the unique explanatory mechanism behind their adoption.

In parallel with the proposition of these various explanatory models and triggers, a number of researchers have called into question whether behavioral modernity is the appropriate concept with which to identify when we became as we are. One such criticism has been directed at the reliance on material culture trait lists to recognize the crossing of the threshold to modernity. An early example of the use of a trait list is by Mellars (1989), who used disjointed elements of the Upper Paleolithic archaeological record to establish a supposed cognitive threshold between Neanderthal and AMH, suggesting that the latter had crossed the Rubicon to behavioral modernity by the beginning of the Upper Paleolithic. However, Deacon (1990) cautioned against the use of a Eurocentric yardstick for measuring cognitive modernity by pointing out that there were indications that these criteria were not pertinent in other regions of the world, where this process appeared to have followed a different tempo and mode. After the publication of the more comprehensive trait list proposed by McBrearty and Brooks (2000), d’Errico (2003) noted that instead of being based on universal features found in all present-day human cultures, this list was a mixture of traits that the authors had recognized in the Middle Stone Age and the Upper Paleolithic. This naturally led them to recognize behavioral modernity in the records on which their list was based and create the misleading impression of a gradual accretion of these traits in Africa. In his view these trait lists cannot necessarily be applied to human populations that lived in dramatically different environments and that had different cultural trajectories. While proposing that behavioral modernity played a useful role in highlighting the inconsistencies of the “human revolution” model and showing that more gradualistic patterns of cultural change existed outside of Europe, d’Errico (2003) argued that behavioral modernity was no longer a useful operational concept and that one should instead explore the emergence of cultural innovation in each region of the world irrespective of the taxonomic affiliation of the population in question.

Zilhão (2011) points out that the real problem with behavioral modernity is that it is based on the notion that different species of *Homo* were each characterized by a unique set of behaviors and that modern behavior is unique to AMHs. He argues that attempts to define “modern human behavior” in opposition to “Neanderthal behavior” have consistently shown that some modern humans were “behaviorally Neanderthal” and some Neanderthals were “behaviorally modern” (Zilhão 2006). In his view, there is no such thing as Neanderthal behavior because the archaeological record in both Europe and the Near East demonstrates that Neanderthal adaptations span the entire range of ethnographically documented settlement-subsistence strategies. Nowell (2010) also highlights the concept of modernity’s ambiguous status due

to its routine association with the development of AMH societies, which is at odds with the presence of many instances of modernity in Neanderthal populations.

Henshilwood and Marean (2003) argue that behavioral modernity is too loose a concept and that we should rely on clear evidence for symbolically mediated actions as the best way to recognize societies that have acquired “fully symbolic *sapiens* behavior.” However, when applying this concept to the archaeological record of southern Central Africa, Barham (2007) highlights how difficult it may be to identify the emergence of such a capacity in records that hint at the presence of modernity but do not have the full suite of material culture that supports its “formal” recognition. This problem may be due to our lack of heuristic tools for recognizing fully symbolic behavior when expressed in ways other than our preconceived notions. His answer to this shortfall is to combine structuralist and ecological theory to recognize individual regional trajectories that could be influenced in part by historical contingencies. Belfer-Cohen and Hovers (2010) concur in that they consider behavioral modernity to be a loose and poorly operational concept that does not create a link between cognitive theory and the typical work of archaeologists. They argue that modernity is multifaceted and cannot be boiled down to a rigid checklist of presence/absence characteristics, and they propose that we should focus instead on the circumstances and contexts in which the phenotypic expressions of modernity, which were at first erratic, became fixed features in the archaeological records of different regions of the world.

Additional criticism has been leveled at this concept by Langbroek (2011), who proposes that the concept of modernity as it is typically applied leads us to frame the evolution of cognition in a unilinear and exponential manner when we should rather envision this process as a branching one that mirrors Darwinian evolution. Within such a framework, “cognitions” associated with different members of our lineage would be submitted to varying selective pressures, thereby creating a variety of cognitive outcomes that cannot be classified as more or less modern.

Shea (2011), like many others, criticizes the fact that behavioral modernity is derived from a trait list founded on the Upper Paleolithic archaeological record, and he echoes d'Errico's (2003:189) argument that archaeologists from different cultural backgrounds could propose different features to define modernity. Furthermore, he adds that the concept has been constructed on a paleoanthropological narrative tradition that implies the transformation from an inferior state to a superior one. His answer to overcome the behavioral modernity conundrum is to focus on “behavioral variability.” The idea is to take into account “modality, variance, skew, and other quantitative/statistical properties” (Shea 2011:2) to measure how successful specific cultural adaptations were from a cost-benefit standpoint in specific environmental settings. Shea's view is anchored in the notion that whatever approach one takes to address this issue, it is solely the business of *Homo sapiens sapiens* and does not concern archaic

hominins perceived by definition as a behaviorally different biological species and therefore irrelevant in this debate.

Comments on Shea's paper (2011), which was published in *Current Anthropology*, welcome his proposed shift toward the reconstruction of different cultural adaptations in specific environmental situations but point out that his search for behavioral variability does not go very far. Comments by Nicholas J. Conard and Rick Potts in particular highlight the fact that behavioral variability, as Shea describes it, is as vague as behavioral modernity because he does not propose with the concept any clear operational tools with which one can evaluate cultural adaptations within their respective environmental contexts. The tool he used, Clark's system of technological modes, appears to them as highly inappropriate because it is constructed on a logic of unilinear, incremental evolution, which is what Shea (2011) is in principle trying to steer away from. We would add another remark: by placing the analysis of behavioral modernity in the realm of what he perceives as a single species, Shea has unwittingly found the prime mover or “donor” of his underlying definition of behavioral modernity—the processes that led to the emergence of our species in Africa.

From *Pars destruens* to *Pars construens*

The above review of the debate makes clear that behavioral modernity and varying lists of cultural traits associated with it are not useful tools for establishing the way in which we became what we are. Some consensus now exists that the evolution of human societies in the last 300 kyr has followed a multitude of paths, not necessarily progressive in nature, in which the material expression of modern cognition is represented by different mosaics of cultural innovations. Focusing on regional trajectories appears to be the only way to document cultural changes and ultimately the mechanisms behind such changes. In doing so, we must seek ways to integrate environmental, ecological, demographic, and social factors as well as historical contingencies in order to understand how human populations have developed and in some cases lost and reacquired cultural innovations that we recognize to be the cornerstone of the human experience. Among those that accept this frame of thinking (d'Errico 2009; Hovers 2009; Kuhn 2013; Stiner 2013; and comments in Shea 2011 by Lawrence S. Barham, Nicholas J. Conard, James F. O'Connell, and Rick Potts), there is consensus that although these are factors that played a role in the process of cultural innovation, the way that they were organized and the interplay between them remains to be understood, and pertinent heuristic tools with which to interrogate the empirical evidence are lacking.

Some might still question whether this endeavor should be conducted only in archaeological records associated with AMHs or should also include archaic hominins. The former would be a clear mistake in our view because it would constrain, whether one would admit it or not, the analysis of

local trajectories within a conceptual framework in which key behavioral innovations can only be the consequence of anatomical modernity. By equating behavioral and anatomical modernity, no matter what “variability” or “cost-benefit” balance is found, we will not get rid of the mind-set that biological change is the prime mover. Such a stance would also deprive us of examining a significant number of cultural trajectories, thus compromising our ability to compare how different populations reacted to comparable suites of external stimuli. Encompassing all local trajectories is in our view the best way to obtain a full picture of the many rapid cultural experiments that are key features of the cultural evolution of our lineage.

With this paper, we propose a methodological framework that moves away from “narrative” explanations toward a focus on material culture and the evaluation of the potential interplay between cultural adaptation and environmental change. We think that by applying this approach to the many different instances of cultural change as well as stasis that characterize the last 300 kyr of human societies, we may identify the mechanisms that have led us to become what we are and the underlying trends, if any, that guided this process.

Causes versus Mechanisms

We argue that the primary problem with most of the scenarios proposed to explain the emergence of behavioral modernity is that they are based on single-cause models. Such models are founded on the teleological notion that a unique cause will continuously act as the sole or the dominant factor in producing the observed outcome. Some of the proposed causes would have acted as long-term stimuli, such as altruism or enhanced working memory. Others, such as genetic mutation or a bottleneck event (e.g., Toba super eruption: Ambrose 1998), would have been short lived in nature and have had a relatively immediate effect. Both types of causes, however, are not sufficient to explain the complex paths and multitude of adaptations that a growing body of archaeological data from Africa and Eurasia denotes.

Rather than causes, we need to focus on identifying the mechanisms that have led different societies to develop specific cultural adaptations as a means of coping with external stimuli (both environmental and cultural). “Mechanism” is a term that has been defined in a number of ways, and Kuorikoski (2009) points out that it is difficult to come up with a definition that satisfies all theoretical needs and potential research practices. Drawing from the work of Bechtel and Abrahamsen (2005), Kuorikoski (2009), and MacHamer, Darden, and Craver (2000), we define a mechanism as a constellation of factors and components that through the process of their interaction with one another stimulates the trajectory of a system. The investigation of mechanisms functions at two different conceptual levels (Kuorikoski 2009). The first consists of examining a componential causal system by disassembling the role played by each component and factoring

in the multitude of interactions that occur between them. The second is more abstract and seeks to encompass interactions between factors and components with the goal of explaining such interactions with a simple model. The final goal is to move from complexity to the proposition of a general explanatory law (e.g., the mechanism of natural selection in biological evolution).

When put in the context of the debate surrounding Middle Stone Age and Middle Paleolithic cultural trajectories, the first concept of mechanism can be seen as a useful operational tool, and the second points to the ultimate goal of identifying the long-term trends and rules that have shaped the cultural evolution of our lineage. One of the interests in approaching cultural evolution from the standpoint of mechanism is that we can describe cultural change dynamically through the analysis of setup and termination conditions (Machamer, Darden, and Craver 2000). The former typically represent in the investigation of mechanism the relevant components, their “structural” properties, spatial relations, and the causal factors thought to influence the relationships between different components. Each component has some degree of variability and independence such that identical setup conditions can result in two systems following different trajectories. Between setup and termination, intervening factors or entities can influence the interactions between components within the mechanism, thus influencing the direction the system follows. Termination conditions are idealized states that represent a point from which one can infer how the mechanism functioned. In this context, “termination” is neither synonymous with equilibrium nor a moment in which the process has necessarily reached a terminal state. In reality, such states are idealized conditions, and their choice by researchers is often determined by the heuristic and analytical tools they have at their disposal to understand the interplay between components and causal factors within a perceivable time frame. This move between setup and termination is analogous to the concept of “adaptive cycle” that is used in resilience theory to characterize the dynamics of a socioecological system with respect to external stimuli and internal processes (Holling 1973; Schoon et al. 2011; Walker et al. 2004).

Setup conditions are of course the result of prior processes, so in the study of mechanisms in a componential causal system framework one is beginning the investigation at a specific point along a continuum. Human cultures follow continuous trajectories in which the various factors that play a role in producing change continuously interact. However, as archaeologists, we identify in the archaeological record discrete and recurrent associations of similar cultural items assumed to reflect cohesive adaptive systems (CASs). We define a CAS as a cultural entity characterized by shared and transmitted knowledge reflected by a recognizable suite of cultural traits that a population uses to operate within both cultural and environmental contexts. The cultural traits used to define a CAS can carry the same well-known ambiguities as those used to define a techno-complex (Clarke 1968; Hodder 1991; Ren-

frew 1977). The archaeological record represents a very pale reflection of the features that constituted a past cohesive cultural group because human adaptation is shaped by cultural rules that govern aspects of human behavior such as kinship systems, marriage, gender politics, and symbolic or belief systems. These rules define human societies as much as and probably more than the environmental contexts they occupy. As archaeologists we have limited means with which to infer those rules for societies of the remote past. It is, however, reasonable to think that those rules, or changes in those rules, shaped the material culture record that we have at our disposal and played a role in how a past group interacted with their environment. The concept of CAS differs from that of a techno-complex (Childe 1929) in that environmental parameters contribute to its definition. The difference lies in the fact that the approach that we detail below effectively explores potential links between cultural traits and ecological parameters and evaluates this relationship through time, thereby providing us the potential to identify general, long-term trends.

Traditionally, archaeologists working with the Middle Paleolithic and Middle Stone Age archaeological records have relied on lithic technology and stone tool typology to define past “cultures” and identify evolutionary trends. Regardless of the multitude of reasons for this focus, examinations of ethnographically documented material cultures indicate that stone tools represent just a small portion of the paraphernalia used by a hunter-gatherer population and do not necessarily reflect the complexity of cultural adaptation or its geography (Hayden 1979). Relying on just a single element of a technical system to represent or infer the complex suite of behaviors and social rules that characterize a past cultural adaptation is clearly illusory. Data accumulated over the last decade in Africa and Eurasia on populations that lived there during the last 300 kyr have broadened our understanding of these CASs by providing insight into a variety of domains beyond those strictly related to lithic technology. These include technological behaviors that certainly are expressions of salient features of those archaeological cultures. These behaviors include pyrotechnology (Brown et al. 2009; Mourre, Villa, and Henshilwood 2010), mastic production (Cârciumaru 2012; Charrié-Duhaut et al. 2013; d'Errico et al. 2012; Lombard 2012; Pawlik and Thissen 2011; Villa et al. 2012; Wadley, Hodgskiss, and Grant 2009), hafting techniques (Lombard 2005; Villa et al. 2009, 2012), projectile technology (Villa and Soriano 2010), techniques for small game capture (Stiner, Munro, and Surovell 2000; Wadley 2010c), use of poison in hunting (d'Errico et al. 2012), bone tool production (Backwell, d'Errico, and Wadley 2008; d'Errico, Backwell, and Wadley 2012; d'Errico, Borgia, and Ronchitelli 2012; d'Errico and Henshilwood 2007), pigment processing and storage (d'Errico et al. 2010; Henshilwood et al. 2011), and use of plants (Mercader 2009; Wadley et al. 2011). Symbolically mediated behavior, which appeared to be largely inexistent or largely out of our grasp a decade ago for the time periods in question, is now well

documented and seems to be clustered in regional traditions. This is the case for personal ornamentation (Caron et al. 2011; d'Errico et al. 2009; Peresani et al. 2011; Vanhaeren et al. 2006, 2013; Zilhão et al. 2010), symbolic use of pigments (Roebroeks et al. 2012; Watts 2010; Zilhão et al. 2010), graphic expressions (d'Errico, García Moreno, and Rifkin 2012; Henshilwood, d'Errico, and Watts 2009; Mackay and Welz 2008; Texier et al. 2010), and mortuary practices (Grün et al. 2005; Pettitt 2011). Although open to debate, we may assume that such CASs also included behavioral features that have not survived in the archaeological record and that made each of these societies unique in the cultural history of our lineage.

As discussed earlier, previous models proposed to explain the emergence of these cultural features and innovations have typically been monocausal in nature and have not been geared toward identifying potential mechanisms and long-term trends. The evolution of a human society cannot be reduced to its demography; systems for transmitting and maintaining cultural innovations depend on a variety of factors. Recent studies have pointed out that a number of ecological, historical, and psychological variables appear to condition the rules that societies impose on individuals and the degree of tolerance a society has toward deviant behavior (Gelfand et al. 2011; Henrich, Heine, and Norenzayan 2010; Norenzayan 2011). The cultural system that one inherits affects basic processes such as perception, reasoning, motivation, and cooperative strategies. This seems to imply that each CAS is characterized by a different potential for cultural transmission, social learning, and the degree to which individuals are open to accept, maintain, and communicate innovations (Gelfand et al. 2011). It has also been argued that each individual society's ability to maintain effective social learning environments is key (Sterelny 2011). It is still unclear whether the reasons behind human behavioral variability are due to purely cultural processes leading to cultural divergence, to ecological constraints, to gene-culture coevolution (Norenzayan 2011), or to some combination of these. Whatever the reason for these differences, each society can be seen as a complex system of attitudes and the potential they offer for change. In this context, we use attitude to refer to the way in which the collective worldviews of individuals in a social group influence behavior. Bar-Yosef and Belfer-Cohen (2011) use such a rationale to explore patterns of human expansion out of Africa with the debatable assumption that lithic technology is a fair reflection of these attitudes and therefore can be used as a proxy to trace successes and failures in hominin expansions. We argue that when identified and combined with the geographic and environmental settings in which societies operated, an array of behaviors related to technical and symbolic systems and reflecting inherited knowledge can be viewed as the setup conditions for the processes at work behind the suite of cultural experiments that took place in regions of Africa and Eurasia between 300 ka and 10 ka.

The approach that we describe below entails means with which one can identify and follow the processes affecting CASs

between setup and termination conditions with no a priori assumption on the trajectories followed by the system being examined. This approach is chosen to avoid the determinism inherent in a “single-cause” frame of thinking as well as the relativism implied in the behavioral variability approach. We perceive the different regional trajectories as unique suites of cultural experiments with their own distinct setup conditions. While these experiments may have components and processes in common, they did not necessarily play the same role within each adaptive system.

Ideally in our field of study, understanding the processes at work between setup and termination conditions would require one to understand the role played by each component and factor in a given region and time—environmental changes, adaptive system-specific material culture characteristics, inferred differences in social rules and attitudes, geography—and to understand how they interacted over time to produce the outcome that we describe as the termination conditions at a particular point in time. This would provide insight into the internal functioning of regional or individual componential causal systems. A second goal would be to understand why for a different componential causal system in a different region and time similar factors interacted in different ways to produce a different outcome. Through the identification of commonalities and differences and by evaluating the role played by specific components and factors within individual trajectories as well as the interplay between them, one should be able to identify overarching trends in the way in which systems operated. This process would allow us to move toward the goal of finding “the general law,” if any, that operated behind the evolution of componential causal systems.

Regional Trajectories as Cultural Experiments

How do we put this approach into practice with the archaeological, chronological, and paleoenvironmental data that we have at hand? Gaining insight into the more remote aspects of cultural systems, socially shared knowledge, and attitudes toward innovations is typically thought of as being a difficult endeavor for archaeologists. We argue, however, that useful inferences can be made pertaining to these cognitive and social domains through the detailed analysis of a wide range of material culture. When such inferences are placed within paleoenvironmental and landscape contexts, we possess an array of data that represent the setup conditions from which an investigation into mechanism can be launched. By applying methods that we detail below, one has the ability to identify the key features and the degree of cohesiveness of these systems and to track the way in which they evolved and possibly responded to environmental change through time. An interest in culture-environment interactions is by no means new, and a number of scholars have already argued that a culture’s “core” (Steward 1955; see also Odum 1971, and for a synthesis Johnson and Earle 2000) can be seen as a society’s means to

solve adaptive challenges. The problem one must address in studies of the distant past is how to operationalize this frame of thinking such that one gives social dimensions and material culture the attention they deserve.

As is already evident to most archaeologists, an important method for inferring behavior and cognition is to view archaeological remains as representing an ordered chain of events, gestures, and processes belonging to a sequence of actions that led to the transformation of a given material to the finished form, that is, the *chaîne opératoire* (Lemonnier 1986; Leroi-Gourhan 1964; Schlanger 1994). This concept is especially pertinent because it permits one to infer from the finished artifact, production waste, and potentially missing elements the socially shared and individual knowledge, cooperation, and amount of short- and long-term memory necessary for the functioning, maintenance, and transmission of a given production sequence. It also allows one to understand to some extent the mental template of the actors.

Different classes of material culture possess different potentials to inform us on cultural cohesiveness, shared knowledge, and underlying cognitive processes. Until 10 years ago, identifying setup conditions of Middle Stone Age and Middle Paleolithic “cultural experiments” would have meant focusing almost exclusively on lithic technology, but now this has become a more complex and potentially informative endeavor considering the many categories of material remains that we have recognized since then (bone tools, pigments, personal ornaments, engravings, mastic compounds, poisons, containers, use of plants and feathers, etc.). Because of their ubiquity and durability, lithic artifacts remain a valuable class of material for identifying the geographic extent of a CAS. In particular, consistencies in lithic technologies and formal tool types have allowed researchers to identify discrete cultural adaptations and begin to piece together their geographic distribution and chronological context in parts of Africa and Eurasia (Barham 2001; Belfer-Cohen and Hovers 2010; Delagnes and Meignen 2006; Discamps, Jaubert, and Bachellerie 2011; Kuhn 2013; Soriano, Villa, and Wadley 2007; Villa et al. 2010, 2012; Wurz et al. 2003). The form that lithic raw material acquisition takes (local or long-distance direct acquisition, trade, etc.) can be a reliable proxy for how an adaptive system is linked to a given territory. The importance assigned to specific types of raw material can provide insight into how rigid or flexible a lithic technical system is and how natural resources became key elements in the cultural system. Acquisition patterns can also reflect the presence of social networks and their complexity. Analysis of debitage techniques can hint at the form and duration of apprenticeship likely necessary to produce certain classes of tools. Shaping techniques to transform knapped blanks into finished tools, the degree of conformity to strict stylistic rules, and whether formal tools were used for single or multiple functions allow us to understand the technical system’s degree of plasticity and to gauge the nature of information needed to maintain and transmit the required know-how. Finally, whether each

phase of the *chaîne opératoire* is found in a unique location or multiple locations can inform us not only about how a population organized its activities across the landscape but also about the planning involved and the complexity of the cognitive maps that characterized an adaptive system.

During the last decade, improvements in excavation techniques and reappraisal of existing collections have identified a variety of material culture remains other than lithics, and methods have been developed to better infer their behavioral significance. During the Middle Stone Age and the end of the Middle Paleolithic, we observe for the first time bone tools produced with techniques specifically conceived for this medium—such as grinding, scraping, and polishing—that allowed their final shape and size to be achieved with a high degree of accuracy. This class of tool is considered particularly appropriate for the characterization of technical systems, tracking technical changes through time, identifying regional variability, disentangling style from function, and inferring the complexity inherent in a given adaptive system (Backwell and d'Errico 2005).

The production of complex compounds entails the ordered combination and modification, often with the use of pyrotechnology, of a variety of raw materials in order to produce an end product that has physical properties not found in the natural world. Beyond the important ability to develop such technologies through experimentation, what is paramount is the ability to maintain and transmit these innovations. Once adopted, each recipe and the way it is employed can become key features of a CAS and have a feedback effect on other aspects of the technical system as well as on how knowledge is accumulated and shared. We now possess means to infer how these compounds were made and used by specific human populations in the Middle Paleolithic and the Middle Stone Age (Böeda et al. 1996; Cârciumaru et al. 2012; Charrié-Duhaut et al. 2013; d'Errico et al. 2012; Hauck et al. 2013; Henshilwood et al. 2011; Mazza et al. 2006; Pawlik and Thissen 2011; Villa et al. 2012; Wadley 2010a; Wadley, Hodgskiss, and Grant 2009). Bitumen, birchbark tar, wood resin mixed with hematite, hematite powder mixed with animal fat: we are starting to understand how different CASs have created and incorporated comparable compound technologies as a response to specific needs in different environmental settings.

We are also moving beyond the simple recognition that instances of symbolic material culture in the form of personal ornaments, engravings, pigment production and storage, and decorated bone items are present in the archaeological record of this period and reflect modern behavior to the exploration of the representativeness and significance of specific instances. First, one can wonder how much evidence has not been preserved or, if preserved, been destroyed during excavation or gone unrecognized. It has been pointed out, for example, that the appearance of symbolic items in the archeological record may be largely conditioned by taphonomic processes (Barham 2007). This problem can be partially overcome by critically examining excavation techniques used at specific sites in the

past. Taphonomic analyses of the various categories of symbolic items may help to identify which classes of artifacts are especially affected by taphonomic processes and infer whether such processes may have led to their disappearance at some sites. Cross-cultural analyses of the raw materials used to produce symbolic items and the evaluation of their respective durability are also means to address the issue of the loss of some elements of symbolic material culture, particularly in contexts in which we observe other material remains pointing to the presence of symbolic mediated behaviors. These behaviors may exist in a society that does not express them through purely symbolic items but rather embodies them in functional items. These items express symbolic meaning by their adherence to strict stylistic norms that archaeologists perceive as modern without having the means to disentangle functional from symbolic traits (Barham 2007). Taking into account such items as components of a CAS is a means of incorporating them, including their potential symbolic value, among the factors that played a role in the relationship between culture and environment. In this way, potentially symbolic aspects of past material culture become full actors in the exploration of mechanisms governing the evolution of cultural systems.

Second, advanced analytical techniques contribute to the disentanglement of accidental from purposeful behavior, thus allowing a precise documentation of the operational chain and underlying cognitive processes. Actualistic studies conducted with the aim of verifying the purposeful alteration of pigment (Wadley 2010b) or shell bead color (d'Errico et al. 2009; Kandel and Conard 2005) as well as assessing whether plant remains are present naturally or because of specific human actions such as use as bedding and as insect repellent (Wadley et al. 2011) are good examples of evaluating the behavioral significance of past human agency. Archaeozoological, taphonomic, chemical, technological, and functional analysis of symbolic items relying on actualistically established criteria, when placed within the framework of a *chaîne opératoire*, have provided new means to identify and analyze early instances of symbolically mediated behavior. This provides insights into the way in which material expressions of symbols were created, assembled, and displayed, how and for how long they were used, and to what degree those early symbolic systems are comparable with those created by ethnographically documented human societies. Adapted theoretical frameworks are proposed to understand the amount and nature of information that one can convey through each category of the identified type of symbolic material culture (Kuhn and Stiner 2007) and the function personal ornaments may have played in prehistoric societies (d'Errico and Vanhaeren 2007). By establishing to what degree specific instances of symbolic behavior are representative of a CAS and exploring patterns of variability through time and space, we are able to verify whether these instances are inherent features of the system or simply the expression of subregional or successive cultural trajectories (Vanhaeren et al. 2013).

A key additional dimension that must be considered when establishing setup conditions of any cultural experiment is space. This is particularly relevant in the case of hunter-gatherer economies because we know, apart from a few cases in which particular adaptations allowed them to be sedentary or semisedentary, that one key feature of these populations is that they were mobile. Although hunter-gatherer economies and their organization across the landscape can be broadly classified as logistical or residential (Binford 1980; Foley 1992), we know that reality is more complex and must have been so in the past. We must delve deeper into each individual case and attempt to understand the unique logic behind each settlement-subsistence system within its particular landscape framework. We now have the means to reconstruct, at both continental and regional scales, the effects that ice-sheet and sea-level changes (Lambeck, Esat, and Potter 2002) had on the landscape. Information pertaining to environmental conditions has traditionally been reconstructed on the basis of proxies from individual sites or groups of sites such as faunal or plant remains and soil characteristics, among others. These certainly provide important information, but if one wishes to explore the systemic and dynamic relationship between culture and environment, one must move beyond the site scale and find a way to examine this relationship at regional and continental scales.

An Integrative Approach

Research seeking to understand the relationship between human and/or cultural evolution and climate change during the Middle and Upper Pleistocene is becoming an increasingly widespread field of study (Bocquet-Appel et al. 2005; Carto et al. 2009; Compton 2011; deMenocal 2011; d'Errico and Sánchez-Goñi 2003; Discamps, Jaubert, and Bachellerie 2011; Gamble et al. 2004; Jacobs et al. 2008; Lowe et al. 2012; Maslin and Christensen 2007; Osborne et al. 2008; Richerson, Boyd, and Bettinger 2009; Sepulchre et al. 2007; Van Andel and Davies 2003). Most of this research has attempted to explore the role played by climate on either long-term or sudden evolutionary/cultural changes/replacements, but they do not detail means with which to verify the proposed causal connection or test alternative hypotheses. Only a handful of studies have designed tools to test the relationship between these factors and explore their interaction at regional scales (e.g., Bocquet-Appel and Tuffreau 2009). These studies attempt to test the correlation between a single and often qualitative climatic variable (e.g., isotopic stage, cold/warm) and the function of sites or the nature of the material record in a given region. Such an approach, however, does not evaluate the various components of a given CAS against multiple and quantitative climatic environmental variables. Other studies use a variety of modeling techniques to contrast Neanderthal and AMH population dynamics and interactions (Barton et al. 2011; Fabre et al. 2011), but they produce results that are difficult to test against the archaeological record and do not

realistically incorporate the environmental conditions of each phase that characterize the variable climatic conditions of this period.

In a series of papers published during the last few years, we have outlined an approach with which we can explore the interactions between CASs and paleoenvironment and understand how environmental dynamics may have influenced these adaptations and the distribution of prehistoric hunter-gatherer populations (Banks et al. 2008*b*, 2009, 2011; d'Errico and Stringer 2011). This approach, termed eco-cultural niche modeling (ECNM), integrates archaeological, chronological, geographic, and paleoclimatic data sets via biocomputational architectures derived from biodiversity studies (Peterson et al. 2011) to estimate ecological niches and distributional areas occupied by prehistoric hunter-gatherer populations and to identify and quantify the environmental factors that shaped these niches.

An eco-cultural niche is defined as the range of environmental conditions (i.e., the ecological niche) exploited by a CAS (see Banks, d'Errico, and Zilhão 2013 for a detailed discussion of eco-cultural niches). ECNM assumes that we can characterize a past cultural niche by employing methods used to reconstruct and study ecological niches. A key feature of such predictive architectures is that they can project the ecological niche predicted for a climatic phase onto the environmental conditions of a subsequent period. The resulting niche projection is compared with the locations of known occurrences for the latter period to see whether or not it successfully predicts their presence within the niche. In this way, one can evaluate whether an adaptive system, in the event of its persistence, exploited the same ecological niche across different climatic phases or significantly expanded or contracted it. This approach parallels the inquiry into the mechanism driving the evolution of a componential causal system because it allows one to define the setup conditions of the process at work, in our case an individual cultural experiment, and evaluate its termination conditions (i.e., the attributes and distribution of a CAS at the end of the process) within either the framework of environmental change or relative stasis.

For data inputs, ECNM requires the geographic coordinates of archaeological sites bearing cultural features that are considered distinctive of a particular CAS or consistent subsets within that system along with a set of raster geographic information system data layers summarizing environmental dimensions potentially relevant to shaping the eco-cultural niche exploited by the CAS as well as its spatial expression during a specific climatic phase. Geographic variables are assumed to have remained relatively constant over the past 300 kyr, and thus one can use high-resolution present-day data (e.g., ETOPO1). Reconstructions of past sea-level fluctuations at both general and regional scales are available and can be used to reconstruct coastlines and related paleogeography for the region of study. Reconstructions of ice-sheet volume and location are available for most of the last climatic cycle and

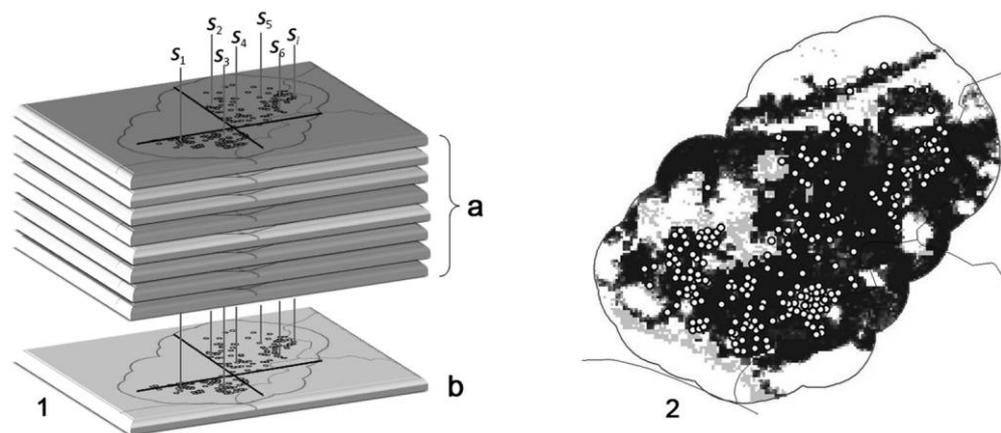


Figure 1. Schematic rendition of how one of the predictive architectures, in this case genetic algorithm for rule-set prediction, reconstructs an eco-cultural niche. 1, Occurrence data (i.e., location of archaeological sites belonging to a cohesive adaptive system) are resampled randomly by the algorithm to create training (b) and test data sets. An iterative process of rule generation and improvement then follows in which an inferential tool is chosen from a suite of rule types and applied to the training data (S_1 – S_6) and paleoenvironmental raster data layers (a) to develop specific rules (Stockwell and Peters 1999). These rules evolve to maximize predictivity by several means (e.g., crossing over among rules), mimicking chromosomal evolution. Predictive accuracy is evaluated based on an independent subsample of presence data and a set of points sampled randomly from regions where the species has not been detected. 2, The resulting rule set defines the distribution of the subject in environmental dimensions (i.e., the ecological niche; Soberón and Peterson 2005), which is projected onto the landscape to estimate a potential geographic distribution (Peterson 2003).

can be inferred, with some incertitude, for more ancient periods. With respect to paleoclimatic variables (temperature and precipitation), there exists a variety of modeling techniques for obtaining reconstructions that can be integrated into a niche modeling approach. One can run (1) a coupled ocean-atmosphere general circulation model (e.g., IPSL CM4 and CM5A; Dufresne et al. 2013; Kageyama et al. 2013), (2) an atmosphere-only model with a slab ocean component (representing the top 50 m of the water column; Kang et al. 2008), or (3) an atmosphere-only model with imposed sea surface temperature (SST) values (Kageyama et al. 2005). With all three, boundary conditions (orbital parameters, greenhouse gas concentrations, ice-sheet volume) appropriate for the targeted climatic event are assigned. The atmosphere-only model with imposed SSTs also can be run with a refined resolution (~ 50 km) over the region(s) of interest (see Banks et al. 2008a; Sepulchre et al. 2007).

The results from the different methods listed above can be statistically downscaled (e.g., Vrac, Stein, and Hayhoe 2007) to increase the resolution of the simulated paleoclimatic data. A final option is to use a regional model forced by general circulation model outputs as boundary conditions, thereby producing climatic simulations with a resolution as fine as 5 km (Frei et al. 2006). This high level of resolution, or even finer when possible, is most appropriate for examining cultural and niche trajectories at a regional scale. The outputs of this simulation process can be used to force a dynamic global vegetation model (e.g., Orchidee, Spitzfire) in order to

obtain reconstructions of vegetation cover compatible with the targeted climate state. In this way, one obtains values for precipitation, temperature (mean annual, coldest month, warmest month), and broad vegetation types. During this process, outputs are compared with paleoenvironmental data to test whether the simulations capture past conditions satisfactorily, and if they do not, there exist means to improve subsequent generations of simulations in an effort to better capture past paleoclimatic conditions.

Other methods exist, such as using statistical techniques to infer past climatic conditions from a variety of vegetation data (for a review, see Tingley et al. 2012), but so far they lack the spatial resolution required for our purposes. Of course, models are just that, models, and one must keep in mind that they only approximate past climatic conditions. Also, our goals are different from those of paleoclimatologists who seek to understand the functioning and evolution of the earth's climate system. We wish to have at our disposal the most accurate simulation for paleoclimatic conditions at a specific time in the past and seek to improve our means for evaluating the pertinence of paleoclimatic simulations. Because of the pressure of the threat of global warming, climate modeling is a rapidly evolving field of research, and it is clear that means to evaluate the pertinence of high-resolution simulations at regional scales will rapidly improve in coming years. We will greatly benefit from such improvements.

A number of predictive modeling approaches are available (climatic envelope range, generalized linear model, general-

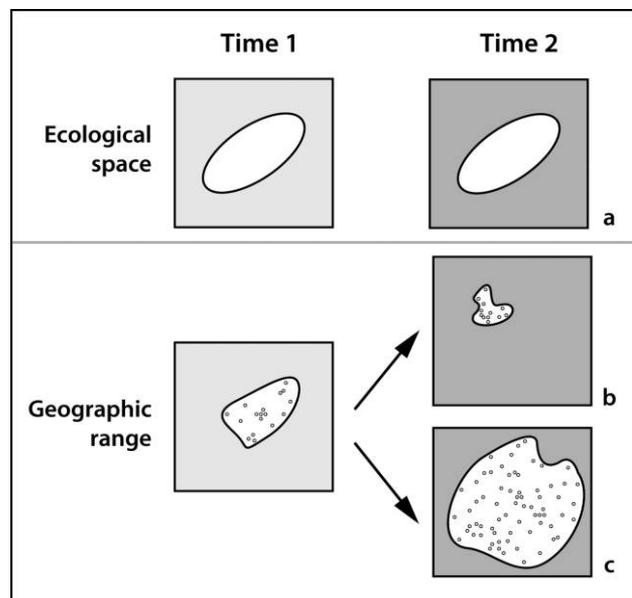


Figure 2. Schematic illustration of how, following a climatic change, the conservation of an eco-cultural niche (a) may result in either a contraction (b) or an expansion (c) of the niche's geographic range.

ized additive model, genetic algorithm for rule-set prediction, maximum entropy, ensemble approach; for a review see Araújo and New 2007 as well as Pearson et al. 2006) for reconstructing the ecological niche of a CAS and its geographic distribution using the above data. Araújo and New (2007) point out that ideally one should use multiple modeling methods and compare their outputs. Therefore, in our previous applications of ECNM we have employed genetic algorithm (genetic algorithm for rule-set prediction) and maximum entropy (Maxent) methods. At a very general level, these architectures first identify shared paleoenvironmental parameters among the geographic locations of archaeological sites belonging to the same culture and then find other geographic regions where these parameters are present, thus predicting the total ecological range of the target population (fig. 1). When estimating ecological niches, it is important to consider the geographic areas that would have been accessible via dispersal to the population in question and that have been sampled such that occurrences could have been detected (Barve et al. 2011; see Banks, d'Errico, and Zilhão 2013 and Banks et al. 2013 for archaeological examples); this area is termed "M" in the BAM framework of Soberón and Peterson (2005). Once meaningful ecological niche estimations have been produced, statistical methods are used to identify the environmental factors that shaped these niches and to measure their breadth. Similarly, a variety of methods exist (e.g., background similarity test: Warren, Glor, and Turelli 2010; partial-ROC test: Peterson, Papeş, and Soberón 2008) to test whether two CASS' eco-cultural niches are significantly different or whether

they are interpredictive either within a single climatic event or between two different events. Two niches are interpredictive when their observed degree of similarity is greater than would be expected by chance.

The interest in following this approach lies in that we move beyond the analysis of site distributions to that of niches and can evaluate and quantify patterns of continuity or niche shifts. Predictive algorithms allow us to evaluate whether a CAS has conserved, expanded, or contracted its ecological niche in the time span between two different points in time. It is noteworthy that such changes may not necessarily be reflected in observed changes of their geographic range. In the event of climatic change, if an adaptive system conserves its ecological niche and simply tracks its shifting footprint, this can result in either an expansion or contraction of its geographic range depending on the range that the related climatic envelope occupies following the climatic shift (fig. 2). With this approach, changes in eco-cultural niches are assessed without a priori assumptions on the role played by environment. ECNM can identify cases in which significant cultural change, potentially reflecting changes in social rules and related organization along with niche shifts, appear to be unrelated to environmental variability. Also, it is often intuitively assumed that cultural innovations indicate an ability to better exploit environments and increase a population's geographic range. However, in some instances innovations may reflect responses to environmental change such that they allow a population to maintain its niche and avoid niche contraction. Situations may exist in which cultural innovations are associated with a niche contraction. This may occur either because a CAS copes with climate change by targeting a smaller subset of its previous niche or because, in spite of innovations, the CAS is unable to maintain its previous niche.

We can envision four different scenarios in the evolution of a CAS between setup and termination conditions (fig. 3). In the first scenario, the material culture characterizing a CAS remains the same between these two points in time. The second scenario features changes in some aspects of the material culture, but one can identify a clear continuity through time. From the perspective of resilience theory, these two situations can be characterized as ecological resilience (Peebles, Barton, and Schmich 2006), which describes the situation in which an adaptive system is changed and reorganized while maintaining its key features and functions. For the third scenario, material culture disappears from the archaeological record, indicating that populations are no longer present in the region or that they are archaeologically invisible. In the fourth scenario, the material culture associated with the termination conditions is clearly different from that of setup conditions (e.g., a different techno-complex). Of course, the recognition of scenarios 1, 2, and 4 assumes that archaeologists have the means to identify and follow the cultural processes at work in the various aspects of the technological and symbolic domains. Scenarios 3 and 4 imply that at some undetermined point in time between setup and termination

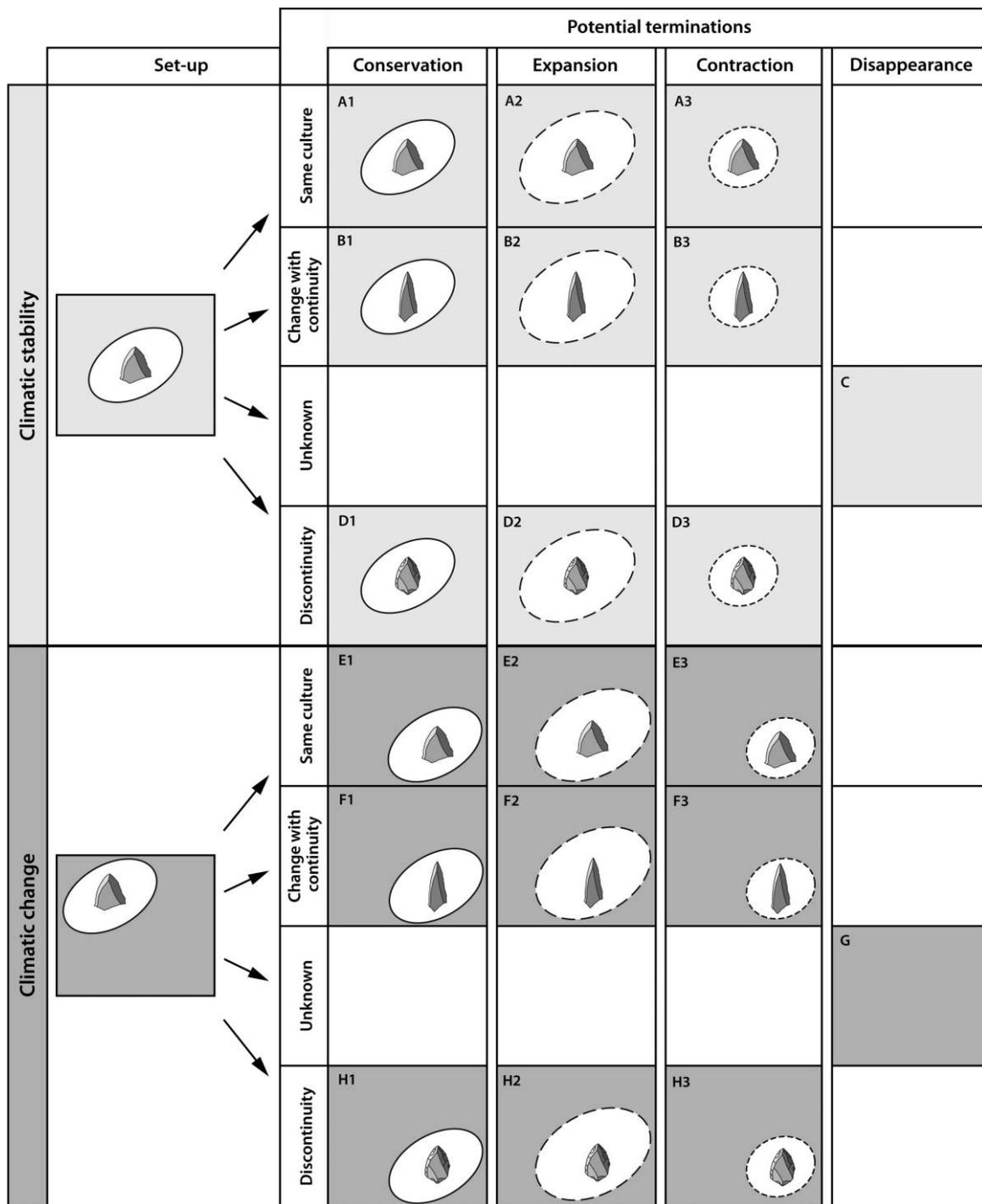


Figure 3. Scenarios of a cohesive adaptive system's (CAS's) evolution between setup and termination conditions within the framework of climatic stability (A–D) or climate change (E–H). Columns depict setup conditions and one of four possible termination conditions: (1) niche conservation, (2) niche expansion, (3) niche contraction, or (4) disappearance. A and E illustrate situations in which material culture remains essentially unchanged (described as scenario 1 in the text). B and F depict situations in which the material culture changes but clear continuity between setup and termination conditions can be recognized (scenario 2). In instances C and G, a CAS disappears or becomes archaeologically invisible at termination, representing either an extreme instance of niche contraction or migration (scenario 3). D and H are instances in which clear discontinuities in the material culture are observed between setup and termination (scenario 4). The potential for shifts in geographic range is indicated by displacement of the eco-cultural niche within the frame representing termination conditions.

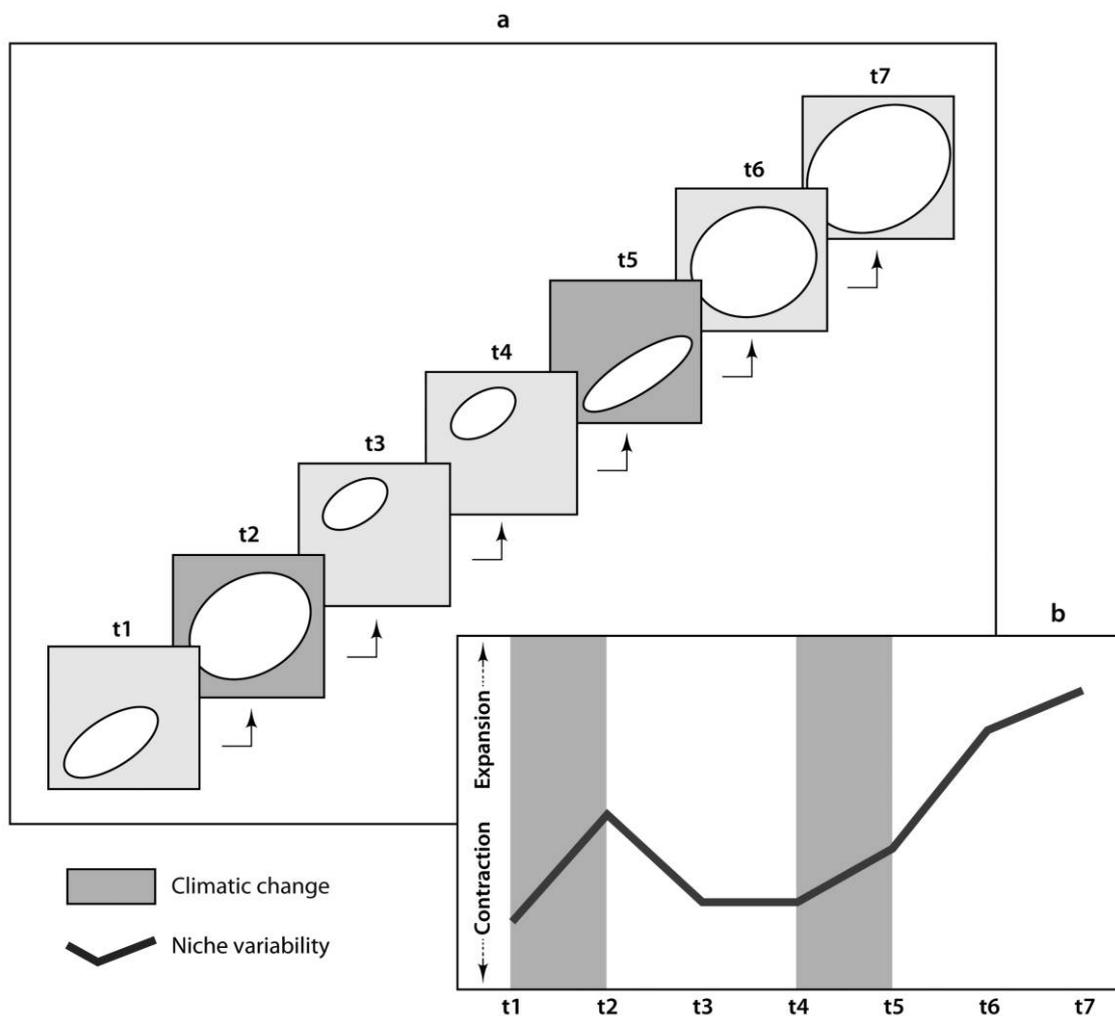


Figure 4. Idealized example of a long-term regional cultural trajectory (a) composed of multiple stages in which termination conditions become setup conditions for the subsequent stage, all of this encompassing multiple periods that may be characterized by either relative climatic stability or climatic change. Trends in niche variability (b) synthesize long-term trends in the relationship between cohesive adaptive systems and environmental variability at a regional scale.

conditions, a process or event occurred that led to the disappearance of the initial CAS or to its evolution into a significantly different cultural system, respectively.

Climate change may or may not have occurred between setup and termination conditions for the above scenarios. The outcome of these eight different trajectories (the four scenarios with or without climate change) may involve niche stability, contraction, or expansion (i.e., 20 possible different outcomes; fig. 3). Once one has determined into which scenario the archaeological record under investigation falls, ECNM tools allow one to determine whether ecological factors played a role in a given CAS's trajectory or whether it was influenced to a greater extent by cultural processes. More importantly, in the first case, dedicated statistical tools allow one to quantify whether these changes are significantly different from what would be expected by chance. For the sce-

narios taking place during a period of relative climatic stasis, comparing the initial and final eco-cultural niches and quantifying potential differences can be accomplished with background similarity tests (Warren, Glor, and Turelli 2010; for an archaeological application see Banks et al. 2011). For scenarios that occurred across a period characterized by a climatic change, the setup eco-cultural niche is projected onto the climatic conditions of the termination period to evaluate whether or not it changed or remained stable. These initial and projected eco-cultural niches can be compared with a variety of statistical methods (e.g., partial-ROC comparisons: Peterson, Papeş, and Soberón 2008; cumulative binomial statistic: Banks et al. 2008a; background similarity test: Warren, Glor, and Turelli 2010), again with the goal of evaluating whether or not there was an eco-cultural niche shift during the process.

By determining whether or not an eco-cultural niche remained stable, along with an identification of the key environmental variables that played a role in the definition of the initial and final niches, and in conjunction with a detailed reconstruction of the behaviors reflected in the material culture record, we should be able to identify the different factors and components involved in the mechanism at work behind the evolution of a CAS. When one steps back to look at the bigger picture, each transition between setup and termination represents a single stage within a long-term regional process in which the termination conditions of each stage become the setup conditions of the following stage (fig. 4). This subsequent stage in turn may not resemble the previous one and can potentially fall into another of the 20 possible scenarios outlined above. When viewed at a regional scale and across a long span of time encompassing a number of climatic phases, this process may reveal trends (e.g., random, punctuated, unilinear, exponential) in the way CASs respond to climate variability. In this way trends may be revealed that would not be evident at the stage level of analysis. We may, for example, face at the stage level minor niche expansion that is not statistically significant but that may become so when multiple, successive stages are considered. This could reveal trends that underlie a long-term regional trajectory. We do not expect regional trends to mirror one another. It is possible, however, that by comparing them, consistencies may become apparent. The identification of such consistencies may allow us to move from the analysis of multiple successive componential causal systems to the formulation of a general or overarching theory that explains the mechanisms that governed the evolution of human cultures and their relationship to the environment before the development of production-based economies.

Conclusions

Documenting regional cultural trajectories is worthwhile, but it is not enough. While the direction that archaeological investigations into behavioral modernity have taken in recent years has been useful in that it has provided us with a wealth of detailed empirical data, this research has so far fallen short of examining the dynamic relationships between the multitude of factors that were at play between human populations and the environments within which they operated. Focusing on the various paths that human populations around the world have taken to become what we are today certainly presents the advantage of escaping previous gross approximations or misleading and generalized scenarios accounting for the origin of modernity. A growing body of evidence is demonstrating that such scenarios, founded on single causes, do not account for the complex processes at work in each region of the world. This raises the question of how detailed compilations of existing data and results from new research on individual regions can lead us forward. Such approaches can quickly fall into the trap of cultural relativism: each cul-

ture is viewed as unique, and one implicitly assumes that our job as archaeologists is to simply document cultural variability without the ability to identify underlying trends in the behavioral evolution of our lineage. Alternatively, intrinsic in a number of regional examinations is the idea that one can better identify, at that scale, one or more points in time during which significant behavioral transformations occurred that lead human populations in that region to cross one or more Rubicons on the path to modernity. Proposing a best-fit factor at play in those passages from the available menu (demography, environment, cognitive changes, climate change, speciation, etc.) often equates to transferring a single-cause scenario from a general to a local scale. The same holds true for more environmentally deterministic approaches seeking to reconstruct climatic changes at a regional scale with the aim of identifying a local prime mover behind a behavioral shift identified in that region: contemporaneity does not equate to a causal link.

We argue that meaningful advances in this field of study cannot be achieved without integrating detailed information on past human behavior into a research strategy that allows one to interrogate, rather than simply document, past material culture with the aim of identifying short- and long-term mechanisms at work in the evolution of CASs within their respective, dynamic paleoenvironmental frameworks. To effectively do so, we must apply the same methods to individual regional trajectories and conceive heuristic tools that enable us to quantitatively compare and evaluate different regional trajectories and their associated behavioral changes through time. Integration of paleoanthropological and paleogenetic data can be important but should probably represent a later stage of the inquiry into mechanisms, as implied by Lalueza-Fox (2013), rather than being used as a prime mover as is now the case in the more popular single-cause models. Cognition does not exist in nature as a given but rather as the result of a continuous interaction between conspecifics as well as between them and the environment. Hypotheses on the behavioral implications of genomic variability need to be tested by finding ways to explore possible interactions between aptitudes and genes rather than attributing to our ancestors an assumed cognitive potential based on our taxonomic reading of the fossil record.

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