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Assessing relationships between human adaptive responses and ecology via eco-cultural niche modeling

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Thèse d'Habilitation à Diriger des Recherches

Université de Bordeaux 1

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UMR 5199 PACEA – De la Préhistoire à l'Actuel : Culture, Environnement et Anthropologie

Assessing Relationships between Human Adaptive Responses and Ecology
via Eco-Cultural Niche Modeling

Soutenue le 14 novembre 2013

devant un jury composé de:

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SUMMARY OF PAST RESEARCH

INTRODUCTION

All human cultures, whether they be complex societies that practice food production or hunter-gatherer societies at the other end of the spectrum, exist within an environmental context. Therefore, many of their cultural solutions related to food resource acquisition and social organization are directly or indirectly influenced by the environment(s) within which they operate. One important preoccupation within the discipline of archaeology is how to identify and capture the complexity of these influences through examinations of the particularities and geographic distributions of past material culture. The purpose of this document is describe the theoretical and methodological efforts I have made to investigate such influences and interactions.

My research has always been oriented towards understanding the complex relationships that exist between prehistoric hunter-gatherer cultural systems and the environmental contexts that they exploited. One of my key objectives has been to identify and interpret the processes of cultural adaptation that have occurred across periods of environmental change. Throughout my career, I have pursued this objective by applying a wide-range of methodologies to a variety of archaeological records. These include:

- Typo-technological and functional studies of lithic industries associated with the Paleoindian and Archaic records of the North American Great Plains and the European Upper Paleolithic;

- Studies of settlement-subsistence systems and chronology within the Central Plains;
- Investigations on the impact of rapid-scale climatic variability during MIS 3 and 2 on Paleolithic hunter-gatherer and large mammal populations.

These various research endeavors have allowed me to study, at differing geographic scales, the complex relationships between a cultural system and its environmental framework. This work, conducted both in the field and in the laboratory, has led me to acquire expertise in high-power use-wear analysis, the examination of lithic economies and reduction sequences or "chaînes opératoires", the calibration and Bayesian modeling of ^{14}C ages, the construction and management of archaeological relational databases, Geographic Information Systems, paleoclimatology, and ecological niche modeling. These expertise are necessary for conducting interdisciplinary studies and serve as the foundation of eco-cultural niche modeling (ECNM), the methodological approach to which I have devoted my attention since obtaining my Ph.D. Before describing ECNM in detail, I think it is necessary to briefly summarize the research that led me in this direction.

HUMAN-ENVIRONMENT INTERACTIONS AT THE SITE SCALE: SOLUTRÉ

The microscopic wear traces left on the surface of stone tools reflect the relationship between lithic technical systems and their human users. Use-wear traces serve as tangible evidence of a culture's adaptation to and exploitation of its environment. My doctoral dissertation detailed a high-power use-wear analysis of the Upper Paleolithic stone tool assemblages recovered from the site of Solutré (Banks, 2004, 2009). That study allowed me to investigate the interface

between culture and environment at a specific spot on the landscape and evaluate how it varied over time.

Solutré is an ideal site for such an analysis since it served as a kill-butchery site throughout the Upper Paleolithic despite the major cultural, technological, and environmental changes documented for this same period. I thought that it was highly probable, however, that these cultural and environmental changes influenced the way in which the site was incorporated into the settlement-subsistence systems of different Upper Paleolithic populations. I used high-power use-wear methods to identify changes in secondary site function through time, characterizing these collateral activities, as well as to identify how specific tool types performed within the larger technical system (e.g., changing relationships between tool type and function, maintenance of tools, recycling of tools to be used in different functions).

The results of these analyses indicated that secondary site functions at Solutré varied significantly through time and served to improve our understanding of how Solutré was incorporated into various settlement-subsistence systems throughout the Upper Paleolithic. However, it became evident to me that I needed to develop and employ methods with which I could better determine how environmental changes influenced the way in which human groups organized their activities within a larger landscape.

HUMAN-ENVIRONMENT INTERACTIONS AT THE REGIONAL SCALE

My research on the late Pleistocene and Holocene archaeological records of the Central Plains of North America focused on technological and settlement systems in order to understand how hunter-gatherer populations adapted to specific environmental settings and environmental change in general. To do so, I focused on use-wear, spatial/distributional, and chronological data (Banks 2003; Banks et Wigand 2005; Banks et el. 2001; Hoard et Banks 2006).

Again, these studies highlighted the need to develop a multi-disciplinary, methodological approach with which one could: 1) interactively combine archaeological, chronological, and climatic data so that the behavioral variability observed in the archaeological record could meaningfully evaluated, 2) better elucidate culture-environment interactions and, 3) more importantly, identify the mechanisms, both long- and short-term, that operated behind observed behavioral shifts. It was these analytical objectives, combined with the organizational and exploratory efforts of a few key individuals who would serve as close collaborators, which led me to pursue the development of an approach that has been termed eco-cultural niche modeling.

ECO-CULTURAL NICHE MODELING

In the spring of 2004, the University of Kansas' Biodiversity Institute, with funding from the National Science Foundation, held a workshop to explore the feasibility of applying ecological niche modeling techniques to the archaeological record. Participants included ecologists, archaeologists, climatologists, geographers, and computer scientists, and discussions centered

on whether ecological niche and species distribution modeling techniques could serve useful in interpreting archaeological data pertinent to investigations of human-environment interactions. In addition to establishing the current state of ecological niche modeling at the time, the workshop participants decided to establish a number of proof-of-concept projects that would serve to test the application of niche modeling tools to both the Old and New World archaeological records. This first exploratory workshop was followed up with a second one a year and a half later (September 2005) in Les Eyzies, France. The second workshop was jointly funded by the National Science Foundation and the European Science Foundation (co-organized by Drs. Harold Dibble and Francesco d'Errico), and participants presented and discussed research pertaining to the geography, mobility and settlement systems, and adaptive solutions of human populations with respect to environmental variability. The application of ecological niche modeling methods to the archaeological record figured among the subjects covered, and additional discussions were held as to how one might operationalize the approach and the types of data that could be used. An article providing a summary of these discussions and a presentation of research perspectives was published a few months later (Banks et al., 2006).

One of the proof-of-concept projects that arose out of the first workshop was directed by Dr. Francesco d'Errico and integrated into a broader European Science Foundation-funded research project termed RESOLuTION (ESF EUROCORES on EuroCLIMATE). RESOLuTION's principal goal was to link high-resolution, multi-proxy marine, terrestrial, and ice core records by means of geochronological analyses and the identification of tephra horizon 'fingerprints'. Work package

5 of the project aimed to explore the impact of rapid-scale climatic fluctuations on Paleolithic hunter-gatherer populations via the use of ecological niche modeling methods.

In the fall of 2005, I was hired by the Centre National de la Recherche Scientifique (CNRS) as a post-doctoral research fellow within the framework of the RESOLuTION project. I was charged with the task of operationalizing the application of ecological niche modeling methods to the Paleolithic archaeological record. This was not a straight-forward task since these methods are dependent on occurrence data, meaning the geographic coordinates of where a specific population or species has been observed. However, one potential limitation of the archaeological record, regardless of the time period of interest, is sampling and whether or not the known sites for a given technocomplex are representative of a past human population, both in terms of its geographic distribution and its range of settlement and subsistence behaviors. Furthermore, these methods are dependent on a variety of other data that are not used by archaeologists on a routine basis (e.g. paleoclimatic simulations). Thus, the research objectives at the core of this post-doctoral position required that certain choices be made, most notably those concerning: 1) the types of archaeological data that should be examined and how they should be sampled in order to obtain the occurrence data necessary to make reliable and robust ecological niche predictions, 2) the types of paleoclimatic data to be used as the environmental data layers input into the predictive modeling architectures, and 3) which modeling architectures should be employed. This ESF-funded CNRS post-doctoral fellowship, therefore, served as the launching pad for my pursuit of developing an approach with which one could effectively apply ecological niche modeling methods to the archaeological record in order to

better understand the intricacies of human-environment interactions specific to prehistoric hunter-gatherer populations. This approach, how it has been implemented over the past several years, and the methodological avenues that I intend to pursue in the coming years, along with my history of graduate student supervision in France, are described in the sections that follow.

EXAMINING HUMAN-ENVIRONMENT RELATIONSHIPS VIA ECO-CULTURAL NICHE MODELING

INTRODUCTION

One goal of Paleolithic archaeology is to describe and understand human behavior by documenting archaeological cultural variability and identifying cultural mechanisms behind the range of adaptations observed in the archaeological record. Paleolithic hunter-gatherers were not divorced from the environmental frameworks within which they operated, so to achieve the above goal we must understand the physical environments they occupied, identify the ecological niches they exploited, and understand how they changed through time. Recent years have seen a multitude of studies aimed at understanding hunter-gatherer responses to environmental change (e.g., Bar-Yosef and Belfer-Cohen, 2011; Binford, 2001; Bocquet-Appel and Tuffreau, 2009; Bradtmöller et al., 2012; Weber et al., 2011). This recent work has benefited from the accumulation of high-resolution climatic data (ice, marine, and terrestrial records: e.g., Harrison and Sanchez-Goni, 2010; Svensson et al., 2008), improvements in ^{14}C dating methods (Higham et al., 2011; Talamo et al., 2012), and refined radiocarbon calibration curves (Bronk-Ramsey, 2012; Reimer et al., 2009). Despite these research efforts, however, it can be argued that there has been too little focus on how culture-environment interactions might be intertwined with ecological niche dynamics.

One should not have the impression, however, that an interest in culture-environment relationships is a recent phenomenon. For a number of decades, numerous approaches have

been used by anthropologists to examine how human cultures interact with their environments and how these environmental contexts may influence cultural adaptations and the material culture variability that we observe. While a detailed treatment of this anthropological research history is beyond the scope of this document's purpose of presenting the research that I have conducted since obtaining my Ph.D., a brief summary of these different schools of thought will serve to place eco-cultural niche modeling into context.

Some of the earliest examples of anthropological studies conducted from an ecological perspective are the research work conducted by Julian Steward and Leslie White in the 1950's and following decades (Steward, 1955; White, 1959). Steward's approach, termed 'Cultural Ecology', examined the relationship between specific environmental features and certain cultural traits, most notably those associated with technology, social organization, and demography. His approach was not environmentally deterministic in that he proposed that environmental factors influenced only certain elements within a culture, elements which he referred to as the cultural core. In essence, Steward was interested in identifying similarities between historically and geographically distinct cultures so that consistencies in how human cultures interacted with their environments might be elucidated. White's research was also focused on material cultural traits. However, he was more concerned with long term cultural evolutionary trends and how resource use and energy capture influenced cultural evolution (Orlove, 1980).

Subsequently, in the 1960's and 1970's, a new school of thought emerged and is commonly referred to as the Neofunctionalist approach (Orlove, 1980). This paradigm attempted to explain cultural variability in terms of how cultural behaviors reflected adaptations to specific environments (e.g., Vayda and MacKay, 1975). In this sense, one could consider this approach to lean more strongly towards environmental determinism, but despite this shortcoming, it had a number of strong points. First, it focused on populations as the unit of study rather than larger cultures. Second, and more importantly, this research was specifically interested in human-environment interactions, and human populations were not viewed as passive participants in these relationships. Furthermore, the environment was not seen as an inert backdrop against which human cultural variability could be studied (Orlove, 1980). Finally, it is with Neofunctionalism that we see the first explicit use of the concept of ecological niche in anthropological research endeavors (Hardesty, 1972, 1975).

In the 1970's, but more importantly in the 1980's, anthropology, and more specifically the sub-discipline of archaeology, saw the emergence of the processual approach. Processualism also targeted culture-environment interactions but was more focused on methods with which one could identify the mechanisms at work behind cultural adaptation and culture change through time. One principal aim of the processual approach applied to archaeology is to use ethnographic, environmental, and experimental data to construct frames of reference that can be used to interpret the variability observed in the archaeological record (for a detailed review, see Binford, 2001). Ultimately, the goal of this approach is to understand the processes and

mechanisms that operate behind the complex relationships between human cultures and the environments within which they operate.

A concept that proved important in the neofunctionalist and processual approaches, and that also serves as the basis of my analytical approach for investigating prehistoric human-environment relationships, is that of ecological niche. This concept was formalized by Grinnel (1917), who defined it as the geographical expression of a species' climatic and habitat requirements. Later, Elton (1927) proposed that an ecological niche should be viewed as the functional role of a species within a community. Thus, the Grinnellian niche considers the role that unlinked, non-consumable environmental variables play in the geographic distribution of a given species, while the Eltonian niche is focused on how a species interacts with a larger community and attempts to take into account its resource consumption and how that influences community structure, i.e., the functional niche. Hutchinson (1957) defined what is known as the fundamental niche, which is based on the Grinnellian concept and represents the total range of environmental conditions within which a species or population can exist indefinitely. Recently, in an attempt to better characterize the factors affecting how a species is distributed and the ecological niche that it occupies, Soberón and Peterson (2005) proposed a static framework that summarizes the different factors involved—the BAM framework (Figure 1). Unit 'A', which Peterson et al. (2011) refer to as the 'existing fundamental niche', represents Hutchinson's fundamental niche and its intersection with the set of environments that are actually present on the landscape. Unit 'B' represents variables that are dynamically linked to the species, which include food resources, the presence and influence of competitors and

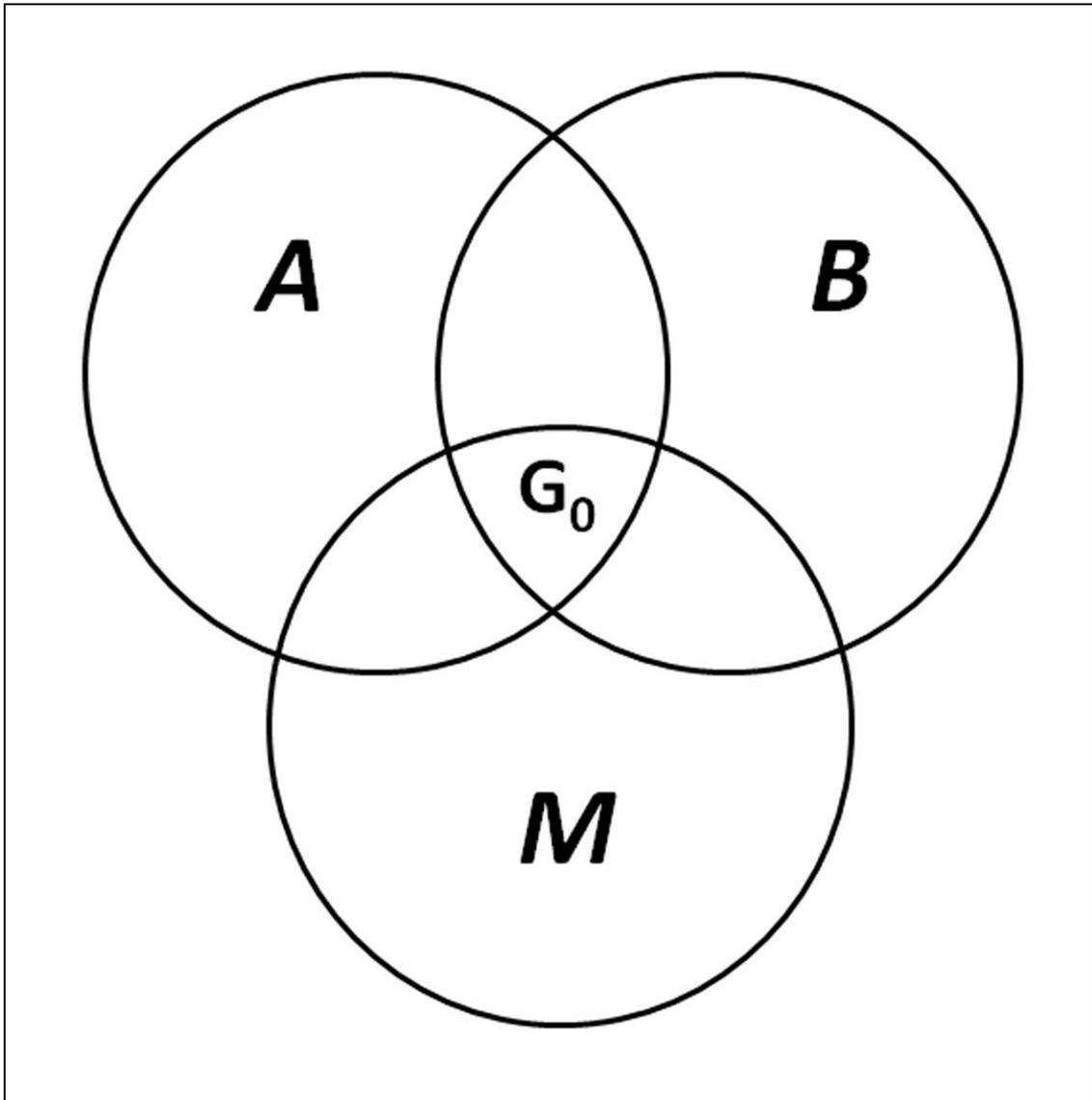


Figure 1: BAM schematic (adapted from Soberón and Peterson, 2005). *A* represents abiotic conditions (the fundamental niche or the realized fundamental niche), *B* represents dynamic inter-species interactions (the functional niche), *M* represents the geographic region(s) accessible to a species, and the 'realized niche' is the intersection of these three factors, indicated by G_0 .

predators. Therefore, this unit is a representation of those variables that can be used to quantify how a species functions within its niche. At large geographic scales, as well as in situations that cannot be directly observed and studied (i.e., the prehistoric past), this aspect of a species' niche is extremely difficult to quantify and operationalize. Finally, unit '*M*' represents the geographic regions that would have been accessible to the species or population in question via dispersal within the time period under examination and that have been sampled such that occurrences could have been detected.

Since a given population's ecological niche is in large part dependent on environmental conditions, then it logically follows that when climatic changes induce the restructuring of environments, a population's ecological niche, or at the very least the geographic expression of its ecological niche, will be altered. With respect to Paleolithic hunter-gatherers, we know that these populations lived during a period marked by abrupt and dramatic climatic changes. For example, Marine Isotope Stages (MIS) 3 and 2 (ca. 60–12 kyr BP) are characterized by closely spaced stadial (cold) and interstadial (temperate) climatic events referred to as Dansgaard-Oeschger cycles (Bond et al., 1993; Bond et al., 1997). Within some of these cycles, stadial events were especially severe and associated with a near shut-down of the Atlantic meridional overturning circulation caused by significant influxes of freshwater and icebergs into northern regions of the Atlantic Ocean. Such events are referred to as Heinrich Stadials (Bond and Lotti, 1995; Heinrich, 1988). It has been demonstrated that these millennial-scale climatic changes had profound impacts on vegetation regimes and therefore terrestrial ecosystems (e.g., Fletcher et al., 2010; Harrison and Sánchez Goñi, 2010). Thus, it follows that Paleolithic hunter-gatherers

were also likely impacted by such changes, and that geographic and adaptive shifts observed in the archaeological record may reflect human responses to the reorganization of the environments that they occupied.

Despite a relatively large corpus of research into culture-environment interactions during the Paleolithic and the variety of analytical approaches taken, there has been no consensus on how to best evaluate and interpret the adaptive changes observed in the archaeological record. In fact, many questions remain unanswered or even uninvestigated. For example, were prehistoric human adaptive shifts and material culture changes undertaken so that populations could continue to exploit the same environments in the face of environmental change (i.e., ecological niche conservatism)? Or, in contrast, are such cultural changes associated with occupation and exploitation of new ecological niches (e.g., ecological niche expansion)? Are there common mechanisms behind various cultural adaptive responses, and if so, how can we best identify them? Such questions can be addressed through eco-cultural niche modeling (ECNM; Banks et al., 2006).

ECO-CULTURAL NICHE MODELING

As was introduced above, numerous attempts, utilizing a variety of datasets and methods, have been made to investigate the relationships between Paleolithic archaeological cultures and environment. However, their primary handicap has been a lack of focus on how these interactions might be intertwined with ecological niche dynamics. Recent improvements in chronology and paleoclimatic reconstructions, in conjunction with eco-cultural niche modeling,

have made it possible to examine cultural variability within more precise temporal frameworks, better relate these to specific paleoclimatic events, and evaluate if and how such variability is related to ecological niche dynamics.

Recent advances in biodiversity studies (for a review see Peterson et al. 2011) have seen the development of biocomputational predictive architectures used to reconstruct ecological niches of species and their geographic distributions, predict their responses to environmental change, and forecast the geographic potential of species' invasions (Araújo and Rahbek, 2006; DeVaney et al., 2009; Kozak and Wiens, 2006; Pearson et al., 2007; Peterson, 2003; Peterson et al., 2007). Research over the past several years has demonstrated the potential of these predictive architectures when applied to archaeological data for understanding past human-environment interactions (Banks et al. 2008a; Banks et al. 2008b; Banks et al. 2009; Banks et al. 2011; Banks et al. 2013a, Banks et al., 2013b). Ultimately, ECNM provides us with the heuristic means with which to potentially identify both the long- and short-term mechanisms implicated in these interactions (d'Errico and Banks, 2013) and understand how they influenced cultural, genetic, and linguistic geography.

ECNM represents a step forward in that it interactively integrates paleoclimatic, geographic, chronological, and archaeological data in order to estimate the ecological niche and geographic range occupied by a past hunter-gatherer population. ECNM is founded on the fact that any given cohesive adaptive system operates within an environmental framework (i.e., its ecological niche). A cohesive adaptive system is defined here as a cultural entity characterized by shared

and transmitted knowledge, reflected by a recognizable suite of cultural traits, that allows a population to adapt to a given set of environmental conditions. Thus, an eco-cultural niche represents the range of environmental conditions exploited by a particular cohesive adaptive system (see Banks et al. 2011, 2013a). This methodological approach employs the Grinnellian concept of ecological niche described above. In such a framework, the combination of paleoclimatic and geographic variables employed, detailed below, can be used to effectively approximate a past ecological niche for a given human population or archaeological culture. The concept of M is extremely important to incorporate into niche estimations because it represents the geographic area within which absences are meaningful in ecological terms. Because the functional niche (i.e., B in Figure 1) is difficult, if not impossible, to accurately quantify in reconstructions of prehistoric ecological niches, such predictions are essentially estimating the realized fundamental niche of a particular human population, in other words the area represented by the intersection of A and M in the BAM framework (Figure 1).

The utility of ECNM is that it provides the ability to evaluate quantitatively whether links exist between a given adaptive system and ecological conditions, and equally as important, determine if a given technocomplex's material culture and geographic distribution may have been influenced more by non-ecological (i.e. cultural) processes. ECNM is particularly relevant for the study of human adaptive system flexibility as it relates to eco-cultural niche variability. It can identify ecological processes (i.e. niche conservatism, niche expansion, etc.) involved in the relationship between an adaptive systems and its environment and track these relationships through time (Figure 2).

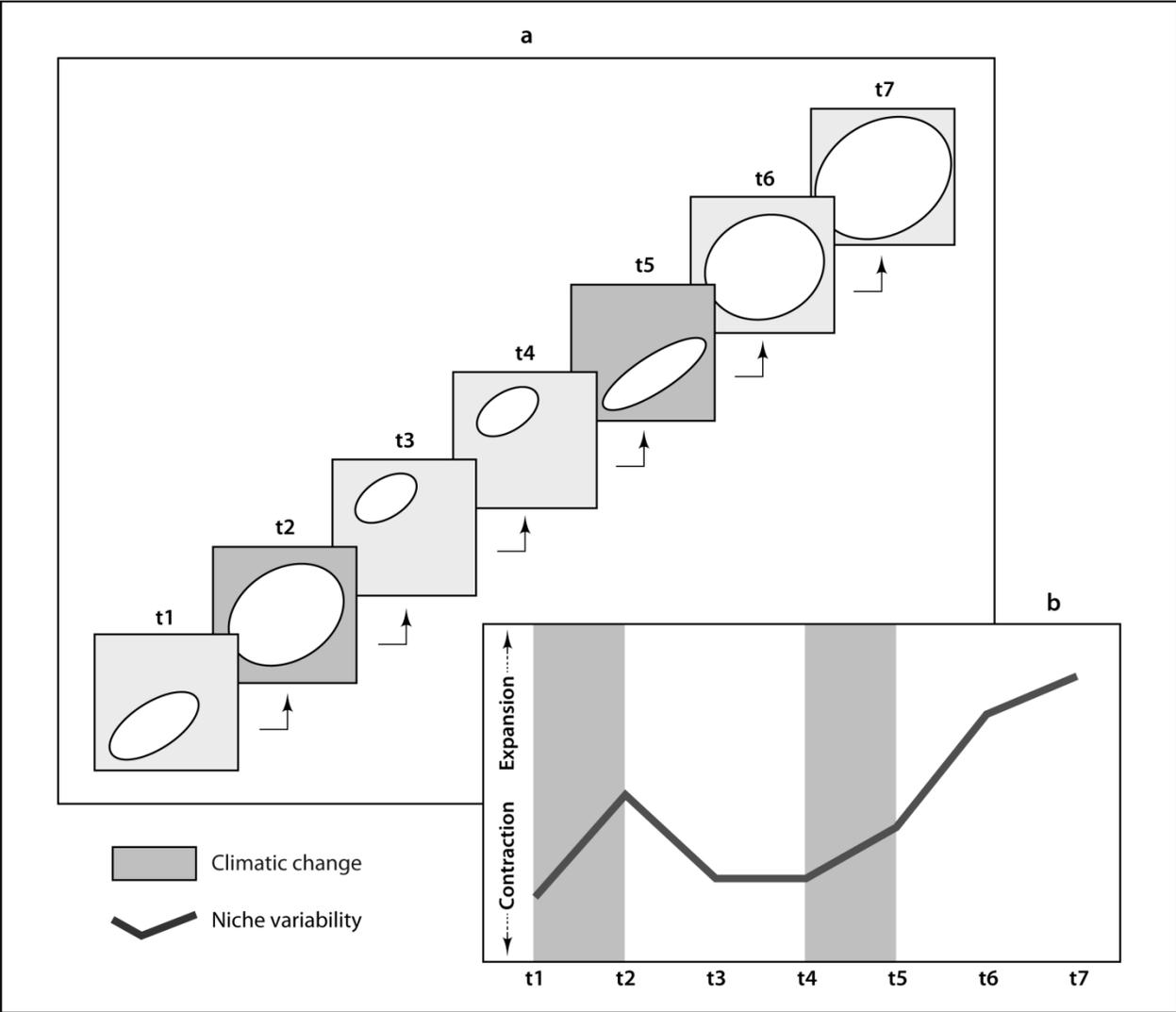


Figure 2: Idealized example of a long-term regional cultural trajectory: (a) composed of multiple stages in which termination conditions become setup conditions for the subsequent stage, all of this encompassing multiple periods that may be characterized by either relative climatic stability or climatic change. Trends in niche variability (b) synthesize long-term trends in the relationship between cohesive adaptive systems and environmental variability at a regional scale. Taken from d'Errico and Banks (2013).

More specifically, when faced with rapid-scale climatic change and subsequent reorganization of environments, a hunter-gatherer population can respond in a number of ways. First, groups may maintain existing settlement, subsistence, and technological systems, conserve the ecological niche they exploit, and simply track its shifting geographic footprint (Figure 3). Such a situation is inferred by Wobst (1974) who proposed that moves between ecological niches would have been rare since such shifts potentially would require new and different adaptations. There also exists the possibility that during periods of environmental change a hunter-gatherer population could avoid geographically tracking a shifting niche footprint by increasing its exploitation of particular environmental settings within the broader conserved ecological niche. Existing, flexible adaptations would serve as a buffer against environmental change in such a scenario (Riede, 2009). This pattern is described for northwestern Central Europe where flexible technologies and mobility patterns allowed late Upper Paleolithic populations to adjust to conditions of the Younger Dryas event without substantially shifting their territories (Weber et al., 2011).

In another scenario, environmental changes could negatively impact demography and social networks, thereby preventing the maintenance of cultural traditions (e.g., Henrich, 2004). This could lead to the loss of certain technological and social adaptations and, ultimately, niche contraction. In other words, the population would only make use of a subset of the environmental conditions it did previously and other portions of the former niche would be completely excluded because groups no longer possessed the means to exploit them.

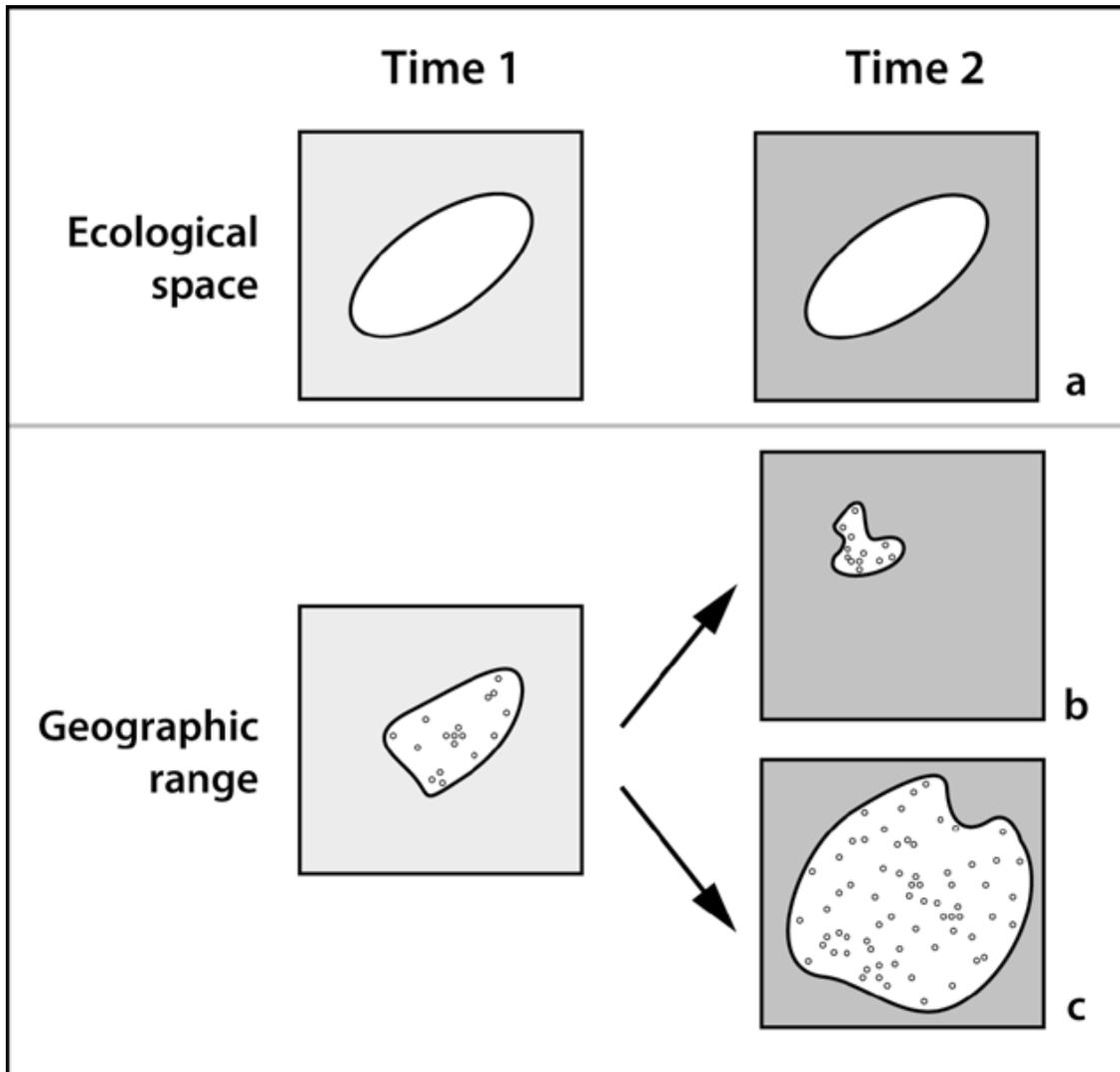


Figure 3: Schematic illustration of how, following a climatic change, the conservation of an ecological niche (a) may result in either a contraction (b) or expansion (c) of the niche's geographic range (d'Errico and Banks, 2013).

Lastly, one needs to take into account the fact that culture allows for rapid adjustments and adaptations to changing climatic conditions and new environments (Richerson and Boyd, 2005; Richerson et al., 2009). Such cultural adaptations open the door for the potential expansion of the exploited ecological niche as a means of adjusting to abrupt restructuring of environments brought about by rapid-scale deterioration (or amelioration) of climatic conditions. This adaptive and behavioral flexibility among hunter-gatherers may be recognized archaeologically by technological changes (bone and lithic toolkits), shifts in subsistence and settlement systems (e.g., mobility structure, geographic ranges, etc.), and shifts in social network structure. Because the success of technological innovations and adaptations is linked to effective population size and density (Shennan, 2001), the maintenance of geographically-broad social networks would become increasingly important if groups rapidly expanded their ecological niche and geographic range, effectively reducing population density. Similarly, social networks would be of increased importance for groups operating at the limits of their expanded ranges (see Whallon, 2006).

Logically, if demography is not adversely affected, the potential for niche expansion would increase during instances in which there was an increase in the level of ecological risk faced by human populations; ecological risk being defined as the amount of variation (seasonally or inter-annually) that a population faces in its food supply over time (see Collard and Foley, 2002; Nettle, 1998). Studies focused on animal taxa have shown, however, that niche conservatism is common (e.g., Peterson, 2011). Does the use of culture as a means of adaptation mean that the general tendency towards niche conservatism may not necessarily apply to human hunter-gatherer populations in certain situations?

Data Requirements and Selection

For data inputs, ECNM requires the geographic coordinates of archaeological sites bearing cultural features that are recognized as distinctive of a particular archaeological culture, along with a set of raster GIS data layers summarizing environmental dimensions potentially relevant to shaping the eco-cultural niche exploited by that culture during a specific climatic phase.

Occurrence Data

With respect to archaeological occurrence data, early ECNM studies were focused strictly on archaeological sites belonging to a particular archaeological culture (e.g., Solutrean, Early Epigravettian, Aurignacian) and that had been radiometrically dated to a particular climatic event or interval. Since most archaeological cultures span a number of rapid-scale Dansgaard-Oeschger Events, it was thought that this was the best way to avoid introducing occurrence data that were not associated with the climatic window under investigation. Furthermore, it was reasoned that if these chronological data were examined critically, one could effectively eliminate erroneous sites and restrict the data sample to those that had the highest likelihood of representing a human presence at a location on the landscape within a relatively narrow window of time. Later studies, while still focused on the idea of targeted a human population during a specific climatic event, or chronological sequence of D-O events, expanded the data selection process to include non-dated sites that had levels containing lithic diagnostics (i.e., index fossils) known to be associated with a particular archaeological culture and time period due to the fact that they had been reliably dated at other sites (Banks et al., 2009; Banks et al.,

2011; Banks et al. 2013a). This more exhaustive procedure of occurrence data evaluation and selection allows more robust eco-cultural niche predictions to be generated.

Environmental Data

Geographic variables are assumed to have remained relatively constant over the past 300 ka 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 can be inferred 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, HadCM3), 2) an atmosphere-only model with a slab ocean component (representing the top 50 meters of the water column), or 3) an atmosphere-only model with imposed Sea Surface Temperature (SST) values. 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. 2008b; Sepulchre et al. 2007). The results from the different methods listed above can be statistically downscaled (e.g., Vrac et al. 2007), to increase the resolution of the simulated paleoclimatic data. A final option is to use a regional model forced by GCM outputs as boundary conditions, thereby producing climatic simulations with a resolution as fine as 5 km (Frei et al.

2006). These higher levels of resolution are most appropriate for examining cultural and niche trajectories on a regional scale. The outputs of this simulation process can be used to force a dynamic global vegetation model (e.g., ORCHIDEE, SPITFIRE) 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 in an ASCII-format. During this process, outputs are compared to paleoenvironmental data to test whether the simulations capture past conditions satisfactorily, and if they do not, there exist means to improve the next generation of simulations in an effort to better capture past paleoclimatic conditions.

Selected Predictive Modeling Architectures

Using the above data, a number of predictive modeling approaches are available (climatic envelope range, generalized linear model, generalized 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 an eco-cultural niche and its geographic distribution. Araújo and New (2007) point out that ideally one should use multiple modeling methods and compare their outputs. While early ECNM studies only employed a single genetic algorithm (GARP: Genetic Algorithm for Rule-Set Prediction; Stockwell and Peters, 1999), more recent applications have incorporated maximum entropy methods (Maxent; Phillips et al., 2006) in addition to GARP. At a very general level, these two 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 (Figure 4).

Genetic Algorithm for Rule-Set Prediction

More specifically, with GARP, occurrence data (i.e., presence-only data) are resampled randomly by the algorithm to create training and test data sets. An iterative process of rule generation and improvement then follows, in which a method is chosen randomly from a set of inferential tools—Atomic, Range, Negated Range, and Logistic Regression—and applied to the training data to develop specific rules (Stockwell and Peters, 1999). These rules evolve to maximize predictivity by several means (e.g., crossover, mutation) via a process that evaluates predictive accuracy based on an independent subsample of presence data and a set of points sampled randomly from regions where the species has not been detected. The final rule-set defines the distribution of the target population in environmental dimensions (i.e., the ecological niche: Peterson et al., 2011), which is projected onto the landscape to estimate a potential geographic distribution. For each GARP model, 1000 replicate runs are performed with a convergence limit of 0.01, using 50% of the occurrence points for model training. A best subsets protocol (Anderson et al., 2003) is typically employed, with a hard omission threshold of 10% and a commission threshold of 50%, and summed the resulting 10 grids to create a consensus estimate of the geographic range of the ecological niche associated with the archaeological occurrence data.

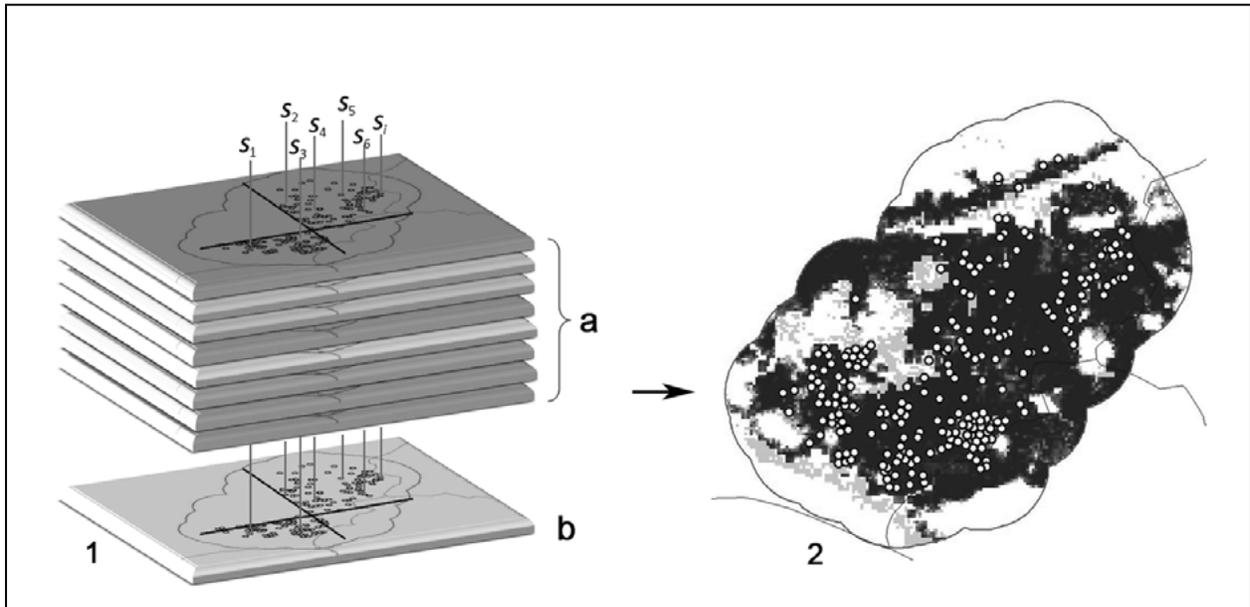


Figure 4: Schematic rendition of how one of the predictive architectures, in this case the Genetic Algorithm for Rule-Set Prediction (GARP), reconstructs an eco-cultural niche (taken from d'Errico and Banks, 2013). 1) Occurrence data (i.e., location of archaeological sites belonging to a cohesive adaptive 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 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).

Maxent

The maximum entropy (Maxent) modeling architecture uses the distribution of known occurrences to estimate a species' ecological niche by fitting a probability distribution of maximum entropy (i.e., that which is closest to uniform) to the set of pixels across the study region (Phillips et al., 2006). This estimated probability distribution is constrained by environmental characteristics associated with the known occurrence localities, while at the same time it aims to avoid making assumptions not supported by the background data. To produce eco-cultural niche reconstructions, the following parameters for Maxent version 3.3.3a are used: random test percentage = 50, maximum iterations = 500, background points = 10,000, and convergence limit = 10^{-5} . This configuration approximates that used to produce the GARP predictions, in that half of the available occurrence data are set aside for evaluating and refining model rule-sets.

When estimating ecological niches, it is important to consider the geographic areas that would have been accessible to the species or population in question via dispersal (*M* in Figure 1), and which have been sampled archaeologically such that such occurrences could have been detected (Barve et al., 2011). One should incorporate *M* into model training because it represents the geographic area in which presences may exist and within which absences are meaningful in ecological and environmental terms. Barve et al. (2011) point out that using overly broad designations of *M* can significantly influence predicted geographic distributions. Therefore, when estimating an eco-cultural niche for a past hunter-gatherer population, it is important to attempt to estimate *M*, based on hypothesized settlement systems or known raw

material circulation networks (see Banks et al., 2011; Banks et al., 2013a). No matter the data used to estimate M , it is important to not employ the entire geographic coverage represented by the environmental data layers plugged into the predictive algorithm. Initial eco-cultural niche modeling studies did not take this geographic concept into consideration as it was not until recently (Barve et al., 2011; Peterson et al., 2011) that the influence of M on ecological niche reconstructions and species distributions was recognized.

One also must consider the likelihood that some of the occurrence data employed in an eco-cultural niche modeling analysis may be in error (e.g., erroneous or incorrect cultural attribution, lack of temporal correspondence to the targeted time period due to poor chronological resolution), and the potential influence of such data on niche predictions can be corrected for by thresholding each eco-cultural niche prediction. To do this for the ecological niche predictions produced by GARP and Maxent, each grid cell is assigned a value that represents model agreement or probability of occurrence, respectively. Given the frequent problem of overfitting (i.e., excessive model complexity) in highly dimensional environmental spaces, continuous outputs are best thresholded to produce binary results (Peterson et al., 2007). Therefore, one can follow the procedure detailed by Peterson et al. (2008) for incorporating a user-selected error parameter E , which summarizes the likely frequency in the occurrence data set of records that are sufficiently erroneous as to place the species in environments outside its ecological niche. This parameter is typically set at 5% (i.e., $E = 5$). Such a value is appropriate for occurrence data that are likely to include a small degree of error and is appropriate considering the ambiguity of material cultural assemblages typically encountered

for a specific archaeological culture. Hawth's Tools extension to ArcGIS 9, or the stand alone software Geospatial Modelling Environment (Ver. 0.7.2.0; Beyer, 2012), can be used to identify the GARP and Maxent output levels that included $(100 - E)\%$ of the training occurrence points; this value is used to reclassify the grid cells from the prediction into a binary map. For example, with a hypothetical occurrence data set of 40 points for model training and $E = 5$, one would find the threshold that includes 38 of the points and reclassify all grid cells with values below it as unsuitable and all grid cells with values at or above it as suitable. This thresholding procedure is applied to the raw predictions, and then each resulting binary raster grid is saved as an integer data layer.

Characterizing Eco-cultural Niche Predictions

Once robust ecological niche estimations have been produced, statistical methods are used to identify the environmental factors that shaped these niches and measure their breadth.

Likewise, a variety of methods exist (e.g., background similarity test: Warren et al., 2010; partial-ROC test: Peterson et al., 2008) to test whether two populations' eco-cultural niches are significantly different or if they are interpredictive, either within a single climatic event or between two different events.

Recent years have seen a proliferation of techniques for reconstructing ecological niches and predicting species' distributions, but debate has focused on how best to evaluate resulting models statistically (Araújo and Guisan, 2006; Peterson et al., 2008; Warren et al., 2008). Hence, a variety of methods should be used to evaluate and compare the outputs from the two

employed modeling algorithms. Warren et al. (2008) described new methods and statistical tests for evaluating overlap between ecological niche models quantitatively, and provided an implementation of these methods with the software package ENMTools version 1.3 (Warren et al., 2010; <http://enmtools.blogspot.com/>). ENMTools allows one to generate ecological niche models (ENMs) with Maxent, calculate niche breadth and similarity measures, as well as develop randomization-based comparisons of niches.

To characterize an eco-cultural niche (ECN), traditional descriptive statistics as well as Principal Component Analyses are effective. To examine patterns of niche similarity, a useful tool is ENMTools' niche breadth measure (inverse concentration), overlap measures I and D (Warren et al., 2008), and background similarity tests. Niche breadth is a measure of the range of abiotic conditions within which a species can maintain populations (Carnes and Slade, 1982; Levins, 1968; Soberón, 2007). Overlap measures I and D compare two ECNs and measure the similarity between them. The background similarity test evaluates whether the observed degree of similarity between two ECNs is greater than would be expected by chance. This comparison is accomplished by generating a null distribution for ECN model difference expected between one region and another based on occurrence points drawn at random from within a relevant geographic area (Warren et al., 2010), which corresponds to the M s defined for the archaeological cultures being examined (described above). If the calculated overlap value is significantly greater than the distribution of overlaps from the pseudo-replicates, the null-hypothesis of niche identity cannot be rejected and the two niches can be considered inter-predictive. If niche overlap is significantly less than the pseudo-replicate overlaps distribution,

the null hypothesis of no difference can be rejected, meaning that the two niches are more different from one another than would be expected by chance.

A key feature of the two predictive architectures described above 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 to the locations of known occurrences for the latter period to see whether or not it successfully predicts their presence. To evaluate the possibility of changes in niche dimensions through time, one can use partial ROC (Receiver Operating Characteristic) tests (Peterson et al., 2008) to evaluate model predictivity among time periods. The partial ROC method calculates the Area Under the Curve (AUC) of the ROC as per normal ROC AUC testing, but truncates the curves to reflect a sensitivity threshold for the niche predictions being compared. In other words, the user-chosen error parameter E is used to target and evaluate different critical area thresholds for the two ROC curves (see Peterson et al., 2008 for a detailed discussion). This AUC value and the AUC null expectation (i.e., the straight line connecting 0,0 and 1,1 in ROC plots) are used to calculate an AUC ratio. Bootstrapping manipulations, via 50% resampling with replacement, use the predicted suitability value associated with each occurrence point along with the proportion of the area predicted present (with respect to the total coverage area of the environmental layers) for each suitability value to calculate a set of AUC ratios for each niche prediction (Barve, 2008). One-tailed significance of differences between each niche prediction's AUC ratios is assessed by direct count, summing the number of partial ROC ratios that are ≥ 1 and calculating a P -value as

the proportion out of 1000. If the probability is low (i.e., below 0.05), one can conclude that the niches are significantly differentiated, thus indicating a niche shift through time.

The method described above represents an improvement over the comparative methodology employed in earlier examination of possible niche variability through time (Banks et al., 2008b; Banks et al., 2008c). In those studies, GARP's capability of projecting an ecological niche prediction onto a different climatic episode was used. The resulting projection was compared to the locations of known occurrences for the latter period to see whether or not the model successfully predicts their spatial distribution. The degree of inter-predictivity (i.e., niche stability) was evaluated statistically by determining the proportional area predicted present by the projected model at each predictive threshold (i.e., 10 out of 10 best subset models in agreement, 9 out of 10 in agreement, etc.) along with the number of occurrence points correctly predicted at each threshold. A cumulative binomial statistic was applied to these values to determine whether the coincidence between projected predictions and independent test points is significantly poorer than random expectations. Thus, this approach, like the partial ROC method, evaluates whether the two distributions are more differentiated from one another than would be expected by chance, albeit at a lower degree of resolution.

ECNM APPLIED TO THE PALEOLITHIC ARCHAEOLOGICAL RECORD

As is evident above, a wide variety of data are needed in order to examine the relationships between culture and environment via eco-cultural niche modeling. In order to acquire these data, it has been necessary to forge numerous relationships with a variety of experts. Close

collaborations with paleoclimatic modelers such as Masa Kageyama and Gilles Ramstein (LSCE - UMR 1572) have yielded state-of-the-art high resolution paleoclimatic simulations, and the expertise of Maria Fernanda Sánchez-Goñi (EPOC - UMR 5805) has been critical for evaluating their accuracy. The necessary critical examinations of the relevant archaeological data have benefited from collaborations with a number of Paleolithic archaeologists, including Francesco d'Errico and João Zilhão (ICREA - University of Barcelona). Finally, numerous interactions with ecologists, such as A.Townsend Peterson and Andrès Lira-Noriega, have served to refine strategies for best applying ecological niche modeling methods to archaeological data and lines of questioning.

The archaeological questions that one can attempt to answer with ECNM are highly dependent on available datasets. With respect to paleoclimatic data, the collaborations referenced above have provided high-resolution paleoclimatic simulations for climatic events that occurred during the Middle-to-Upper Paleolithic transition as well as the Last Glacial Maximum. It is for this reason that most ECNM studies, to date, have focused on examining how Upper Paleolithic cultures responded to rapid-scale climatic variability. As it concerns archaeological and chronological data, ECNM studies have benefited from the collation of data from the archaeological literature and in turn the construction of relational databases. There is an extensive body of material culture and radiometric data pertaining to the archaeological record of Europe for the period covering Marine Isotope Stages 6 through 2, but for the most part, compilations of these data tend to be regionally and/or temporally specific. Thus, to facilitate applications of ECNM to the European Paleolithic record, it is has been necessary to construct a

continental-scale relational database that records the geographic locations of archaeological sites, each site's specific cultural levels, and their associated material culture, technological, and chronological data, in addition to related bibliographic information. Such relational database structures are of extreme utility as they allow one to explore and analyze associations between different data classes in a manner that is not possible with more commonly used spreadsheet architectures. An extract, in spreadsheet format, of cultural and chronological data pertaining to the European Paleolithic archaeological record, which was assembled in a collaborative effort by a number of individuals in the PACEA laboratory and figured prominently in applications of ECNM, has been published recently (d'Errico et al., 2011).

The Middle-to-Upper Paleolithic transition

One important debate in Paleolithic archaeology is centered on the issue of whether climatic change or competition with newly arrived modern human populations was the prime mover behind the disappearance of Neanderthal populations in Europe. Eco-cultural niche model reconstructions for Neanderthal and modern human populations across a number of climatic phases between 43–37k cal BP demonstrated that Neanderthal disappearance is best explained by competition with newly arrived modern humans and not by climate change (Banks et al., 2008b). This conclusion was reached by using the predictive architecture GARP to project the Neanderthal eco-cultural niche for Heinrich Stadial 4 (HS4) onto the climatic conditions of the subsequent phase termed Greenland Interstadial 8 (GI 8). The results indicated that the Neanderthal niche was present across the majority of the European continent during GI 8, but that their actual geographic distribution during this period was restricted to Mediterranean

regions (Figure 5). During this same time interval, the geographic expression of the modern human ecological niche expanded. Neanderthal populations moved south, and eventually disappeared, once they came into contact with modern human populations, despite the fact that the ecological niche to which they were adapted was present across Europe. Thus, competitive exclusion is the most parsimonious explanation for Neanderthal disappearance.

Adaptive shift between the Proto- and Early Aurignacian

The Aurignacian technocomplex comprises a succession of culturally distinct phases. Between its first two subdivisions, the Proto-Aurignacian and the Early Aurignacian, we see a shift from single to separate reduction sequences for blade and bladelet production, the appearance of split-based antler points and a number of other changes in stone tool typology and technology as well as in symbolic material culture. Bayesian modeling of available ^{14}C determinations indicates that the material culture changes between the Proto- and Early Aurignacian are coincident with abrupt and marked climatic changes between GI 10–9 and HS4, respectively. ECNM was used to quantitatively evaluate whether these shifts in material culture are correlated with environmental variability and, if so, whether the ecological niches exploited by human populations shifted accordingly (Banks et al., 2013a).

Results indicate that the transition between the Proto-Aurignacian and the Early Aurignacian was associated with an expansion of the ecological niche (Banks et al., 2013a). These shifts in both the eco-cultural niche and material culture are interpreted to represent an adaptive response to the relative deterioration of environmental conditions at the onset of HS4. This

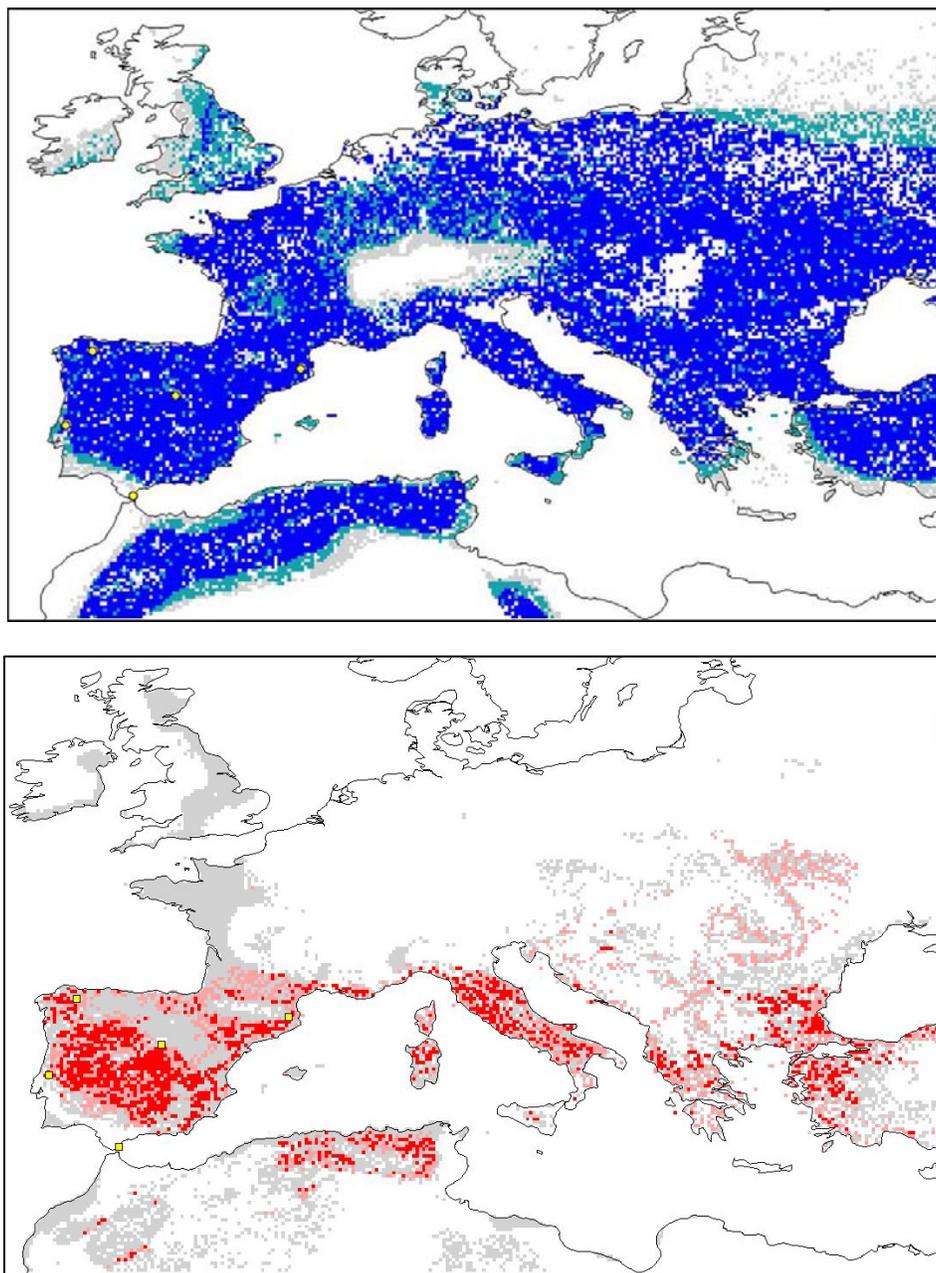


Figure 5: The upper prediction (dark blue) is the projection of the HS4 Neanderthal niche onto GI 8 climatic conditions. The lower prediction (dark red) is the actual occupied Neanderthal niche during GI 8 based on known sites. This contraction of the realized Neanderthal niche, thus, cannot be explained by climate change. Rather, it is best explained by competition with AMH, whose ecological niche geographically expanded during the same period (Banks et al., 2008b).

exemplifies a situation in which cultural flexibility was used by hunter-gatherer populations to quickly adapt to a rapid-scale and severe climatic fluctuation. Moreover, this is the first time that ecological niche expansion has been demonstrated for an archaeological cultural transition. Thus, the trend towards niche conservatism among most animal species over relatively short spans of time (Peterson, 2011) does not appear to hold true for human populations, or at least Upper Paleolithic hunter-gatherer cultures. A logical question that warrants further research is whether the use of cultural solutions to expand the exploited ecological niche is unique to modern humans, or were there similar instances of such shifts among anatomically archaic humans?

The Last Glacial Maximum

ECNM research on this time period is comprised of four different studies, each of which took into account methodological lessons learned from previous analyses. The first targeted technocomplexes during the height of the LGM at a broad scale in order to identify possible differences in their ecological niches. The second study used a more exhaustive archaeological database to examine Upper Solutrean technological and ecological variability. The third used improved niche modeling and statistical measures to examine whether the relatively homogenous lithic industry of the Badegoulian was used to exploit distinct ecological niches. Finally, the fourth study examined the ecological niches and distributions of two principal prey species, reindeer and red deer.

In the first study, a high-resolution paleoclimatic simulation for the LGM, a sample of Solutrean and Early Epigravettian sites dated by AMS between 23 and 21k cal BP, and GARP were used to reconstruct the eco-cultural niches for these two technocomplexes (Banks et al., 2008a). The results clearly indicate that the latitudinal limits of human populations during this time period correspond to the known limits of periglacial conditions (Figure 6). The Solutrean niche prediction shows that, as inferred from the known site distribution and documented subsistence systems, this archaeological culture was adapted to arctic conditions, in contrast to the contemporaneous Early Epigravettian. One also notes that Epigravettian populations did not occupy their entire ecological niche. While competition for resources and cultural boundaries likely played a role, it was argued that differing levels of ecological risk (cf., Collard and Foley, 2002; Nettle, 1998) were the main reason behind this observed pattern. Epigravettian populations were subjected to lower levels of ecological risk, and therefore did not occupy the entire geographic range of the niche they exploited.

The implications of ecological risk were investigated further by examining the Upper Solutrean (Banks et al., 2009). In this study, eco-cultural niche variability between the Middle and Upper Solutrean (i.e., between HS 2 and the early LGM), as well as within the Upper Solutrean, was examined. The results indicated that the cultural choices behind the production of specific armature types during the Upper Solutrean had an ecological basis since they are associated with particular environmental conditions. However, it was proposed that the diversification of armature types was the by-product of cultural drift that occurred due to increased territoriality, which was the result of lowered levels of ecological risk associated with the slight climatic

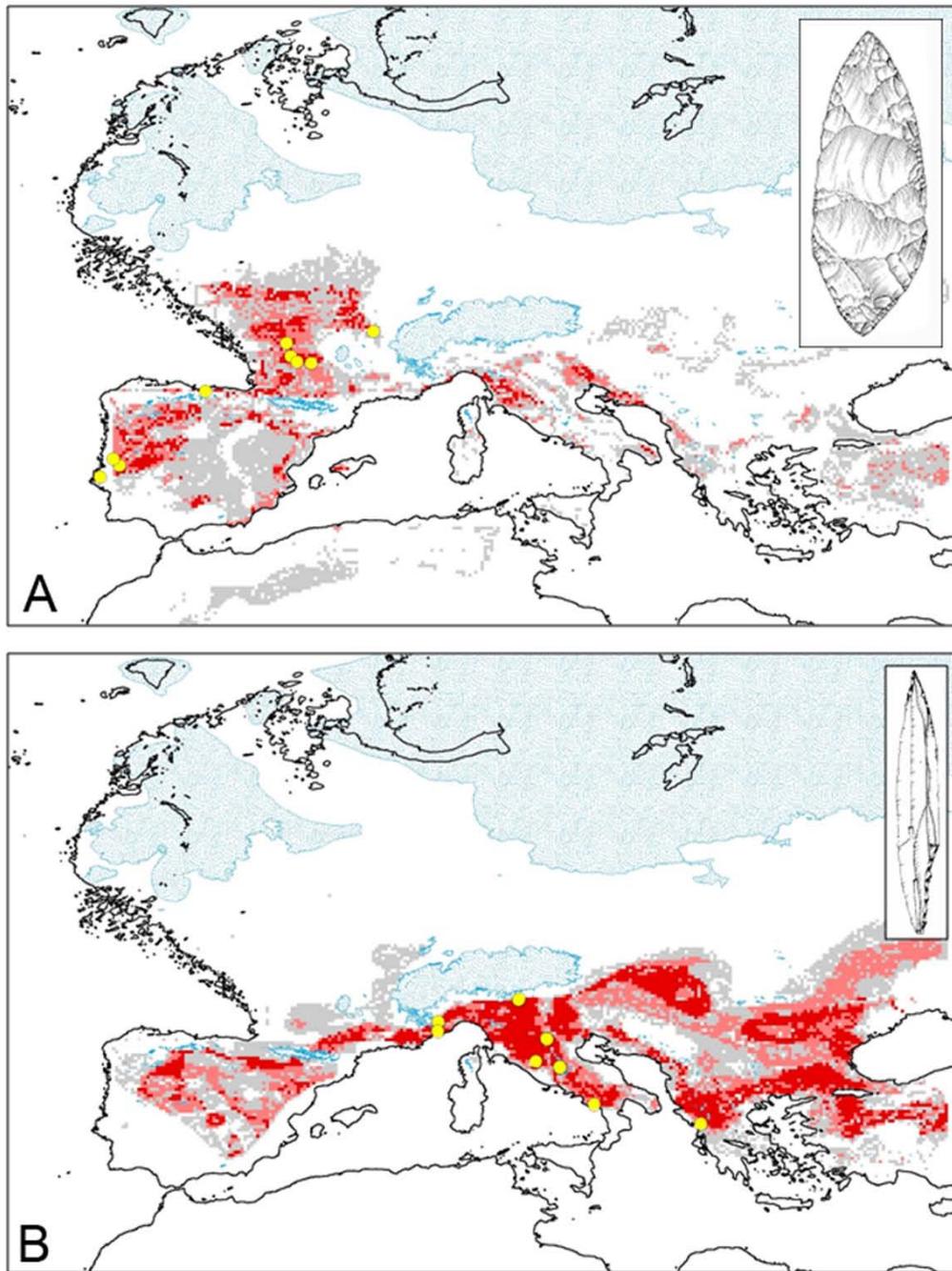


Figure 6 : Eco-cultural niche predictions for the Solutrean (A) et early Epigravettian (B) during the Last Glacial Maximum (adapted from Banks et al., 2008a).

amelioration between HS 2 and the early LGM. This study demonstrated that ECNM is an effective means with which to identify both ecological and cultural factors that influenced material cultural variability.

The third study targeting the LGM focused on the Badegoulian archeological culture. First, the existence of two distinct cultural territories based on the circulation of lithic raw material types was identified (Figure 7), and it was shown that these territories were contained within a broad ecological niche (Figure 8; Banks et al., 2011). These circulation networks reflected the exploitation of particular conditions within a single ecological niche by distinct social groups that shared a common lithic industry. It was argued that the existence of these Badegoulian social territories represents a carryover of the regional territories established during the preceding Upper Solutrean. This study illustrated our ability, using ECNM, to identify and evaluate diachronic trends in cultural continuity for situations where such patterns might be missed when the focus of study is restricted solely to lithic technology and typology.

Finally, the application of ecological niche modeling methods to reindeer and red deer populations of the LGM was used to evaluate whether their respective distributions were the result of ecological niche conservatism or if niche shifts might be implicated (Banks et al., 2008c). Such a study was warranted because traditional approaches only allow for crude characterizations of species distributions, while niche modeling methods allow us to understand the ecological and geographic processes that shaped these distributions. The results indicate that reindeer and red deer distributions during the LGM were characterized by niche

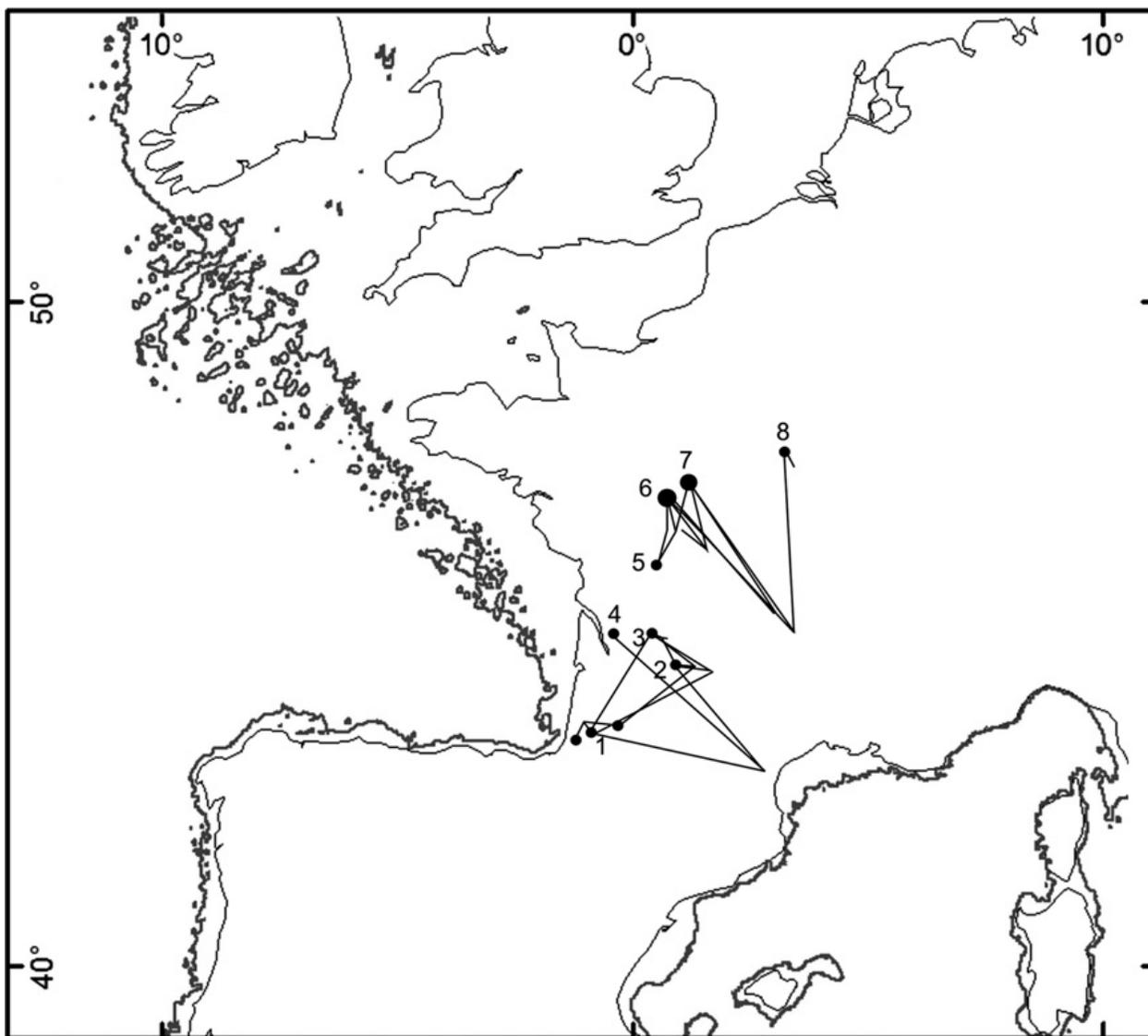


Figure 7: Depiction of lithic raw material source areas and circulation for the Badegoulian archaeological culture. Source areas are indicated by solid black circles, while lines indicate the direction and distance of source material circulation. LGM coastlines are depicted in bold grey and are contrasted with those of the present-day (taken from Banks et al., 2011).

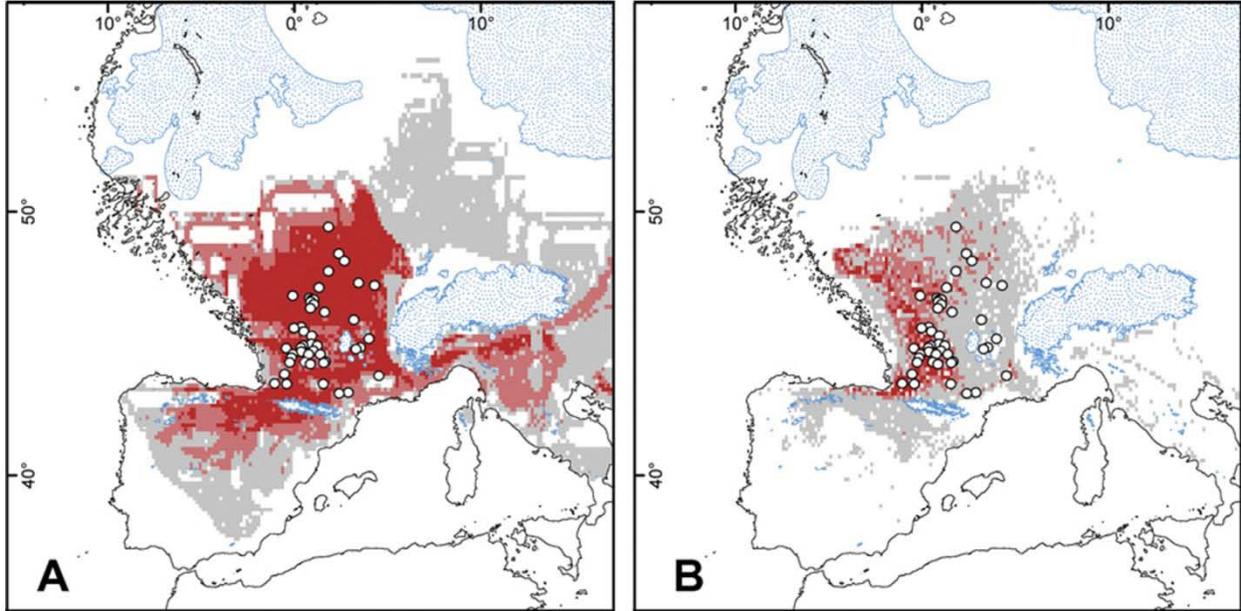


Figure 8: Badegoulian eco-cultural niche reconstructions: A) GARP prediction for the entire technocomplex; B) Maxent prediction for the entire technocomplex. Background similarity tests indicated that the two distinct territories inferred from the differential circulation of lithic raw materials were not significantly ecologically differentiated (Banks et al., 2011).

conservatism and were the result of these two species following the contracting geographic footprint of their respective stable ecological niches. Interestingly, the eco-cultural niches of Solutrean and early Epigravettian populations correspond closely to those of reindeer and red deer, their respective principal prey species. This type of study represents an example of Middle Range Research (see Binford, 1978, 1983) and has implications for investigations targeting prehistoric hunter-gatherer subsistence economies.

Over the past few years, each ECNM study has served to refine and improve this methodological approach, both in the nature of the archaeological data used and the methods used to examine them. First, as discussed earlier, ECNM has moved away from using only sites that are reliably dated to a strategy that also includes undated sites with cultural diagnostics that are unambiguously associated with a specific archaeological culture. Such an approach allows for more robust niche predictions. Secondly, it has become evident that Bayesian age modeling techniques are extremely important for correlating archaeological cultures with specific climatic events. This is especially the case for periods near the temporal limits of the radiocarbon dating method. With respect to niche modeling techniques, it has become evident that we must take into account the geographic regions that would have been accessible to prehistoric populations when predicted their eco-cultural niches. Finally, more robust methods for statistically comparing different niche predictions have been employed, thereby improving the possibility of identifying eco-cultural niche shifts.

In summary, it is important to highlight the fact that this corpus of research carried out over the past several years has required an ability to work with a number of specialists in a variety of disciplines. Such work necessitates excellent management and professional relationship skills. With these collaborations, I have needed to continuously learn new skills and update existing areas of expertise (Bayesian statistics, paleoclimatic modeling, GIS). My research and publication records demonstrate that, not only am I an effective communicator and collaborator, but that I have the ability to formulate and investigate research questions important to the field of Archaeology. My work over the past several years serves to demonstrate that I have the personal and professional skills necessary to direct and carry out research at departmental, university, and international scales.

RESEARCH PERSPECTIVES

It is clear that with adequate archaeological and chronological data, and high-resolution paleoclimatic simulations, one can apply ECNM to a variety of archeological questions. In the coming years, I envision using this approach to examine cultural adaptations across with entire Upper Paleolithic in order to test the hypothesis that millennial-scale climatic variability and resulting ecological niche shifts played a role in the appearance of specific adaptations. I also envision the completion of work focused on determining whether the appearance of cultural innovations among anatomically modern humans in South Africa during MIS 5 and 4, as well as among Neanderthal populations in Europe during MIS 3 were associated with ecological niche shifts. This work will be completed within the framework of the ongoing European Research Council project entitled "TRACSYMBOLS", co-directed by Dr. Christopher Henshilwood and Dr.

Francesco d'Errico. Finally, ECNM offers the possibility of identifying long-term mechanisms that worked to shape the cultural evolution of our lineage.

Eco-cultural niche variability across the Upper Paleolithic

It has been demonstrated that ECNM is an effective means with which to evaluate the paleoecological pertinence of archaeologically defined artifact types and identify ecological mechanisms and cultural processes behind material culture variability (Banks et al., 2009; Banks et al., 2011; Banks et al., 2013a). I propose to enlarge my focus and examine eco-cultural niche variability across the Upper Paleolithic.

I possess a number of high-resolution paleoclimatic simulations that will allow me to reconstruct and compare eco-cultural niches for the principal Upper Paleolithic technocomplexes (i.e., Aurignacian, Gravettian, Solutrean, Magdalenian) and investigate whether documented technological shifts are associated with possible eco-cultural niche shifts. I recently demonstrated that the transition between the Proto- and Early Aurignacian is characterized by an expansion of the exploited ecological niche (Banks et al., 2013a). In contrast, a conservation of the exploited ecological niche has been documented between the Middle and Upper Solutrean, or Heinrich stadial 2 and the early LGM, respectively (Banks et al., 2009). Therefore, it is clear that Upper Paleolithic human populations did not always respond to D-O climatic variability in the same manner. There is a need to understand if and how the major Upper Paleolithic cultural transitions are linked to ecological niche dynamics, and ECNM provides the quantitative tools to do so.

At a finer scale, examinations of cultural-ecological dynamics within a specific archaeological culture are also needed. Are the patterns that we were able to identify for the Upper Solutrean and Badegoulian cultures unique, or do similar patterns exist within other archaeological cultures and time periods? For example, did Early Epigravettian populations in Central and Southern Europe respond to climate change in similar ways to those documented in Western Europe? How does Magdalenian material cultural variability relate to environmental changes brought about by Heinrich Event 1 and subsequent Greenland Interstadial 1?

Since links between lithic technology and ecology have been identified with ECNM, this method should be applied to other aspects of Upper Paleolithic material culture beyond that of subsistence technologies. For example, Vanhaeren and d'Errico (2006) concluded that regional variations in personal ornament types reflect ethnolinguistic variability during the early Upper Paleolithic. Furthermore, my examination of the Badegoulian (Banks et al., 2011) identified distinct social territories associated with distinct environmental conditions, and stressed the need to expand the scope of study to incorporate a broader range of material culture. With ECNM, one can determine if identified social territories (defined by raw material circulation networks, material culture variability, etc.) were associated with specific ecological niches and better understand how cultural systems were organized within their environmental contexts.

Adaptive responses during Marine Isotope Stages 5a–4

One reason for an intense research focus on South Africa is that this region saw the origin of AMH who later spread across the African continent before migrating out to other regions of the world (Forster and Matsumura, 2005; Mellars, 2006; Tattersall, 2009). It is with the Still Bay technocomplex in southern Africa at the end of the last interglacial (MIS 5a, just prior to 75 kyr cal BP) that we see a complex combination of symbolic behaviors such as the systematic use of ochre, personal ornaments, and the manufacture of bone tools and foliate points (d'Errico et al., 2009; d'Errico and Henshilwood, 2007; Henshilwood et al., 2009). At present, chronological data indicate that these symbolic behaviors disappeared at the beginning of MIS 4, and human settlement in South Africa either ceases or becomes archaeologically invisible for a few thousand years (Henshilwood, 2012; Jacobs et al., 2008). Lithic technologies were episodic or discontinuous in nature and those that appear during the latter part of MIS 4 (Howieson's Poort technocomplex) are different from those that preceded them. The material culture lacks the same innovations seen earlier, and symbolic behaviors changed as well (e.g., ostrich shell engravings: Texier et al., 2010). The reasons and mechanisms behind this gap in the archaeological record and subsequent changes are unknown. It is possible that rapid-scale environmental changes during MIS 4 are implicated, although contrary hypotheses exist (Jacobs and Roberts, 2009). Thus, ECNM can contribute to resolving this issue by evaluating whether these cultural changes are linked with environmental variability (i.e., climate change), and if so, determine the exact scale and nature of this relationship.

During the latter stages of MIS 4 in Europe, the Neanderthal archaeological record indicates that they began to develop behaviors that in Africa are associated with AMH populations. These include burials, the use of pigment (Soressi and d'Errico, 2007), and lithic technologies that are similar to those manufactured by AMH in southern Africa (Villa et al., 2005). Recent work has shown that many later Neanderthal technological developments occurred prior to contact with AMH populations (e.g., Zilhão et al., 2010). Therefore, important research questions are: (1) are these cultural developments associated with Neanderthals related to possible changes in the ecological niches they exploited, and if so, how?; (2) does the appearance of these cultural innovations follow a similar trajectory to that observed for AMH in Africa?

Europe and southern Africa are two areas of the world where we see biologically and geographically distinct human populations displaying similar cultural behaviors during MIS 5a–4. In the near future, I intend to integrate available archaeological, chronological, and paleoclimatic data, via eco-cultural niche modeling, in order to: (1) address whether millennial-scale climatic changes resulted in eco-cultural niche shifts for these biologically and geographically distinct human populations; (2) evaluate whether climatic and eco-cultural niche variability influenced the appearance/disappearance of complex human behaviors (e.g., technological developments, symbolic behavior); and (3) identify the cultural processes behind documented changes in the material culture records.

Identifying long-term mechanisms

It is becoming increasingly evident that "behavioral modernity" is associated with various members of the human lineage, not just AMH, and that cultural and demographic factors, arguably triggered by climate change, could explain the asynchronous emergence, disappearance, and re-emergence of key cultural innovations among both African Middle Stone Age and Eurasian Middle Palaeolithic populations (Conard, 2008; d'Errico and Stringer, 2011; Langley et al., 2008; Nowell, 2010; Zilhão, 2007). Some consensus now exists that the evolution of human societies in the last 300 ka 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.

With ECNM, we can evaluate the potential interplay between cultural adaptation and environmental change. This is the best way to move away from single cause models and instead towards identifying the possible multitude of mechanisms that have led different societies to develop specific cultural adaptations as a means of coping with external stimuli (both environmental and cultural; d'Errico and Banks, 2013). Thus, the research proposals that I

describe above will provide the results and data necessary to identify and evaluate the long-term trends and rules that have shaped the cultural evolution of our lineage.

Ultimately, a long-term research perspective that I envision is the examination of eco-cultural niche variability in Europe since the arrival of hominins on the continent. The well-documented European archaeological record provides one the potential to examine human-environment relationships for a number of different hominin species. Were there common trends in how these different species culturally responded to climatic change? Were there common mechanisms at work?

RESUME

INTRODUCTION

L'objectif principal de mes recherches est de comprendre les relations complexes qui existent entre les systèmes culturels (ex : techniques, territorialité) des populations de chasseur-cueilleurs du passé et les systèmes environnementaux dans lesquels ils évoluaient. J'ai poursuivi cet objectif en menant des recherches dans des domaines variés, tels que :

- L'étude de la technologie et de la fonction des outillages lithiques des populations paléoindiennes et archaïques du centre de l'Amérique du Nord et du Paléolithique supérieur en Europe ;
- L'étude de la paléogéographie et des adaptations des populations préhistoriques dans les grandes plaines d'Amérique du Nord ;
- L'impact des changements climatiques sur les populations humaines et animales en Europe pendant les stades isotopiques 3 et 2.

Ces approches, développées de manière complémentaire, me permettent d'appréhender, à différentes échelles analytiques, les mécanismes complexes qui ont régi la relation entre le savoir-faire de ces populations et leur milieu. Un des objectifs clés de mes recherches a été également de comprendre les implications de ces mécanismes dans les processus d'innovation culturelle lors de changements environnementaux.

Ces activités, menées sur le terrain et en laboratoire, m'ont permis d'acquérir des compétences spécifiques dans des domaines variés tels que la tracéologie à haute résolution, la technologie lithique, la calibration de datations ^{14}C et la modélisation Bayésienne, la création et la gestion de bases de données géoréférencées, l'analyse SIG, la paléoclimatologie, et la modélisation des niches écologiques. La maîtrise de ces compétences est un atout majeur pour mener à bien des études interdisciplinaires de qualité y compris, et surtout, dans le cadre de l'approche que j'ai développée, nommée « Eco-Cultural Niche Modeling ».

ECO-CULTURAL NICHE MODELING

Les études qui se sont attachées à comprendre l'impact de la variabilité climatique rapide des stades isotopique 2–3 (oscillations de Dansgaard-Oeschger et événements de Heinrich) sur la géographie humaine en Europe sont peu nombreuses. Ces études ont croisé des données archéologiques et climatiques variées afin de mettre en évidence le comportement des chasseur-cueilleurs préhistoriques et mieux comprendre leurs distributions et adaptations dans un contexte environnemental donné. Malheureusement, il n'a pas encore été trouvé de consensus quant à la façon d'évaluer et interpréter les réponses adaptives que des populations humaines préhistoriques pourraient avoir eu en réponse aux changements environnementaux.

Nous savons, au regard des importantes conséquences que les oscillations climatiques ont engendrées dans l'océan et dans l'atmosphère, que cette variabilité a dû avoir de profonds impacts sur les communautés végétales, animales, et humaines.

Mon approche analytique est dérivée des sciences de la biodiversité. Des avancées récentes ont permis le développement d'outils aptes à reconstituer les niches écologiques d'espèces, à prédire leurs réponses face aux changements environnementaux et à déterminer les facteurs environnementaux les plus influents dans la création des niches.

Ces méthodes ont un potentiel considérable pour l'étude des populations et des adaptations humaines. Par rapport à leur application aux registres archéologique et ethnoarchéologique, j'ai nommé cette approche « eco-cultural niche modeling ». Dans le cadre de deux bourses postdoctorales (une du CNRS, et une de la National Science Foundation) et d'un contrat de l'Institut Ecologie et Environnement (InEE), j'ai pu développer et mettre en œuvre cette approche. Le but a été d'intégrer diverses données afin d'évaluer, de manière précise, de quelle façon les populations humaines du passé ont modifié leurs territoires culturels, leurs systèmes de subsistance, et leurs systèmes techniques, face aux changements climatiques et environnementaux rapides. Mes recherches sur ces questions, et avec cette toute nouvelle méthodologie, constituent une suite naturelle de mon parcours professionnel.

«Eco-cultural niche modeling » (ECNM) utilise des données géographiques, archéologiques, chronologiques et climatiques, en combinaison avec des architectures prédictives (e.g., GARP – Genetic Algorithm for Rule-Set Prediction; Maxent - Maximum Entropy). Cette approche permet de reconstituer la niche écologique d'un technocomplexe donné, afin de mettre en évidence les conditions environnementales dans lesquelles ce technocomplexe aurait pu maintenir une adaptation viable. Mon postulat de base est le suivant : en reconstituant les niches écologiques

exploitées par des populations humaines du passé, il est possible d'identifier les processus culturels cachés derrière les interactions entre un système adaptif et son milieu. On entend par système adaptif la totalité des systèmes technologiques et des modes d'occupation d'un territoire, partagés et transmis par une population culturellement cohésive, dans un cadre paléoenvironnemental donné.

Les systèmes adaptatifs humains ne sont pas restés stables au cours du temps, comme cela a été généralement le cas pour d'autres espèces animales. Les cultures humaines peuvent changer leurs systèmes adaptatifs rapidement, par des innovations techniques et sociales, en réponse à divers facteurs. ECNM est particulièrement adapté pour rendre compte des changements des systèmes adaptatifs humains par rapport au cadre environnemental dans lesquels ils opéraient. Un autre avantage de cette approche est que l'on peut identifier les mécanismes écologiques (i.e. conservation de niche, contraction de niche, etc.) qui se trouvent derrière des changements culturels se produisant à travers le temps. Cependant, des comportements observés dans le registre archéologique peuvent répondre uniquement à des facteurs culturels. Un autre atout de l'ECNM est qu'il est possible d'identifier les situations dans lesquelles des facteurs écologiques ont joué un rôle mineur, ou même nul, dans les transformations culturelles observées au cours du temps.

Il est important de souligner que cette approche ne présuppose aucun déterminisme environnemental. Des visions différentes existent chez les archéologues quant à l'influence du climat sur les cultures humaines. Les "culturalistes" considèrent que la variabilité culturelle

dépend de processus entièrement culturels, que l'archéologie tente de documenter et de reconstituer. Les "déterministes" pensent que la culture est fortement influencée par l'environnement et certains d'entre eux considèrent que les règles régissant cette relation sont identifiables. Loin d'être définitivement antagonistes, ces deux visions sont rendues compatibles par l'ECNM. Nous ne stipulons pas que des règles existent, mais considérons que si tel est le cas, des moyens peuvent être mis en œuvre pour les identifier.

Dans les applications que je réalise, la reconstitution de la niche écologique d'un système adaptif (cf., la niche éco-culturelle) est réalisée par l'intégration de :

- simulations paléoclimatiques à haute-résolution, intégrant les reconstitutions de la végétation si elles sont disponibles ;
- coordonnées géographiques des localités (ex : sites archéologiques) où un technocomplexe (culture archéologique) est identifié et qui appartiennent à une phase climatique particulière.
- algorithmes prédictifs qui nous permettent de reconstituer une niche écologique potentielle.

Dans le cas des populations archéologiques, ECNM établit une distribution de base représentant le territoire dans lequel la niche écologique exploitée par cette population humaine pourrait avoir été présente. Cette approche permet également de projeter la niche éco-culturelle d'une époque donnée dans une autre phase climatique, de façon à évaluer, après comparaison avec la distribution réelle des sites archéologiques dans la deuxième phase, si la niche originelle a subi

une contraction ou une expansion au cours du temps. Des implications importantes concernant l'étude diachronique des dynamiques culturelles des populations de chasseurs-cueilleurs en résultent.

Applications diverses

En appliquant cette méthode au registre archéologique européen, j'ai abordé plusieurs questions :

- Comment les changements environnementaux ont influencé la colonisation de l'Europe par les Hommes modernes et l'extinction des Néanderthaliens (Banks et al., 2008b) ?
- Les premiers hommes modernes en Europe (porteurs de la culture aurignacienne ont-ils conservé leur niche écologique pendant ces processus de peuplement initiaux (Banks et al., 2013) ?
- Comment les conditions environnementales ont influencé l'adaptation humaine ainsi que la variabilité archéologique pendant le Dernier Maximum Glaciaire (DMG) (Banks et al., 2008a; Banks et al., 2009) ?
- Les territoires du Badegoulien, définis par la circulation des matières premières lithiques, sont-ils liés à des niches écologiques distinctes et reflètent-ils des territoires culturels (Banks et al., 2011) ?
- Comment deux espèces de proie réagissent-elles aux changements environnementaux pendant le DMG (Banks et al., 2008c) ?

PERSPECTIVES DE RECHERCHE

Mes perspectives de recherche représentent une continuation naturelle du développement et de l'application de cette approche novatrice. C'est dans ce cadre que je propose de :

1) reconstituer et évaluer les niches écologiques exploitées par chaque culture archéologique du Paléolithique supérieur afin de déterminer si ces niches ont changé au cours du temps.

Mes études précédentes ont montré que les différentes populations humaines du Paléolithique supérieur n'ont pas réagi aux changements climatiques de la même façon.

Donc, il existe un besoin fort de comprendre si et comment les transitions culturelles majeures du Paléolithique supérieur sont liées aux dynamiques de niches

écologiques. L'ECNM nous fournit les outils quantitatifs nécessaires pour répondre à ce besoin.

2) reconstituer les niches écologiques et éco-culturelles exploitées par les populations humaines au cours des stades isotopiques 5a-4 (~75-60 ka cal BP) en Afrique australe (hommes modernes – AMH) et en Europe (Néanderthaliens), afin de tester différentes hypothèses concernant le rôle joué par la variabilité climatique dans l'émergence de comportements humains complexes ex : changements de technologie, symbolisme, etc.) ainsi que dans la disparition d'innovations culturelles à certaines périodes.

3) mener des études qui ont pour but d'identifier de possibles mécanismes ayant pu opérer sur les changements culturels documentés dans le registre archéologique. Une focalisation sur les trajectoires régionales semble être le seul moyen pour documenter des changements culturels et les mécanismes sous-jacents. Nous devons poursuivre nos recherches pour

intégrer des facteurs environnementaux, écologiques, démographiques et sociaux, ainsi que des évènements historiques, afin de comprendre pourquoi des sociétés humaines ont développé, et parfois perdu, des innovations culturelles clés dans l'histoire de notre lignée.

TEACHING STATEMENT

When teaching in a university environment, one has two very different audiences (sometimes in the same course, e.g. introductory courses). The first is composed of those students who are taking an anthropology class either as a requirement or out of general interest, while the second group is composed of those individuals that will eventually become the next generation of professional anthropologists. With respect to the former, it is important that our teaching allows them to come away with a broader view of the human experience and an ability to appreciate the past and present diversity of cultures. This is especially relevant in today's global society. Concerning the future anthropologists, we must work to nurture their passion for the study of culture. It is key that we teach these individuals to be free and critical thinkers and provide them with a solid foundation of anthropological theory, methods, and data. In this way, we can form anthropologists that will move our discipline forward and in directions that we ourselves as educators and researchers may not be able to envision at present. I firmly believe that our ultimate goal as professional educators is to help produce anthropologists that have the ability to surpass us.

I think these goals can be achieved in a number of ways. First, hands-on activities are important since learning cannot be based solely on reading the available literature and listening to lectures. This allows students to place concepts in context, which serves to better retain information. This is especially true for courses with a focus on material culture or analytical methods (e.g. lithic technology). Secondly, discussion should be incorporated into the learning environment as much as possible. The reason being that two individuals can examine the same

body of theoretical or methodological literature and come away with different reactions to it. Both reactions may be equally legitimate, but nonetheless still incomplete. Two heads think better than one, and by incorporating discussion into the classroom experience, students are able to refine their understanding of a concept, thereby further developing their own unique perspective. Furthermore, students must learn to express themselves—both orally and in writing. The latter is especially critical for graduate students. Thirdly, as educators we must be sure that students can think critically. Just because an idea has been published does not mean that it is infallible. To become good scientists, students must learn to critically evaluate hypotheses, methods, and interpretations. It is in this way that these future anthropologists can build on what has already been done. Finally, anthropology has become increasingly interdisciplinary, and it is critical that we pass this openness to other disciplines on to our students. With respect to archaeology, this includes introducing students to concepts in ecology, paleoclimatology, and statistics. Many of the advances in archaeology during the past decade have been accomplished through the incorporation of concepts and methods originally developed outside of anthropology. I think that the application of this philosophy can serve to produce a body of professionals that will be capable of advancing our discipline.

I have been present in France since August 2005 and have always been attached with the CNRS laboratory PACEA (UMR 5199)—De la Préhistoire à l'Actuel: Culture, Environnement et Anthropologie. I have worked within the framework of a number of European-funded projects, both as a post-doctoral research fellow and as a contractual researcher, as well as my own National Science Foundation-funded project. My role in these projects has always been strictly

related to research. Nevertheless, when first presented the opportunity to supervise a graduate student in the 2009–2010 academic year, I seized the opportunity because I think it is important for all active professionals to play a role in educating the next generation of anthropologists.

This first teaching opportunity I had was to serve as a co-supervisor (principal supervisor: Dr. Francesco d'Errico) for Nicolas Antunes, who at the time was a Master 2 student at the University of Toulouse. He was interested in exploring the application of predictive algorithms to archaeological data, and he performed his internship in the PACEA laboratory. I worked with him on exploring ways to improve methods of producing eco-cultural niche estimations and quantitatively evaluating niche predictions. During the 2011–2012 academic year, I also served as a co-supervisor (principal supervisor: Dr. Arnaud Lenoble) for Eric Andrieux who was a Master 2 student at the University of Bordeaux 1. His research focus was on the geoarchaeological, paleoenvironmental, and chronological records of archaeological cultures in France during Heinrich Stadial 2 and the early part of the Last Glacial Maximum. My supervision of his work centered on the calibration and Bayesian modeling of radiocarbon data pertaining to the archaeological record associated with these two climatic periods.

With respect to the supervision of doctoral candidates, I have also taken advantage of opportunities to do so, either directly or indirectly, even though such a role has never been a requirement of the numerous CNRS contracts that I have held. At present, I am the co-supervisor (principal supervisor: Dr. Francesco d'Errico) of my former Master 2 student Nicolas Antunes, who is now a candidate in the doctoral school at the University of Bordeaux 1. As a

continuation of his earlier work, his doctoral dissertation is in part focused on exploring ways in which multiple predictive algorithms can be used collectively in order to produce highly robust eco-cultural niche predictions. Another important component of his doctoral work centers on the application of ecological niche modeling methods to archaeological and ethnographic records of the historic period, as well as the more recent archaeological past (the Neolithic record). One case study involves eco-cultural niche modeling analyses of the Viking Settlement of Greenland during the Medieval Warm Period and the subsequent Little Ice Age. Another application of these methods is concerned with ethnographic data related to symbolic material culture and ethnolinguistic groups in Papua New Guinea. The utility in examining these historic archaeological and ethnographic records is that their more detailed material cultural records, as well as settlement and subsistence systems, can lead to more detailed understandings of culture-environment interactions. Therefore, the inferred ecological and cultural mechanisms that operated within these human adaptive systems can be used to aid in the interpretation of culture-environment relationships for more ancient, prehistoric populations.

Even though Nicolas Antunes is still an active doctoral candidate with another year left before he defends his thesis, my ability to serve as an effective supervisor is attested to by the fact that I have published a peer-reviewed article with him in an international journal (Banks et al. 2013b). The subject of this article is the application of eco-cultural niche modeling methods to the Neolithic archaeological record, a study that we conducted together and that serves as one of the building blocks of his doctoral research. This collaboration with him in designing the study, conducting the analyses, and writing up the results for publication in a high-ranking

journal, serves as a clear demonstration of my ability to actively and effectively educate doctoral students.

Additionally, my involvement in the training of doctoral students has not been restricted to Mr. Antunes. I was also involved, albeit not as intensively as is the case with Mr. Antunes, with the doctoral work conducted by Dr. Solange Rigaud and Lucas Sitzia, both at the University of Bordeaux 1. Dr. Rigaud defended her doctoral dissertation in 2011 and Mr Sitzia will defend his Ph.D. before the end of this academic year (2013). Furthermore, Dr. Rigaud is a co-author on one of my recent publications (Banks et al., 2013b), and I am a co-author along with Mr. Sitzia on a study that is central to his doctoral dissertation (Bertran et al., 2013).

Finally, the University of Bordeaux, along with other major universities in France, has begun to incorporate graduate-level teaching modules in which classes are conducted in English. One advantage in such a trend is that it will attract international students to pursue their graduate studies in French institutions of higher learning. It is reasonable to assume that the number of foreign students coming to France to pursue their doctoral studies will increase. Therefore, by having my Habilitation à Diriger des Recherches, not can I serve as a principal supervisor to French students pursuing studies in Archaeology, but I can also attract and directly mentor foreign doctoral students. I was trained as an archaeologist in the United States, have spent well over a decade studying the European archaeological record, and am very familiar with analytical approaches to this record that are more typical of the French method of gathering and interpreting data. Therefore, with an HDR degree, I will be able to supervise doctoral

students, both French and foreign, and expose them to these different but complementary ways of examining archaeological data—a task that will serve to enrich and broaden their doctoral studies on their path to becoming active professionals in the field.

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- Peterson, A.T., 2003. Predicting the geography of species' invasions via ecological niche modeling. *Quarterly Review of Biology* 78, 419–433.
- Peterson, A.T., 2011. Ecological niche conservatism: a time-structured review of evidence. *Journal of Biogeography* 38, 817–827.

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- Peterson, A.T., Papeş, M., Soberón, J., 2008. Rethinking receiver operating characteristic analysis applications in ecological niche modeling. *Ecological Modelling* 213, 63–72.
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- Warren, D.L., Glor, R.E., Turelli, M., 2010. ENMTools: a toolbox for comparative studies of environmental niche models. *Ecography* 33, 607–611.
- Weber, M.-J., Grimm, S.B., Baales, M., 2011. Between warm and cold: Impact of the Younger Dryas on human behavior in Central Europe. *Quaternary International* 242, 277–301.
- Whallon, R., 2006. Social Networks and information: non-"utilitarian" mobility among hunter-gatherers. *Journal of Anthropological Archaeology* 25, 259–270.
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- Zilhão, J., 2007. The Emergence of Ornaments and Art: An Archaeological Perspective on the Origins of "Behavioral Modernity". *Journal of Archaeological Research* 15, 1–54.
- Zilhão, J., Angelucci, D.E., Badal-García, E., d'Errico, F., Daniel, F., et al., 2010. Symbolic use of marine shells and mineral pigments by Iberian Neanderthals. *Proceedings of the National Academy of Sciences USA* 107, 1023–1028.

Curriculum Vitae

William E. Banks

EDUCATION

2004 Doctor of Philosophy, Anthropology, University of Kansas, Lawrence, KS.
"Toolkit Structure and Site Use: Results of a High-Power Use-Wear Analysis of Lithic Assemblages from Solutré (Saône-et-Loire), France." Degree conferred with Honors.

Committee:

Co-Advisors: Drs. Anta Montet-White and Ivana Radovanovic
other members: Dr. Marvin Kay (University of Arkansas), Dr. Leonard Krishtalka (University of Kansas), Dr. Brad Logan (Kansas State University).

1996 Master of Arts, Anthropology, University of Kansas, Lawrence, KS.
"Archaeology of a Small Catchment Basin: Farra Canyon, Oklahoma.
Advisor: Dr. Jack Hofman

1992 Bachelor of Arts, Anthropology, University of Wyoming, Laramie, WY

PROFESSIONAL EXPERIENCE

At present Adjunct Researcher, affiliated with the CNRS – UMR 5199 PACEA
2009–2013 **Contractual Researcher**, Centre National de la Recherche Scientifique (CNRS), Talence, France. Contracts provided by the Institut Ecologie et Environnement and the European Research Council-funded project entitled TRACSYMBOLS.
2010–present **Adjunct Research Associate** with the Biodiversity Institute, Univ. of Kansas.
2008–2009 **Independent Researcher** affiliated with the CNRS - UMR 5199 PACEA.
2007–2008 **Post-doctoral International Research Fellow** with the CNRS and funded by the National Science Foundation.
2005–2007 **Post-doctoral Research Fellow** with the CNRS and funded by the European Science Foundation
1999–2005 **Archaeologist** with the State Historic Preservation Office, Kansas State Historical Society, Topeka, KS.

TEACHING EXPERIENCE

2005–present Several invited lectures for Masters and PhD level students (detailed below).
2011–present Ph.D co-supervisor (principal supervisor: Dr. Francesco d'Errico) of Nicolas Antunes, University of Bordeaux, France. Dissertation topic concerns the

evaluation and comparison of multiple ecological niche modeling methods applied to the archaeological record.

- 2011–2012 Master's Thesis co-supervisor (principal supervisor: Arnauld Lenoble) of Eric Andrieux, University of Bordeaux, France. Thesis: "Paleoenvironnement et cultures préhistoriques contemporains de l'évènement d'Heinrich 2: revue critique des données."
- 2009–2010 Master's Thesis co-supervisor (principal supervisor: Dr. Francesco d'Errico) of Nicolas Antunes, University of Toulouse, France. Thesis: "Apport des algorithmes prédictifs à la compréhension des relations Homme-Environnement."
- 2002 Adjunct Faculty, Washburn University, Topeka, KS. AN225 - Kansas Archaeology, Spring semester. AN112EA - Cultural Anthropology, Fall Semester.
- 2001 Adjunct Faculty, Washburn University. AN225 - Kansas Archaeology.
- 1997 Graduate Teaching Assistant for the University of Kansas and Kansas State University Archaeological Field School. Directed by Dr. Brad Logan at the DB Site (14LV1071), Fort Leavenworth, Kansas.
- 1996–1997 Graduate Teaching Assistant for Dr. John Hoopes. ANTH 110/310 - Introduction to Archaeology. Fall and Spring semesters. University of Kansas.
- 1995–1996 Graduate Teaching Assistant for Dr. John Hoopes - Anth 110/310 - Introduction to Archaeology (Fall); Dr. David Frayer.- Anth. 104/304 - Introduction to Physical Anthropology (Spring). University of Kansas.
- 1994–1995 Graduate Teaching Assistant for Dr. Jack Hofman. Anth. 110/310 - Introduction to Archaeology. Fall and Spring Semesters. University of Kansas.

Invited Lectures

- 2013 Exploring the emergence of modern human behavior in Africa and Europe. Lecture given for the University of Stockholm (Prof. Barbara Wohlfarth) in Les Eyzies, France. May 16 and May 23.
- 2013 Eco-cultural niche modeling: Theory, implementation, case studies. Seminar lecture given to the Department of Prehistory, Ancient History, and Archaeology, University of Barcelona, March 21.
- 2013 Déchiffrement des interactions home-environnement avec la modélisation des niches éco-culturelles : théorie, mise en œuvre et résultats. Seminar lecture given to the Doctoral School, University of Bordeaux 3, January 30.
- 2012 Exploring the emergence of modern human behavior in Africa and Europe. Lecture given for the University of Stockholm (Prof. Barbara Wohlfarth) in Les Eyzies, France. May and September.
- 2010 Relations entre nature et culture: l'apport des algorithmes prédictifs. Lecture given for a Master's seminar, University of Toulouse, France. February.

GRANTS/FUNDING

External

- 2009 Institut Ecologie et Environnement of the CNRS (21,000 €). 6 month grant to finalize and publish a European chronological database concerning Marine Isotope Stages 3 and 2.
- 2007 National Science Foundation International Research Fellowship Program (Grant No. 0653000: \$55,000). 12 month grant to apply eco-cultural niche modeling methods.

Internal

- 2001 Two Carrol D. Clark Grants, Dept. of Anthropology, Univ. of Kansas, use-wear research.
- 2000 Carrol D. Clark Grant, Dept. of Anthropology, Univ. of Kansas, use-wear research.
- 1999 Carrol D. Clark Grant, Dept. of Anthropology, Univ. of Kansas, use-wear research.
- 1996 Carrol D. Clark Grant, Dept. of Anthropology, Univ. of Kansas, use-wear research.

PUBLICATIONS

Pending Items (under review or in press)

- Banks W.E.**, Aubry T., d'Errico F., Zilhão J. (2013). Paléoenvironnements et Adaptations Humaines au Dernier Maximum Glaciaire: Le cas du Badegoulien. Actes du XXVII Congrès Préhistorique de France, 31 mai–5 juin 2010 Bordeaux-Les Eyzies, (in press).
- d'Errico F., **Banks W.E.** (2013). Identifying mechanisms behind Middle Paleolithic and Middle Stone Age cultural trajectories. *Current Anthropology* (in press).

Books

- Banks W.E.** (2009). *Toolkit Structure and Site Use: Results of a high-power use-wear analysis of lithic assemblages from Solutré (Saône-et-Loire), France*. BAR International Series 1970, Archaeopress, Oxford.
- Hoard R.J., **Banks W.E.** (editors) (2006). *Kansas Archaeology*. University Press of Kansas, Lawrence.

Chapters in Books (peer-reviewed)

- d'Errico F., **Banks W.E.**, Clobert J. (2012.). Human expansion: research tools, evidence, mechanisms. In *Dispersal Ecology and Evolution*, edited by J. Clobert, M. Baguette, T.G. Benton, and J.M. Bullock. Oxford University Press, pp. 433–447.

- Banks W.E.** (2006). Lithic Use-Wear Analysis: Shifting Analytical Scale. In *Confronting Scale in Archaeology: Issues of Theory and Practice*, edited by G. Lock and B. Molyneaux, pp.89–111. Springer, New York.
- Hoard R.J., **Banks W.E.** (2006). Introduction. In *Kansas Archaeology*, edited by R.J. Hoard and W.E. Banks, pp. 1–9. University Press of Kansas, Lawrence.
- Banks W.E.** (2003). Catchment Basins as Islands in West-Central Oklahoma: Farra Canyon. In *Islands in the Plains*, edited by M. Kornfeld and A. Osborn, pp. 67–88. University of Utah Press, Salt Lake City.

Journal Articles (peer-reviewed)

- Banks W.E.**, Antunes N., Rigaud S., d'Errico F. (2013). Ecological constraints on the first prehistoric farmers in Europe. *Journal of Archaeological Science* 40, 2746–2753.
- Banks W.E.**, d'Errico F., Zilhão J. (2013). Human-climate interaction during the Early Palaeolithic: testing the hypothesis of an adaptive shift between the Proto-Aurignacian and the Early Aurignacian. *Journal of Human Evolution* 64:39–55.
- Bertran P., Sitzia L., **Banks W.E.**, Bateman M.D., Demars P.-Y., Hernandez M., Lenoir M., Mercier N., Prodeo F. (2013). The Landes de Gascogne (southwest France): periglacial desert and cultural frontier during the the Palaeolithic. *Journal of Archaeological Science* 40, 2274–2285.
- d'Errico F., **Banks W.E.**, Vanhaeren M., Laroulandie V., Langlais M. (2011). PACEA Geo-Referenced Radiocarbon Database. *PaleoAnthropology* 2011:1–12.
- Banks W.E.**, Aubry T., d'Errico F., Zilhao J., Lira-Noriega A., Peterson A.T. (2011). Eco-cultural niches of the Badegoulian: Unraveling links between cultural adaptation and ecology during the Last Glacial Maximum in France. *Journal of Anthropological Archaeology* 30:359–374.
- Banks W.E.**, Zilhao J., d'Errico F., Kageyama M., Sima A., Ronchitelli A. (2009). Investigating Links between Ecology and Bifacial Tool Types in Western Europe during the Last Glacial Maximum. *Journal of Archaeological Science* 36:2853–2867.
- Banks W.E.**, d'Errico F., Peterson A.T., Kageyama M., Sima A., Sanchez-Goni M.F. (2008). Neanderthal Extinction by Competitive Exclusion. *PLoS ONE* e3972.
- Banks W.E.**, d'Errico F., Peterson A.T., Kageyama M., Colombeau G. (2008). Reconstructing ecological niches and geographic distributions of caribou (*Rangifer tarandus*) and red deer (*Cervus elaphus*) during the Last Glacial Maximum. *Quaternary Science Reviews* 27:2568–2575.
- Banks W.E.**, d'Errico F., Peterson A.T., Vanhaeren M., Kageyama M., et al. (2008). Human ecological niches and ranges during the LGM in Europe derived from an application of eco-cultural niche modeling. *Journal of Archaeological Science* 35:481–491.
- Banks W.E.**, d'Errico F., Dibble H., Krishtalka L., West D., et al. (2006). Eco-Cultural Niche Modeling: New Tools for Reconstructing the Geography and Ecology of Past Human Populations. *PaleoAnthropology* 4:68–83.

Banks W.E., Wigand P.E. (2005). Reassessment of Radiocarbon Age Determinations for the Munkers Creek Phase. *Plains Anthropologist* 50:173–184.

Hoard R.J., **Banks W.E.**, Mandel R.D., Finnegan M., Epperson J.E. (2004). A Middle Archaic Burial from East Central Kansas. *American Antiquity* 69:717–739.

Banks W.E., Kay M. (2003). High-Resolution Casts for Lithic Use-wear Analysis. *Lithic Technology* 28:27–34.

Banks W.E., Mandel R.D., Roper D.C., Benison C.J. (2001). The Macy Site (14RY38): A Multicomponent Early Ceramic Occupation in Northeastern Kansas. *Plains Anthropologist* 46:21–37.

Banks W.E. (1999). A Casting Method Suitable for High-Power Microwear Analysis. *Current Research in the Pleistocene* 16:105–107.

Banks W.E., Hofman J.L., Patterson R. (1994). Paleoindian and Paleoecological Evidence from Farra Canyon, Oklahoma. *Current Research in the Pleistocene* 11:1–3.

Conference Proceedings (peer-reviewed)

Bertran P., **Banks W.E.**, Bateman M., Demars P.-Y., Langlais M., Lenoir M., Prodéo F. (2012). Les Landes de Gascogne : désert périglaciaire et frontière culturelle au Paléolithique. In *Des climats et des hommes*, edited by J.-F. Berger, pp. 141–156. Editions La Découverte, Paris.

d'Errico F., Sánchez Goñi M.-F., **Banks W.E.** (2012). L'impact du Dernier Maximum glaciaire sur les populations européennes. In *Des climats et des hommes*, edited by J.-F. Berger, pp. 125–140. Editions La Découverte, Paris.

Banks W.E. (2002). Analyse Tracéologique de l'Industrie Lithique Aurignacienne de Solutré, Secteur M12. In *Solutré: Les fouilles 1968–1998*, edited by Jean Combier and Anta Montet-White, pp. 243–246. Mémoire 30. Société Préhistorique Française, Paris.

Technical Reports (peer-reviewed)

Benison C.J., **Banks W.E.**, Mandel R.D. (2000). *Phase IV Archeological Investigations at 14RY38: A Multicomponent Early Ceramic Age Campsite Near Manhattan, Kansas*. Contract Archeology Publication No. 21. Archeology Office, Kansas State Historical Society, Topeka.

Conference Proceedings (non peer-reviewed)

Kay M., **Banks W.E.** (2001). Spadzista Kostenki Knives Use-Wear. In *Proceedings of the International Conference on Mammoth Site Studies*, edited by D. West, pp. 117–119. Publications in Anthropology 22. University of Kansas, Lawrence.

Journal Articles (non peer-reviewed)

Banks W.E. (1996). Statistical Analysis of Flake and Blade Dorsal Patterns from Krakow-Spadzista Units E and F: A Study of the Organization of Site Space. *Folia Quaternaria* 67:63–74.

CONFERENCE ORGANIZATION

2008 Co-organizer, along with Dr. Francesco d'Errico, of the Meeting entitled "Us and Them: Modeling past genetic, linguistic, and cultural boundaries", European Science Foundation-funded Workshop, May 15–17, Talence, France. Workshop focused on exploring methods with which we can disentangle and interpret the complicated dynamics that exist between natural and human systems.

PRESENTATIONS

Invited Talks

- 2012 Eco-cultural niche modeling : Theory, implementation, results. Department of Archaeology, University of Köln, December 3.
- 2009 "La modélisation des niches éco-culturelles: une approche pour mieux comprendre les interactions home-environnement." Doctoral Division of the School of Environmental Sciences, University of Marseille. March.
- 2007 Eco-cultural niche modeling: evaluating prehistoric human-environment interactions. Department of Anthropology, University of Cambridge, UK. October.

Invited Conference/Workshop Presentations

- Banks W.E.**, d'Errico F., Zilhão J. 2012. Human-climate interaction in the Early Upper Paleolithic: testing the hypothesis of an adaptive shift between the Proto-Aurignacian and the Early Aurignacian. Symposium entitled "Modelling environment/agent interactions in prehistory." 31st annual meeting of the Canadian Archaeological Association, May 16–20, Montréal, Canada.
- Banks W.E.**, d'Errico F., Peterson A.T., Kageyama M., Sima A., Sanchez-Goni M.F. (2009). Neanderthal Extinction by Competitive Exclusion. Workshop "Approaches to Modelling Interactions between Paleoclimatic Change, Neanderthals, and Anatomically Modern Humans. Spanish National Museum of the Natural Sciences, August 31, Madrid, Spain.
- Banks W.E.** (2008). Investigating Human-Environment Interactions via Eco-Cultural Niche Modeling: Results and Prospects. 4th HERA Annual Conference: European diversities-European Identities. October 8–9, Strasbourg, France.
- Banks W.E.** (2007). Eco-Cultural Niche Modeling: Synchronic and Diachronic Evaluations of Prehistoric Human-Environment Interaction. The Modelling Hominid Dispersals workshop, March 2, Montreal, Canada.

Conference/Workshop Presentations

- Banks W.E.**, F. d'Errico (2011). Exploring human-environment interactions with ecological niche modeling methods. Poster presented at the Royal Society's Theo Murphy international scientific meeting, November 21-22, Buckinghamshire, United Kingdom.
- Banks W.E.**, F. d'Errico, J. Zilhao, M. Kageyama (2011). Testing the hypothesis of an adaptive shift between the Proto- and Early Aurignacian via Eco-cultural niche modeling. Poster presented at the Inaugural Meeting of the European Society for the Study of Human Evolution, September 23–24, Leipzig, Germany.
- d'Errico, F, **Banks W.E.**, Sanchez-Goni M.F., Kageyama M. (2010). Paleolithic chronologies and population dynamics in changing environments: Data and research strategies. Paper presented at the 16th Annual Meeting for the European Association of Archaeologists, 2 Sept., The Hague, The Netherlands.
- Banks W.E.**, Aubry T., d'Errico F., Zilhão J. (2010). Paléoenvironnement et adaptation humaine au Dernier Maximum Glaciaire: le cas du Badegoulien. Paper presented at the 27th Congrès Préhistorique de France, Session F, June 4, Les Eyzies, France.
- Banks W.E.**, d'Errico F. (2008). Eco-Cultural Niche Modeling: What's been done and where we are going. Paper presented at the European Science Foundation RESOLuTION meeting, Sept. 29–Oct. 3, Talence, France.
- Banks W.E.**, d'Errico F., Peterson A.T., Kageyama M., Sanchez-Goni M.F. (2008). Assessing the climatic hypothesis for Neanderthal extinction using Eco-Cultural Niche Modeling. Paper presented at the Sixth World Archaeology Congress, June 29–July 4, Dublin, Ireland.
- Banks W.E.** (2008). Possible relationships between cultural boundaries and large mammal ecological niches during the LGM. Paper presented at the OMLL (ESF-funded) networking meeting "Us and Them: Modeling past genetic, linguistic, and cultural boundaries", May 15–17, Talence, France.
- Banks W.E.**, d'Errico F., Peterson A. T., Vanhaeren M., Kageyama M., et al. (2007). How Environmental Conditions of the Last Glacial Maximum Affected Human Ranges. Poster presented at the Colloque de Restitution du Programme ECLIPSE II, October 15–16, Paris.
- Banks W.E.** (2007). Eco-Cultural Niche Modeling: Synchronic and Diachronic Evaluations of Prehistoric Human-Environment Interaction. Paper presented at the European Science Foundation EUROCLIMATE meeting: Radiocarbon and Ice-Core Chronologies during Glacial and Deglacial Times, March 5–7, Heidelberg, Germany.
- Banks W.E.** (2006). An Examination of Human Ecological Niche Conservatism during OIS 3–2. Paper presented at the second EuroClimate RESOLuTION project workshop, Sept. 28–30, Osterlen, Sweden.
- Banks W.E.**, d'Errico F. (2006). Eco-Cultural Niche Modeling of European Human Populations during the Last Glacial Maximum. Paper presented at the 2006 Paleoanthropology Meetings, April 24–26, San Juan, Puerto Rico.
- Banks W.E.**, Montet-White A., Petereson A.T., d'Errico F., Vanhaeren M. (2005). Eco-Cultural Niche Modeling Applied to the Solutrean: A Feasibility Study. Paper presented at the OMLL-NSF International Symposium on Eco-Cultural Niche Modeling: Exploring the Potential of Eco-Cultural Niche Modeling for Reconstructing the Geography of Past Human Populations, Sept. 22–26, Les Eyzies, France.

- Banks W.E.** (2005). The Application of Eco-Cultural Niche Modeling to Oxygen Isotope Stages 3–2 Human and Ungulate Populations. Paper presented at the first Euroclimate RESOLuTION project workshop, Sept. 29–Oct. 2, Les Eyzies, France.
- Banks, W.E.**, Wigand P.E. (2004). Reassessment of Radiocarbon Age Determinations for the Munkers Creek Phase. Paper presented at the 62nd Plains Anthropological Conference, Billings.
- Banks, W.E.** (2002). Use-wear Analysis of Stone Tools Recovered from 14DO417. Paper presented at the 24th Annual Flint Hills Archaeological Conference, Manhattan, Kansas.
- Banks, W.E.** (2001). The Current State of Kansas Archaeology. Symposium moderated by William E. Banks and Robert J. Hoard, 59th Plains Anthropological Conference, Lincoln.
- Banks, W.E.** (1999). Analyse des Traces d'Usure de l'Assemblage Lithique Aurignacien de Solutré, Secteur M12. Paper presented at the Séance de la Société Préhistorique Française: Le Peuplement Préhistorique du Mâconnais. Mâcon, France, June 5, 1999.
- Banks, W.E.** (1997). Changing Scale: An Analysis of Paleoindian Artifacts from a Small Catchment Basin in Western Oklahoma. Paper presented at the Tertiary and Quaternary Meetings, Lawrence, KS.
- Banks, W.E.** (1997). Solutré, Bloc P16: Investigations of Tool Technology and Tool Use with Analyses of Breakage Patterns. Paper presented at the 62nd Annual SAA Meeting. Nashville.
- Banks, W.E.** (1996). Catchment Basins as Islands in West-Central Oklahoma: Farra Canyon. Paper presented at the 54th Annual Plains Anthropological Conference. Iowa City.
- Banks, W.E.** (1995). Spadzista, Loci E and F: Flake and Blade Dorsal Pattern Analysis and Comparison with other Gravettian Assemblages. Paper presented at the 60th Annual Meeting for the Society for American Archaeology. Minneapolis.
- Banks, W.E.** (1994). An Analysis of the Farra Canyon Lithic Assemblage: The Archaeology of a Small Catchment Basin. Paper presented at the 59th Annual Meeting for the Society for American Archaeology. Anaheim.

REFEREEING: Journals/Funding Agencies

Science

PLoS ONE

Quaternary Science Reviews

Current Anthropology

Journal of Archaeological Science (multiple reviews)

Journal of Anthropological Archaeology

Geoarchaeology

Quaternary International

Global Change Biology

Plains Anthropologist

Leakey Foundation

Fieldwork Experience

- 2007 – Volunteer excavator at Les Rois (Charente). F. d’Errico and M. Vanhaeren - directors.
- 2005 – Geomorphology work at 14SN101 (Kansas) in collaboration with the Univ. of Kansas (KU).
- 2003 – Excavations at the Claussen site (Kansas) in collaboration with KU and the Kansas Anthropological Association Training Program (KATP).
- 2002 – Excavations at the Albert Bell site (Kansas) in collaboration with the KATP.
- 2001 – Director of excavations at 14AT448 and 14AT438 (Kansas) in collaboration with the KATP.
- 2000 – Excavations at Fort Ellsworth (Kansas) in collaboration with the KATP.
- 1998 – Crew chief at Solutré (France), Aurignacian levels, directed by Dr. Anta Montet-White.
- 1997 – Crew chief at several sites in Ellsworth County, KS, directed by Dr. Brad Logan.
- 1997 – Excavations at Solutré, Magdalenian and Solutrean levels, directed by Dr. Anta Montet-White.
- 1997 – Graduate Teaching Assistant at the DB site, KU field school, directed by Dr. Brad Logan.
- 1995 – Field Crew member, Kansas State Historical Society.
- 1994 – Graduate Teaching Assistant at Lovewell Reservoir excavations, directed by Dr. Brad Logan.
- 1994 – Field Crew member, Lovewell Reservoir survey, directed by Dr. Brad Logan.
- 1993 – Field Crew member, Lovewell Reservoir survey, directed by Dr. Brad Logan.
- 1992 – Field Crew member, University of Wyoming excavations, directed by Dr. George C. Frison. And Dr. Charles Reher.
- 1991 – Field Crew member, University of Wyoming excavations, directed by Dr. George C. Frison. And Dr. Charles Reher.
- 1990 – Student excavator, University of Wyoming field school.

FULL TEXTS OF SELECTED PUBLICATIONS

- Banks W.E., d'Errico F., Dibble H., Krishtalka L., West D., et al. (2006). Eco-Cultural Niche Modeling: New Tools for Reconstructing the Geography and Ecology of Past Human Populations. *PaleoAnthropology* 4:68–83.
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Eco-Cultural Niche Modeling: New Tools for Reconstructing the Geography and Ecology of Past Human Populations

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ABSTRACT

Prehistoric human populations were influenced by climate change and resulting environmental variability and developed a wide variety of cultural mechanisms to deal with these conditions. In an effort to understand the in-

fluence of environmental factors on prehistoric social and technical systems, there is a need to establish methods with which to model and evaluate the rules and driving forces behind these human-environment interactions. We describe a new set of analytical tools—an approach termed Eco-Cultural Niche Modeling (ECNM)—that can be used to address these issues and to test current hypotheses. This approach’s modeling architectures are used to reconstruct past human systems in the Old and New Worlds, past natural systems within which they operated—namely geological, paleobiological and paleoenvironmental conditions—and also to develop informed hypotheses concerning the geographic spread, migration, and eco-cultural adaptations of prehistoric human populations. The ECNM approach has recently been developed and explored at two National Science Foundation- and European Science Foundation-funded workshops. We describe the goals and methods of ECNM, the results of the proof-of-concept projects, the analytical issues that remain unresolved, and the potential this approach has to offer the disciplines of paleoanthropology and archaeology.

INTRODUCTION

To what extent have the tempo and mode of human population dispersals and the geography of past cultural traditions corresponded with environmental variability during prehistory? Human populations have adapted to the environment via sophisticated, often specialized, subsistence strategies, allowing human cultures to spread across a wide range of latitudes, altitudes, and ecological zones. Generalized adaptations have the advantage of flexibility. Complex and specialized adaptations have allowed for the exploitation of inhospitable regions, but at the same time may have increased some cultures’ dependence on particular ecological settings and made such adaptations more vulnerable to rapid environmental change. Establishing methods to evaluate the rules and driving forces behind these human-environment interactions is critical if we are to assess and understand the influence of environmental constraints on social and technical systems, cognition, and communication. Identification of the geography and variability of past culturally coherent human groups and variability is critical to understanding the complex mechanisms that have shaped the interactions among genetics, linguistics, cultural affiliation, and climate.

The topic of human-environment interaction is recurrent in the fields of paleoanthropology and human ecology (e.g., Binford 2001; Collard and Foley 2002; deMenocal 2004; Feakins et al. 2005; Foley 1984, 1994; Nettle 1996, 1998; Potts 1996), with some issues and questions being more resolved than others. The disciplines of paleoanthropology and archaeology can now incorporate and refine a new set of analytical tools to address the topics identified above and to test current hypotheses. These new tools and their associated methodological approach, termed Eco-Cultural Niche Modeling (ECNM), are derived from Ecological Niche Modeling (ENM) and the disciplines of biology and evolutionary ecology (Soberón and Peterson 2004). ENM has demonstrated its effectiveness in estimating ecological niches of plant and animal species, and predicting their geographic distributions, based on biotic and environmental data. ECNM applies the same methodological approach to analyses of the archaeological record and prehistoric human cultures.

The feasibility of applying ENM methods and protocols to the archaeological record was first explored at a National

Science Foundation-funded workshop, 11–13 March 2004, at the University of Kansas, Lawrence, organized by two of us (Krishtalka and West). The 23 participants drew from Old and New World archaeology, paleobiology, biodiversity science, climatology, geography, computer science, and informatics to: 1) establish the current state of ecological and eco-cultural niche modeling; 2) identify opportunities and constraints of ECNM; and, 3) determine proof-of-concept projects and an immediate timetable to test applications of ECNM with the New and Old World archaeological records.

A follow-up workshop at the Musée National de Préhistoire in Les Eyzies, France, 22–26 September 2005, was organized by d’Errico and Dibble, and was jointly funded by the NSF and the European Science Foundation (ESF), in keeping with a component of the ESF’s “Origins of Man, Language, and Languages” EUROCORE program aimed at evaluating the size, degree of adaptation to environmental conditions, geography, and movements of past human populations.

ECO-CULTURAL NICHE MODELING OVERVIEW

ECNM and its associated theoretical and methodological underpinnings allow us to explore the complexity of reciprocal impacts between human and natural systems in the history, adaptations, and movements of archaeological peoples. This approach combines multiple disciplines and research emphases to turn centuries of archaeological *description* into *prediction*—to understand and model the ecology of human and hominid populations. Modeling eco-cultural niches across time and space requires capturing, digitizing, and sharing data from numerous disparate sources. Only such cooperation and integration can realize the enormous potential for using ECNM to test archaeological theory and generate quantitatively robust hypotheses regarding ancient human populations.

Colleagues familiar with archaeological predictive modeling and geographic information systems (GIS) will identify many parallels with ECNM. Inductive approaches, exploratory data analysis, and predictive modeling became common in recent decades as data became automated and computation-intensive applications became as close as one’s own desktop (e.g., Allen et al. 1990; Judge and Sebastian 1988; Lock and Stančič 1995; Maschner 1996). Well es-

tablished precedents in archaeology include such seminal works as Jochim's (1976) predictive model of Mesolithic subsistence and settlement and the integration of GIS and multivariate statistics by Kvamme (1983). Several advances proposed by ECNM include the use of new algorithms, more diverse data integration, and greater scales of analysis.

The ENM software platform that has been used in most of the exploratory ECNM applications is the Genetic Algorithm for Rule-Set Prediction (GARP). GARP is part of a larger biocomputational architecture that integrates biotic and environmental data to produce predictive geographic models of species' occurrences, potential distribution patterns, and related complex biodiversity phenomena that were previously intractable (Peterson 2003; Peterson et al. 2003; Peterson et al. 2005a; Sánchez-Cordero and Martínez-Meyer 2000; Thomas et al. 2004). This evolutionary computing application has been applied successfully to a diverse group of topics such as biodiversity conservation (Chen and Peterson 2002; Peterson et al. 2000), effects of climate change on species' distributions (Peterson et al. 2005b; Thomas et al. 2004), geographic potential of species invasions (Peterson 2003; Peterson and Vieglais 2001), and prediction of the spread of emerging diseases (Peterson et al. 2004; Peterson et al. 2005a; Peterson et al. in press).

ENM data requirements include geographic occurrence points for species of interest and raster GIS data layers summarizing landscape, ecological, and environmental dimensions that may be involved in limiting the potential geographic distribution of the species of interest. In GARP, occurrence data are related to landscape variables to develop a heterogeneous rule-set that defines the distribution of a species in ecological space (Soberón and Peterson 2005), which in turn can be projected onto landscapes to predict potential geographic distributions. GARP accomplishes this task by relating ecological characteristics of species' geographic occurrences to background observations randomly sampled from the study region. The result is a set of decision rules that best summarize factors associated with the species' presence, thereby constituting a model of that species' ecological niche.

GARP has seen extensive improvement and testing in recent years, including detailed sensitivity analyses (Peterson and Cohoon 1999; Stockwell and Peterson 2002a, 2002b; Anderson et al. 2002). A recently developed desktop version of GARP offers a greatly improved user interface; in particular, many processes are automated, permitting analysis and testing of different hypotheses: (1) jackknifing inclusion/exclusion of ecological/environmental data layers (Peterson and Cohoon 1999); (2) bootstrapping inclusion of species' occurrence points; and, (3) jackknifing inclusion/exclusion of predictive algorithms within the genetic algorithm. The desktop version of GARP, developed at the University of Kansas Biodiversity Research Center, is now available for free download (<http://www.lifemapper.org/desktopgarp/>).

When ENM is applied to geographic and ecological distributions of human cultures—i.e., ECNM—it is human

culture that occupies an ecological space, and occurrences of archaeological sites and material culture are used to develop eco-cultural niche models in ecological dimensions only. There is still some uncertainty as to what level of specificity ECNM can be used to examine human groups. The biological disciplines have shown these methodologies to be effective in determining the actual and potential distributions of animal species. Thus, at its most basic level, ECNM should be able to be used to examine human adaptive systems. The next issue that needs to be addressed is how to use ECNM to identify and examine the variability seen in the archaeological record with reference to technocomplexes, economies, and ethno-linguistic groups, for example. In applying GARP to the archaeological record, cultural distributions are modeled for specific time periods and then interpreted relative to the associated ecological dimensions. With reference to biological species, ecological niches have been shown to be conservative at regional and continental scales (Peterson 2003; Peterson et al. 2002), so one aim of ECNM is to test if the same holds true for cultural groups—i.e., equally robust and accurate eco-cultural niche models.

ECNM identifies geographic regions for archaeologically defined populations that represent the eco-cultural niches and models potential geographic distributions for those populations. Specifically, GARP and other modeling tools can be used to reconstruct past human systems in the Old and New World, as well as features of past natural systems within which they operated (e.g., distributions of prey species) in the context of geological, paleobiological, and paleoenvironmental conditions. Once initial hypotheses are developed, ECNM can be used to develop informed, testable hypotheses concerning the geographic spread, migration, and eco-cultural adaptations of prehistoric human populations to their respective environments.

CLIMATE, PALEOENVIRONMENTS, AND CHRONOLOGY

ECNM integrates and analyzes a wide range of data. Because human-environment interactions are the focus of ECNM, climate data and environmental reconstructions, derived from a variety of proxy data, are key (e.g., marine sediment cores, ice cores, terrestrial proxy records). For example, the isotopic makeup of air bubbles trapped in Antarctic ice allow for reconstruction of the history of atmospheric gas concentrations over the past 800,000 years (Spahni et al. 2005); the isotopic composition of Greenland ice implies a series of abrupt warming events (Dansgaard-Oeschger events) that punctuated the last ice age (Dansgaard et al. 1993); layers of detritic material accumulated on the North Atlantic sea-floor indicate massive iceberg discharges termed Heinrich events (Heinrich 1988). Past vegetation patterns can be reconstructed from fossil pollen in peat-bogs, lake sediments, and off-shore deep-sea sediments. Moreover, multi-proxy analyses of a variety of terrestrial archives (e.g., lakes, peat bogs, speleothems) provide information on past climatic and environmental changes. However, most detailed and high-resolution re-

cords extend only over the past ca 20 kyr B.P. and only a few long terrestrial records have the necessary resolution to document millennial-scale changes during the whole of the last glacial period. It is therefore challenging to establish accurate chronologies for these long terrestrial records and to link them precisely to other high-resolution records so that the nature of such changes, and ultimately the cause of these fluctuations, can be understood. Such changes certainly had profound impacts on prehistoric human populations.

Using these data in ECNM analyses presents a number of challenges. One common difficulty is building a uniform time scale for all these records. With respect to chronology, we must be reasonably certain that the sample of archaeological sites used to document distributions reflects chronological cultural reality and coincides with the paleoenvironmental data used. Some obvious questions present themselves. What types of dates should be used? What levels of uncertainty are acceptable? What strategy do we use to tackle the issue of ^{14}C calibration for periods prior to 26k BP? Internationally agreed-upon timescales exist for those records that can be radiocarbon dated, and Ménot-Combes et al. (2005) have illustrated recent attempts to develop uniform radiocarbon calibrations. At present, radiocarbon calibration curves, such as the widely accepted IntCal04 (Reimer et al. 2004), have been reliably extended back to 26 kyr B.P. but for older ages, the available “calibration” data series diverge to a large extent and are not included in the recent IntCal04 dataset. Beyond 26 kyr BP, it has been suggested that these data series should be regarded as comparison curves rather than calibration curves (Beck et al. 2001; Richards and Beck 2001; van der Plicht 2000). For the interval between 33,000 and 41,000 cal BP, the record of the Iberian Margin agrees with the IntCal98 coral data and the Cariaco record (Bard et al. 2004). Continued comparative analyses of diverse and complementary records, along with hyperpurification methods associated with AMS dating (Mellars 2006), will help to refine radiocarbon chronologies.

The use of records with independent sources of paleoenvironmental information can minimize problems associated with chronological resolution. A good example is off-shore deep-sea records, which contain marine fossil assemblages (used to reconstruct sea-surface temperatures and hence identify Dansgaard-Oeschger (D/O) events), fossil pollen, and ice-rafted detritus (to identify Heinrich events). Pollen records from deep-sea cores off the Iberian Peninsula provide a detailed record of vegetation changes associated with D/O climatic variability. Transfer functions based on modern pollen spectra applied to pollen data from these sequences predict past temperature and precipitation patterns for the continent (Figure 1). The results indicate that the impact of D/O cycles was spatially variable, and these findings are comparable to the results of modeled vegetation responses for the same region (Sepulchre et al. 2005). Additionally, most paleoenvironmental data sets must be modified before they can be used in ECNM analyses. For example, although ECNM may require tempera-

ture and precipitation data, the actual paleoenvironmental information consists of local fossil pollen assemblages. “Spatial-to-temporal mapping,” a best analogue technique (Guiot 1990; Peyron et al. 1998), can be used to infer past environmental conditions, as well as develop and test environmental models to be incorporated into an ECNM analysis. However, this technique’s accuracy may be limited by various factors, including low CO_2 concentrations during the last glacial era as compared to present-day concentrations (e.g., Cowling and Sykes 1999; Harrison and Prentice 2003; Jolly and Haxeltine 1997).

ECNM also requires data with high spatial resolution, in most cases at landscape scales. Statistical downscaling techniques exist (e.g., Palutikof et al. 2002), but the last glacial period differed so greatly from the present that it is essential to resort to climate models. The best objective source of such information is general circulation models, which reconstruct past, present, and future climates for the entire globe at a resolution of 100–200 km (e.g., the Hadley Centre Model – Gordon et al. 2000). The alternative is regional climate models, but these simulations need to be driven by “boundary conditions” drawn from a general circulation model (Ramstein et al. 2005).

General circulation models are usually run for specific points in time, typically the Last Glacial Maximum (LGM), Last Interglacial, or the Mid-Holocene; scenarios falling between these benchmark dates require interpolation. The only parameters that must be specified are greenhouse gas concentrations, orbital forcing, and land-sea orographic configuration. The results of various climate models are integrated, collated, and archived in a central database (<http://www-lsce.cea.fr/pmip>; Crucifix et al. 2005). The goal behind these simulations is to understand mechanisms of climate change, and as such they may at times be incompatible locally with paleoenvironmental observations. Alternative approaches, in which paleoenvironmental information is assimilated into the simulation process to produce a climatic map simultaneously compatible with data and physical constraints on atmosphere and ocean dynamics, are still under development.

Paleontological data also have the potential to serve as proxies for past regional environmental conditions. An exploration of the ecological dynamics of large mammal communities in southwestern Europe between 45 kyr and 10 kyr BP based on a sample of 230 sites and 755 mammal associations indicates a clear diversity gradient from SW/NE with lower biomass towards the SW (Brugal and Yravedra 2006). These analytical indices have proven to be ecologically and functionally meaningful, but problems associated with a reliance on conventional radiocarbon determinations and the potential for stratigraphic mixing of archaeological and paleontological assemblages must be addressed before such approaches can be reliably incorporated into regional modeling attempts. Prehistoric environmental conditions for portions of Western Africa have been inferred from statistical examinations of archaeozoological bovid assemblages (Jousse and Escarguel 2006). These results are useful in identifying refuge areas for some vegetation communi-

GISP $\delta^{18}\text{O}$ MD95-2042, Atlantic margin

MD95-2043, Alboran Sea

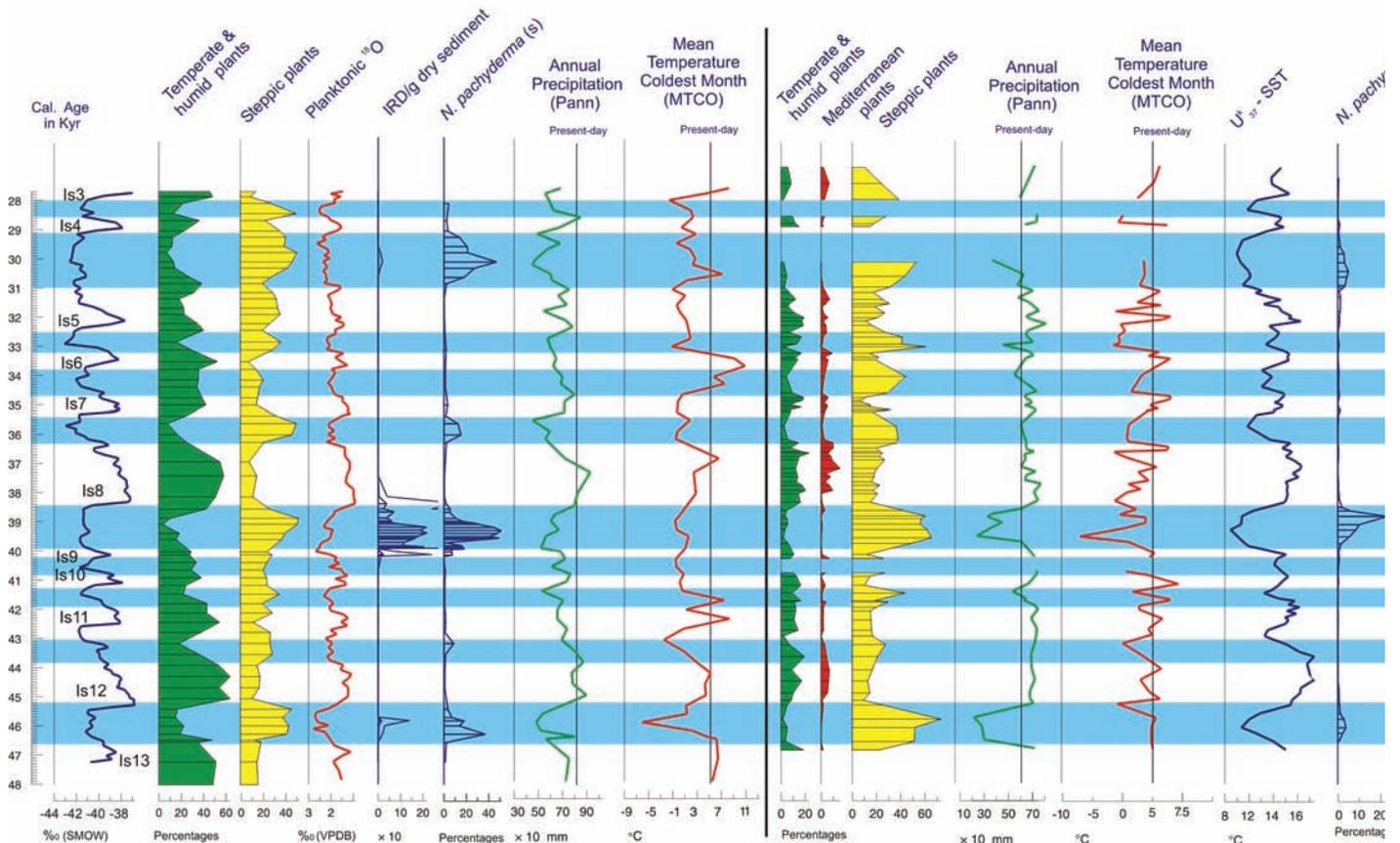


Figure 1. Palaeoclimatic records from the Iberian margin cores MD95-2042 and MD95-2043, and their comparison with the GISP2 $\delta^{18}\text{O}$ curve. Blue intervals indicate Heinrich events (H5, H4 and H3) and the other Dansgaard-Oeschger stadials (from d'Errico & Sanchez Goñi 2003). The curves of the lower and upper standard deviations of annual precipitation and mean temperature of the coldest month are shown in Sánchez Goñi et al. (2002).

ties, have proven to be valid at a local scale, and complement available pollen data. Expanding this approach to more diverse faunal assemblages will likely increase the resolution of regional paleoenvironmental models that can be used to complement ECNM analyses.

ARCHAEOLOGICAL, PALEOANTHROPOLOGICAL, AND ETHNOLINGUISTIC DATA

A primary goal of ECNM is to evaluate, simulate, and reconstruct how ancient human populations could have responded to climatic fluctuations and to understand which climatic factors most impacted these populations. With respect to Upper Paleolithic populations, we would expect more geographically extensive cultural units during stadials and more restricted distributions during interstadials, a prediction based on correlations between ethno-linguistic and environmental parameters (Collard and Foley 2002; Nettle 1998) and partly supported by analyses of AMS-dated site distributions and climatic fluctuations that indicate increased frequency of archaeological sites in Western Europe during each cold event prior to the Holocene (d'Errico et al. 2006). Related relevant evidence consists of linkages between vegetational change, herbivore/ungulate populations, and responses of human groups.

An ECNM analysis based on abiotic environmental parameters and 18 archaeological sites dated by AMS to 21 ± 0.5 kyr BP and associated with the Solutrean technocomplex was performed as a pilot application of the methodology described above. The Solutrean was chosen for a number of reasons. First, it is marked by the use of a specialized process for making highly diagnostic stone tools unique to the Upper Paleolithic in Western Europe. This technology represents a specific cultural adaptation to environmental conditions during the LGM, thus making it ideal for an ECNM study. This technocomplex also had a relatively narrow geographic range (France, Spain, and Portugal) and was present in these regions during a restricted time period of the Upper Paleolithic. Therefore, one is able to avoid the resolution problems typical of studies that cover broader time spans and greater cultural variability.

The GARP modeling results indicate that temperature was the variable that most influenced the potential distribution of the Solutrean technocomplex. The ability to produce ECNMs while jackknifing the inclusion of environmental variables allows for such patterns to be identified (Peterson and Cohoon 1999:163). Such jackknife manipulation involves systematically eliminating each environmental variable from specific modeling runs. In other words, one

uses N-1 of the N variables for a series of modeling runs to determine which environmental variable most influences the predictive model outcome that utilized the full complement of analytical variables.

Additionally, the geographic distributions produced by GARP indicate potential Solutrean populations where they are known to have occurred as well as where we know they did not exist, and a similar pattern is seen with comparative GARP models based on the Epigravettien record of Southern Europe during the LGM (Figure 2). This suggests that cultural adaptations, in addition to environmental conditions, strongly conditioned the distributions of these tech-

nocomplexes. The discord between the GARP models and actual archaeological distributions likely reflects the role of cultural transmission (Nettle 1998) and cultural territory (Collard and Foley 2002) in distributions of archaeological populations.

A similar pattern can be described for North American Paleoindian assemblages. Clovis and related fluted points, which date from ca 13,500 to 12,900 cal BP (e.g., Fiedel 1999, 2004, 2005; Haynes 2005; Roosevelt et al. 2002), occur widely over portions of North America that were unglaciated, cross-cutting a wide range of paleoenvironmental settings. This pilot analysis is based on 1,514 locations where such

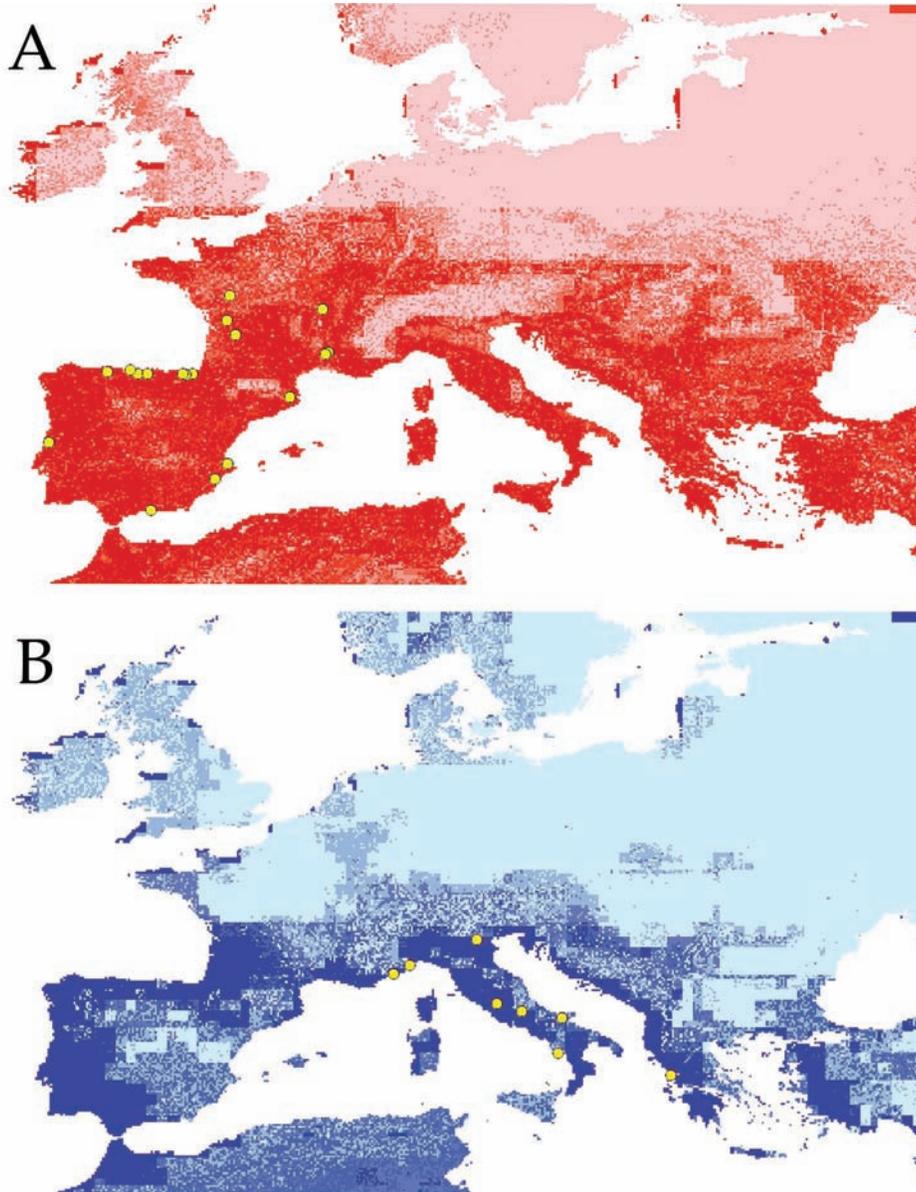


Figure 2. Upper map (A) depicts GARP prediction based on Solutrean sites dated by AMS to 21 ± 0.5 k cal BP. Lower map (B) depicts GARP prediction based on Epigravettian sites from Southeastern Europe dated by AMS to 21 ± 0.5 k cal BP. The darkest colors represent the highest level of agreement among best subset models (Anderson et al. 2003) in prediction of potential presence, whereas the lightest color represents highest levels of agreement among best subset models in prediction of absence. GARP analyses were based on mean temperature and mean precipitation values drawn from a LGM (21k cal BP) General Circulation Model developed by the Hadley Centre (Hewitt et al. 2003) and served through PMIP1 (Paleoclimate Modelling Intercomparison Project) (Joussaume and Taylor 2000).

artifacts have been found, along with related information, all of which has been compiled and made available on-line (Anderson and Faught 1998, 2000; Anderson et al. 2005; <http://pidba.tennessee.edu/>). This Paleoindian Database of the Americas (PIDBA) is as comprehensive and inclusive a compilation of these artifact types and locations as possible, is steadily growing, and has been subject to intensive and generally positive evaluation (e.g., Buchanan 2003; Shott 2002). Given the widespread occurrence of Clovis points, appreciable debate and uncertainty exists as to whether: (1) a common 'high technology foraging' adaptation was in play by widely ranging groups (i.e., Kelly and Todd 1988); or, (2) a number of distinct adaptations were in existence, representing populations adapted to conditions in specific subregions, such as generalized foragers in the deciduous forests of the southeastern United States or more specialized foragers (i.e., caribou hunters) in the northeast and upper Midwest (i.e., Anderson 1990; Meltzer 1988, 2002, 2003). Given the several hundred years attributed to the Clovis phenomenon, both scenarios likely apply. That is, the initial Clovis technology and/or populations using it likely radiated rapidly, but soon became distinct from one another in time and space, and within a relatively brief period localized adaptations and distinctive subregional cultural traditions arose (Anderson 1990, 1995; Anderson and Gillam 2000, 2001; Meltzer 2003). The Clovis niche produced by GARP and based on projectile point data (Figure 3) is so broad that it may represent a single high technology foraging adaptation. More likely, however, the nature of this GARP niche prediction indicates that we must refine our analytical methods and make use of additional categories of assemblage data in order to identify discrete subregional adaptations that probably existed during the Clovis era.

In contrast, the presumably immediate post-Clovis and contemporaneous Folsom and Cumberland adaptations (ca 12,800–12,500 cal BP or later) are much more geographically restricted, largely to the Great Plains and the deciduous forests of the midsouth, respectively, although they exhibit some geographic overlap. The Folsom and Cumberland technocomplexes are thought to represent very different adaptations, respectively directed to specialized bison hunting and more generalized foraging (e.g., Anderson 2001; Clark and Collins 2002). Their GARP predictions overlap appreciably, however, indicating that the distinctive projectile point forms employed by each, which only minimally overlap, are probably strongly culturally determined (Figures 4 and 5). That is, the people using each form could have ranged far more widely, but did not, probably because the landscape was already occupied by peoples belonging to different and distinctive cultural traditions. Again, however, and as with Clovis, we must become better at differentiating these early adaptations, and determine what factors, beside projectile point morphology, make them appear to represent distinctive cultural complexes.

Based on the GARP results, it can be argued that the Solutrean and Epigravettian technocomplexes, as well as the New World Paleoindian cultures that immediately followed Clovis, may be thought of as sympatric cultures

adapted to similar abiotic situations but employing different cultural adaptations. However, with reference to the Solutrean and Epigravettian GARP predictions, one notes that the Epigravettian distributions are confined to more southerly latitudes, while the potential eco-cultural niche distributions for the Solutrean include higher latitudes. This indicates that while in a general sense these two technocomplexes can be viewed as sympatric cultures, they nevertheless represent unique technical systems more or less adapted to specific environments.

One important issue facing ECNM is how to incorporate the occurrences of undated or imprecisely dated material culture diagnostics into analyses. The PIDBA encompasses some 26,000 late Pleistocene and initial Holocene projectile points from over 1,800 locations, spanning a number of archaeological 'cultures' or technocomplexes dating from ca 13,500 to 10,000 cal BP (Anderson et al. 2005). As noted in the discussion above, problems associated with using this database include: equating specific artifact types with specific cultural groups; relying on a group of sites that may in reality only partially represent a settlement system; sacrificing the need for independent temporal evidence and established precision by relying on material diagnostics, and assuming that materials are indeed culturally diagnostic [see also Anderson and Faught (1998) for a discussion of these concerns, as well as Shott (2002) and Buchanan (2003) for in depth critical evaluations of its utility]. Therefore, incorporation of such cultural markers into ECNM must be done with caution recognizing that models based on cultural items from well-dated contexts or datasets that include a wide array of assemblage data categories will have great interpretive potential. For example, seriation and correspondence analyses of personal ornaments from dated contexts have been used to identify distinct geographic and cultural differences across Europe during the initial Upper Paleolithic (Vanhaeren and d'Errico 2006), thus demonstrating the potential of such artifact types for examining the links between artifact types, culture, and biological populations. Future research should examine the impact of climate changes on cultural organization and territories, as reflected in material culture, and test resulting hypotheses against available genetic data.

ECNM also has the potential to model the geography and movements of human and earlier hominid populations; currently, a number of modeling methodologies have been used. For example, GIS has been used to approximate corridors of migration across continents using least-cost paths analysis for Paleoindians in North and South America (Anderson and Gillam 2000). The "Stepping Out" model (Mithen and Reed 2002) and its derivative (Hughes et al. 2005) combine paleoanthropological data and generic climatic conditions to produce models that are in agreement with the East Asian archaeological record, and the latter approach has highlighted the importance of uncertainties in the environmental tolerances of *Homo erectus* for their later arrival into Europe. Foley et al. (2005) describe similar disagreements between the archaeological record of early hominid dispersal routes out of Africa and models that use

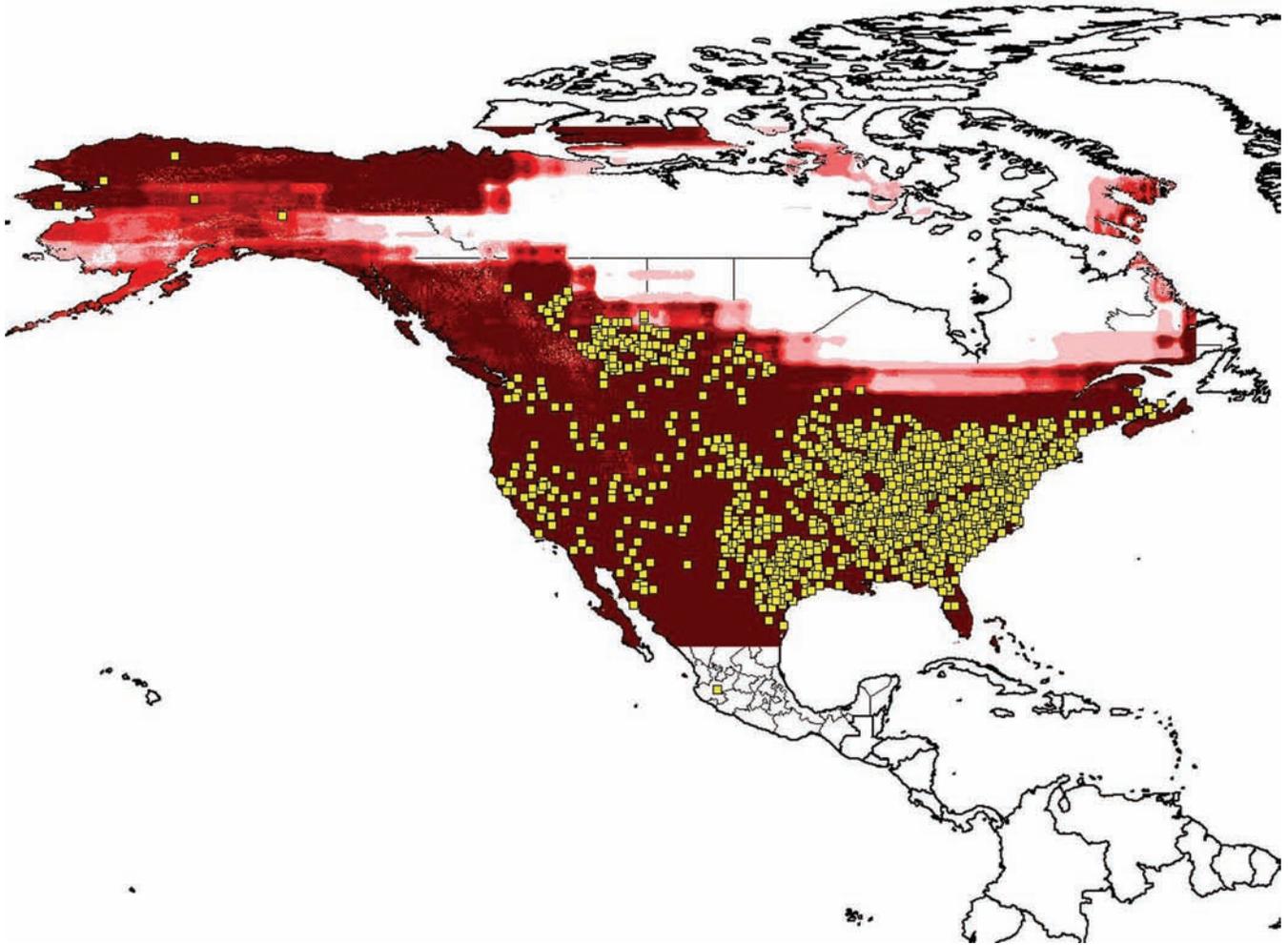


Figure 3. GARP prediction for 13,000 cal BP based on occurrences of all fluted point types ($n=1,514$), excluding known post-Clovis types. Climate data were interpreted linearly between a LGM (21k cal BP) and a mid-Holocene (ca 6k cal BP) General Circulation Models developed by the Hadley Centre and served through PMIP1.

cost matrices based on topographic friction, vegetation, and simulated habitat distributions. Colonization proceeds at different rates in different environments requiring models that approximate resource gradients and incorporate mathematics, GIS, and archaeological data (e.g., diffusion models, wave front models, etc., e.g., Hazelwood and Steele 2004). Population expansion models must resolve discords between the analytical constraints associated with simple models and problematic archaeological data (Steele 2005).

One necessary step is to better integrate paleoenvironmental data with archaeological data, but in order for this to be productive we need to compile exhaustive and detailed regional archaeological databases that are consistent with respect to the information they contain. For example, a number of databases exist for the Acheulean Tradition. A lower Paleolithic database for the Indian subcontinent has been compiled by Shanti Pappu, Sharma Centre for Heritage Education, and another assembled by Naama Goren-Inbar of Hebrew University of Jerusalem concerns the Acheulean

record of the Near East. It is hoped that these databases can be used to facilitate investigations of Lower Paleolithic archaeological diversity, how environmental changes influenced hominid dispersals, and test possible relationships between these technologies and environmental factors (e.g., James and Petraglia 2005). For example, despite the occurrence of Acheulean-like technologies in southern China (Yamei et al. 2000), the Movius line appears to remain a valid concept. ECNM provides an analytical toolkit with which to test the possible relationships between the spread of Acheulean and Acheulean-like technologies and ecological conditions in Asia.

Similarly, compilation and analyses of robust georeferenced databases can increase understanding of the spread of Anatomically Modern Humans in Africa and the correlation between archaeological and environmental records. The Paleogeography of the African Middle Stone Age (PAMSA) database (Marean and Lassar 2005) has been under development for approximately three years. Starting

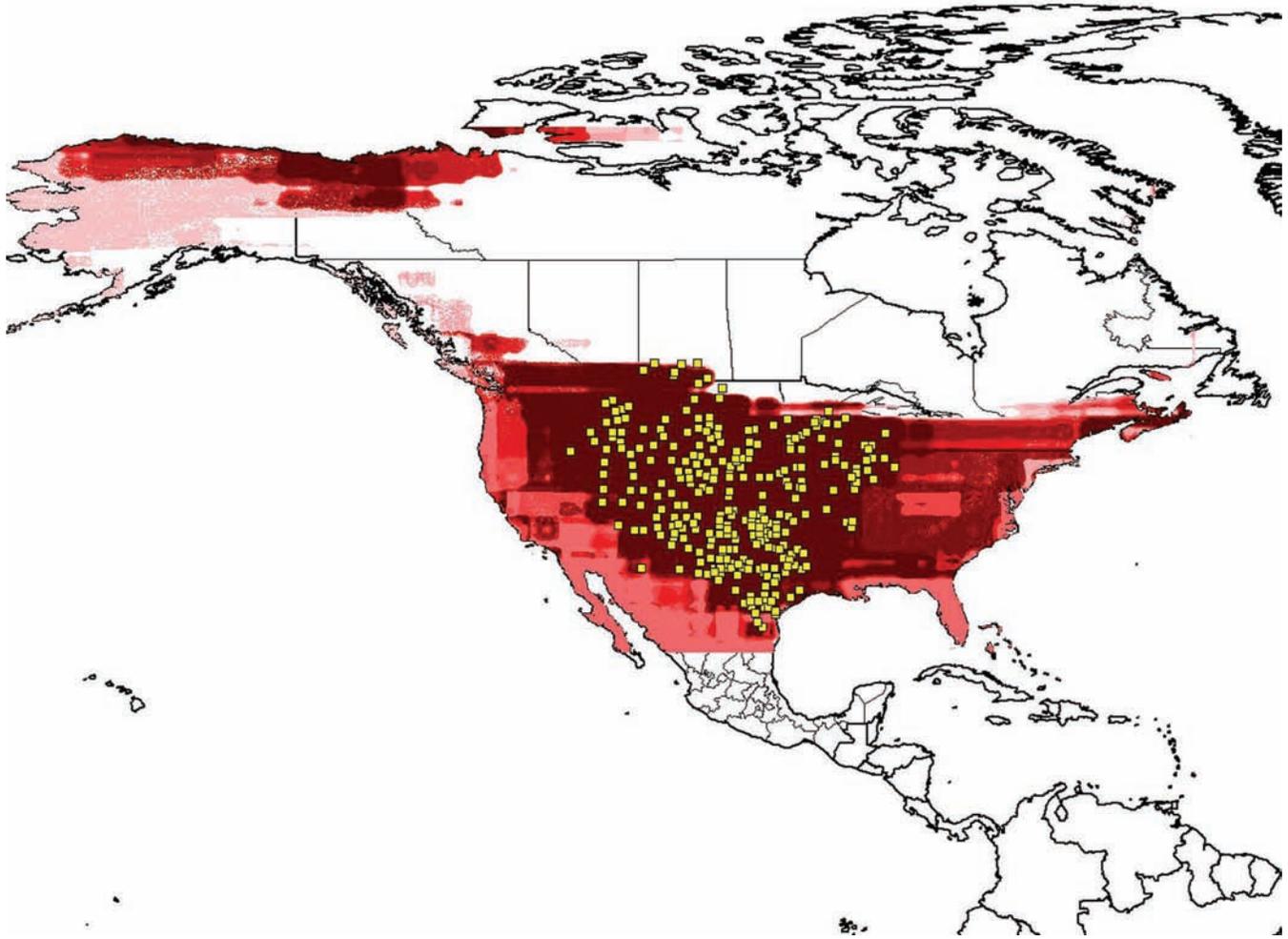


Figure 4. GARP prediction for 12,000 cal BP based on Folsom point occurrences ($n=292$). Climate data were interpreted linearly between a LGM (21k cal BP) and a mid-Holocene (ca 6k cal BP) General Circulation Models developed by the Hadley Centre and served through PMIP1.

with Clark's *Atlas of African Prehistory* (1967), this database has now been updated to the present. It includes the geographic coordinates of all MSA sites and links to tables on site attributes, excavation details, and the composition of the lithic assemblages, as well as hot-links to original data tables and figures. It currently includes approximately 1,800 cases. A spatial analysis of industries characterized by bifacial lanceolate points relative to projected environmental zones suggests these may be adaptive systems focused on hunting in grassland ecosystems (Figure 6).

In the New World, the PIDBA is being developed from state and county-level archaeological records of diagnostic biface types to enable analyses of archaeological distributions and environmental factors related to Pleistocene settlement systems (Anderson et al. 2005; Gillam et al. 2005). Such continental scale databases are ideally suited for ECNM analyses given the rather coarse spatial resolution of climate system models (CSM), land and bathymetric elevation models (e.g., ETOPO2), and other environmental datasets that form the basis of such modeling efforts. As

noted above, the PIDBA's contribution to such modeling efforts will continue to grow as it is expanded to include a more comprehensive array of assemblage and chronological data.

Other databases that focus on the definition of prehistoric cultures and technocomplexes based on material remains are being constructed for ECNM analyses (Svoboda in press). Jaubert's (2005) Middle Paleolithic database is a prime candidate for such investigations once the compilation of geographic coordinates of all its sites is completed. Similar Middle Paleolithic databases for the Caucasus region are also being compiled (Doronichev 2005; Golovanova 2005), and these too have great analytical potential. A large comprehensive database that includes information on lithological, geological, geomorphological, vegetational, paleobotanical, and archaeological data associated with the LGM in Italy has the potential to identify trends such as the spread of the early Epigravettian in Italy and associated environmental influences (Peresani et al. 2005). Research presented at the two workshops revealed that such compi-

lations of environmental and archaeological data from disparate disciplinary domains, geographic regions, and time periods require working with professionals in informatics and close collaboration among researchers in archaeology.

In brief, ECNM offers considerable potential to archaeology and the study of ancient humans. The technique allows investigators to interpret geographic patterns ecologically, which makes for numerous unique inferences. First, and most simply, the models themselves can be interpreted to provide insights into the ecological distributions of ancient humans, teasing apart influences (for example) of temperature and precipitation. Second, the maps produced can be interpreted as depicting potential geographic distributions—within known distributional areas, this result can interpolate between known occurrences to hypothesize a more complete geographic distribution (Soberón and Peterson 2005); when predictions are geographically disjunctive, they may indicate new sites for exploration (Raxworthy et al. 2003). ECNM can also be applied to questions of distributions of prey species or other biological resources—for example, testing hypotheses of reindeer distributions dur-

ing the LGM (Flagstad and Røed 2003), or the distribution of particular forest types, would be most useful (for related ENM examples, see Bonaccorso et al. 2006; Martínez-Meyer and Peterson in press; Martínez-Meyer et al. 2004). Finally, ECNM has the potential to develop quantitative predictions of the effects of events of change on ancient humans—climate change, land use change, etc., all interact with species' ecological potential, and the spatial manifestations of these changes can be reconstructed using such a methodological approach (Sánchez-Cordero et al. 2005, Thomas et al. 2004). As such, ECNM has much to offer to archaeology, providing the potential for many new insights and new questions.

Accurate interpretation of recognized cultural patterns requires incorporation of ecological concepts into ECNM analyses (d'Errico et al. 2006; Vanhaeren and d'Errico 2006). Some features of linguistic systems may relate to environmental conditions, such as ecological risk (Collard and Foley 2002; Nettle 1998). Although there is likely no direct relationship between them, an indirect one may be mediated by the social structures of the speakers and their

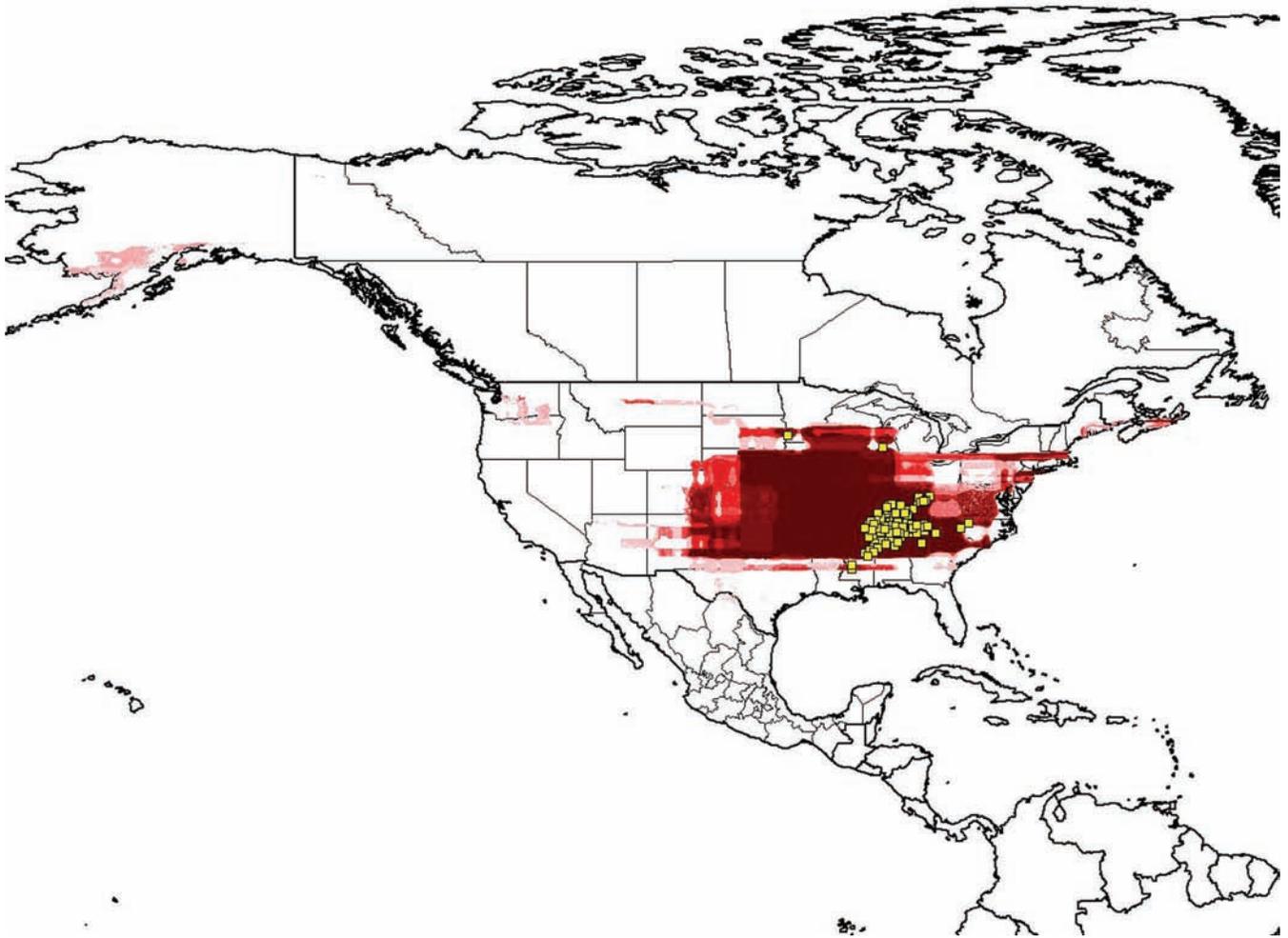


Figure 5. GARP prediction for 12,000 cal BP based on Cumberland point occurrences ($n=103$). Climate data were interpreted linearly between a LGM (21k cal BP) and a mid-Holocene (ca 6k cal BP) General Circulation Models developed by the Hadley Centre and served through PMIP1.

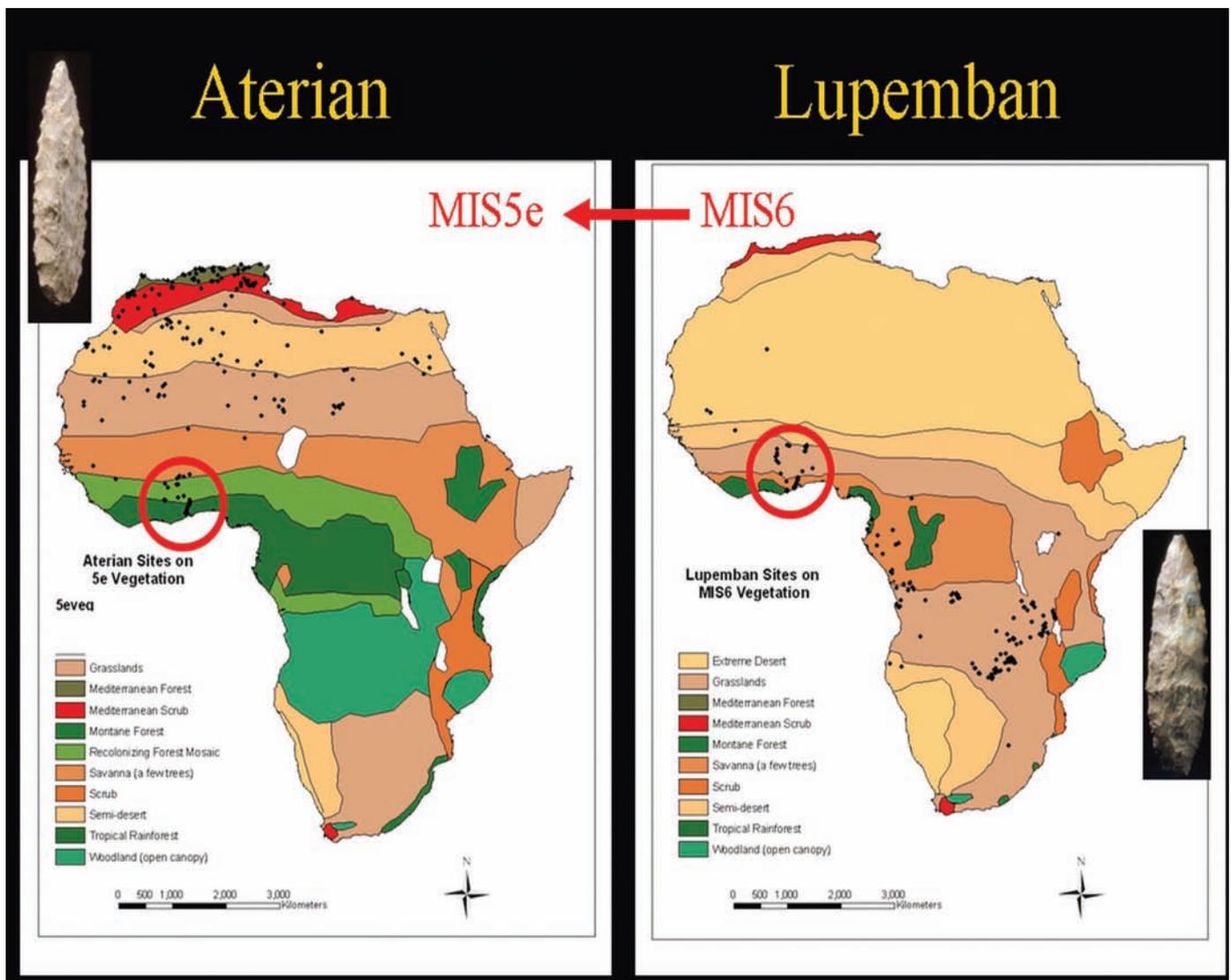


Figure 6. The location of Aterian sites projected on an interglacial vegetation map derived from the early Holocene reconstruction of Adams and Faure (1997), and the location of Lupemban sites on a glacial vegetation map derived from the Last Glacial Maximum reconstruction of Adams and Faure (1997).

behaviors in adapting to specific environments. Although it is difficult to apply these concepts to Paleolithic populations, small group size, localized residence, exogamy, and the size and frequency of aggregations all might explain expected levels of linguistic variability in hunter-gatherer groups (Coupé 2005). Modeling linguistic diversity might yield valuable results, and there should be a focus on the concept of ecological risk among hunter-gatherers, with respect to cultural and climatic variability, and subsequent impacts on the patterns of social interactions and linguistic evolution. Coupé is currently examining the influence of social structure on language evolution, and more specifically how the evolution of language diversity is related to the degree of locality among interacting populations. Such an approach could be used to model the possible size of cultural groups during specific periods of the Paleolithic.

However, the results of a current OMLL project in South America indicate caution in assuming a strict link between

linguistic, ethnic, and genetic data and ecological factors (Hornborg 2005). For example, although geographically isolated groups speak related languages, their neighbors may be linguistically and ethnically different despite sharing similar adaptations and material culture. This pattern is related to the recursive relationship between socio-ecological niches and the construction of ethnic identity (Hornborg 2005), which leaves signatures that could be explored with Eco-Cultural Niche Modeling.

CONCLUSIONS

A current challenge facing archaeology (and other disciplines) is deciphering and understanding coupled natural and human systems and their reciprocal impacts, as well as the constants in their dynamic equilibrium. Such understanding requires enabling access to data across biodiversity, ecology, earth systems science, and anthropology; mining, analyzing, and modeling these data for new

knowledge; and informing decision-makers and the public of the insights discovered. Research that exploits information technology to bridge natural and human systems will advance our ability to study aspects of biocomplexity across these systems.

The two ECNM workshops “proved” a concept and initiated a fusion of multiple disciplines and data domains in eco-cultural niche modeling of past coupled and natural systems, particularly human-environment interactions. The workshops also identified current limitations of applying ECNM to analyses of the archaeological record, especially as regards the quality, quantity, and temporal and spatial resolution of the data. Archaeology lacks network-ready databases that are uniformly detailed, comprehensive, and consistent across the spatial and temporal record. Compiling such resources requires international collaboration in mining literature, collections, and other sources, and capturing and networking the data via modern informatics tools. Biases inherent in these databases are differences in the quality and resolution of regional archaeological surveys, and frequencies and distributions of known sites and dated sites. Precisely because the archaeological record represents the human past imperfectly preserved and discovered, ECNM is a powerful tool in reconstructing the geographic patterns of archaeological populations, as it has proven to be for biological species (Wiens and Graham 2005), of which perhaps only 10% are documented in museum collections, biotic surveys, and the literature.

Specific challenges facing the enhancement of ECNM analyses encompass the chronological record, the climate record, and computational expertise. Chronological resolution is critical to understanding cultural responses to specific climatic events, but because many dates are problematic (e.g., sigmas that are too large), analyses require consistent, compelling criteria in excluding or including particular conventional and AMS radiocarbon dates.

Another issue is the availability and use of interpolated climatic data at a regional level that have the requisite spatial resolution for GARP modeling. Every general circulation model differs in its climatic predictions slightly from higher resolution regional proxy records. For example, many recent high-resolution atmospheric general circulation models underestimate LGM cooling and aridity as compared to pollen records (Jost et al. 2005). Mathematical interpolation of coarser-scale climatic data can yield finer spatial resolution, but different assumptions and mathematical methodologies will produce different results. The consequence will be a need for ensemble predictions and careful rethinking regarding both the implications and limitations of ECNM analyses.

Finally, ECNM requires considerable training and skill in (1) the use of various, complex software packages and computational routines; (2) organizing and integrating disparate datasets for modeling; and, (3) interpretation of model outcomes. The solution, of which the two workshops were an illustration, is to establish multidisciplinary and multisector research teams representing the biological, environmental, anthropological, and information scienc-

es. Such teams can deploy ECNM to heterogeneous data and complex, large-scale research problems in prehistoric coupled natural and human systems that were previously intractable.

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Human ecological niches and ranges during the LGM in Europe derived from an application of eco-cultural niche modeling

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Abstract

We apply eco-cultural niche modeling (ECNM), an heuristic approach adapted from the biodiversity sciences, to identify habitable portions of the European territory for Upper Paleolithic hunter-gatherers during the Last Glacial Maximum (LGM), circumscribe potential geographic extents of the Solutrean and Epigravettian technocomplexes, evaluate environmental and adaptive factors that influenced their distributions, and discuss this method's potential to illuminate past human–environment interaction. Our ECNM approach employed the Genetic Algorithm for Rule-Set Prediction (GARP) and used as input a combination of archaeological and geographic data, in conjunction with high-resolution paleoclimatic simulations for this time frame. The archaeological data consist of geographic coordinates of sites dated by Accelerator Mass Spectrometry to the LGM and attributed to the Solutrean and Epigravettian technocomplexes. The areas predicted by ECNM consistently outline the northern boundary of human presence at 22,000–20,000 cal BP. This boundary is mainly determined by climatic constraints and corresponds well to known southern limits of periglacial environments and permafrost conditions during the LGM. Differences between predicted ecological niches and known ranges of the Solutrean and Epigravettian technocomplexes are interpreted as Solutrean populations being adapted to colder and more humid environments and as reflecting influences of ecological risk on geographic distributions of cultures.

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1. Introduction

The idea of modeling past human–environment interactions is by no means new. Researchers have used archaeological and environmental data sets, and diverse methods, to interpret prehistoric hunter-gatherer behavior in ecological

contexts. Well-known European examples concern prehistoric population distributions during Oxygen Isotope Stages 2 and 3 (Gamble et al., 2004; Van Andel and Davies, 2003), as well as the resettlement of regions following severe climatic episodes (Gamble et al., 2005; Straus et al., 2000). These studies were based on spatial distributions of radiometrically dated sites and generalized climatic reconstructions. Others have used a similar approach to estimate population size and kinetics (Bocquet-Appel and Demars, 2000; Bocquet-Appel et al.,

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2005). More detailed attempts to examine population distributions and human tolerances with respect to environmental variability also exist (Binford, 1999, 2001; Davies et al., 2003; d'Errico and Sánchez Goñi, 2003; d'Errico et al., 2006; Sepulchre et al., 2007). However, no agreement yet exists on how best to evaluate influences of environmental factors on prehistoric human populations and their responses to climatic variability.

One common limitation is the use of coarse-scale climatic data (i.e., simulations with resolutions of 3–5° in latitude and longitude) and imprecise chronological data (i.e., reliance on old conventional ages with large sigmas) that make evaluation of human responses to rapid-scale climatic variability, with adequate resolution, difficult. Another shortfall of previous studies is that they have incorporated environmental data into analyses only passively, such that these data are used as backdrops against which the archaeological record is interpreted. While these studies have obvious value, they are limited in their ability to evaluate prehistoric hunter-gatherer responses to the abrupt climatic and environmental changes of the last glacial period. The need for robust methods with which to evaluate more precisely how past human and animal populations responded to these changes is critical.

An important recent advance in the study of biological diversity has been the development of biocomputational architectures for predictive modeling of complex biodiversity phenomena (Guisan and Zimmermann, 2000; Soberón and Peterson, 2005). Such tools can be used to predict species' range (i.e., ecological niche) expansion or contraction in response to real or simulated climatic changes (Peterson et al., 2002). The ecological niche of a species can be defined as the range of environmental conditions within which it can persist without migrational subsidy (Grinnell, 1924; Hutchinson, 1957). Such methods have considerable potential for reconstructing niches of past human populations and for illuminating the complex mechanisms that regulated the interactions between past hunter-gatherer populations and their environments, which in turn helped shape cultural, genetic, and linguistic geographies. These methods, and related concepts, recently have been termed eco-cultural niche modeling (ECNM) (Banks et al., 2006) when applied to prehistoric human populations. Our application of ECNM interactively integrates climatic, geographic, and archaeological data via a machine-learning genetic algorithm, described below. Comparable work is being pursued by others to analyze North American Paleoindian (Anderson and Gillam in Banks et al., 2006) and Far Eastern Paleolithic (Gillam and Tabarev, 2006) data and have shown promising results. We argue that ECNM is a powerful approach and, when paired with high-resolution climatic simulations, allows one to overcome many limitations of previous studies and evaluate prehistoric human–environment interactions at regional scales.

Here, we apply ECNM to human populations at the Last Glacial Maximum (LGM) in Europe, a well-studied and dated climatic phase known to have had profound impacts on human populations, with three primary objectives: (1) to determine the limits of the potential human range during the LGM, (2) to define the eco-cultural niches of the two main archeological

cultures present in Europe at that time (the Solutrean and Epigravettian technocomplexes), and (3) to identify environmental and cultural factors that shaped their geographic ranges.

1.1. Environmental and cultural context

The last glacial period was marked by dramatic and rapid climatic variability (Dansgaard et al., 1993; Johnsen et al., 1992), with the LGM representing a unique suite of climatic conditions (Ditlevsen et al., 1996; Peyron et al., 1998). This period, centered on 21 kyr cal BP, is characterized by the maximum volume of the ice sheet over Scandinavia and northern Europe, along with cold and generally arid conditions in northern and Western Europe. The LGM archaeological record is characterized by a relatively small number of sites and large gaps in the archaeological record for many regions (cf. Soffer and Gamble, 1990; Straus, 2005; Street and Terberger, 1999). Such a pattern has been interpreted to be the result of the human abandonment of northern Europe and a contraction of the human range to southern regions that served as refugia. Such contraction and consequent demographic reduction is known to have produced a bottleneck in human genetic diversity (Barbujani et al., 1998: p. 490; Torroni et al., 1998, 2001).

In Western Europe, between ca. 22 kyr and 20 kyr cal BP, human groups responded to LGM environmental conditions by developing a suite of new technologies characterized by a variety of diagnostic projectile points and knives produced by bifacial retouch (Fig. 1A), which define the Solutrean (Mortillet, 1873; Smith, 1966). Straus (2005) proposed that Solutrean populations employed more specialized subsistence systems, relative to earlier Upper Paleolithic technocomplexes, to exploit regions rich in game but under harsh climatic conditions.

In the regions of southeastern Europe, hunter-gatherers of the LGM produced a different lithic technology, termed the early Epigravettian (Laplace, 1964; Mussi, 2001), characterized by shouldered and backed projectile points produced by unifacial retouch (Fig. 1B). Leaf-shaped points are rare and have been recovered from only a few sites in northern Italy (Palma di Cesnola, 1990). Contrary to the Solutrean, which appears as a novel technology, the Epigravettian toolkit is interpreted as being derived from the preceding Gravettian technocomplex (Otte, 1990; Palma di Cesnola, 2001).

2. Materials and methods

For ECNM, we employed a machine-learning genetic algorithm originally developed for determining the ecological niches of plant and animal species (Stockwell, 1999; Stockwell and Peters, 1999). This software application, termed the Genetic Algorithm for Rule-Set Prediction (GARP), has been applied to topics as diverse as habitat conservation, effects of climate change on species' distributions, the geographic potential of species' invasions, and anticipation of emerging disease transmission risk (Adjemian et al., 2006; Martinez-Meyer et al., 2004; Peterson et al., 2004; Sánchez-Cordero and Martínez-Meyer, 2000; Soberón and Peterson,

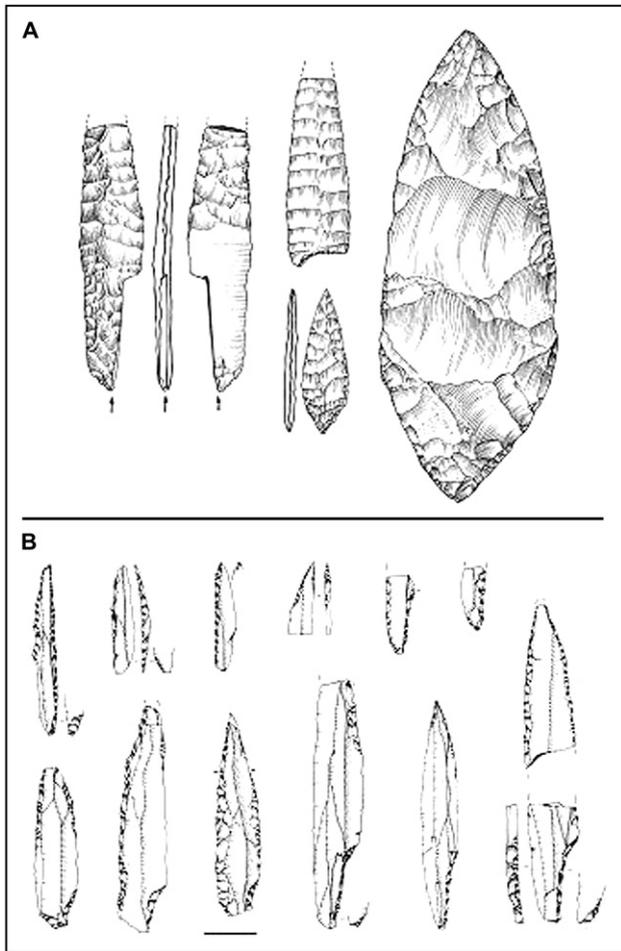


Fig. 1. (A) Examples of Solutrean projectile points. Drawings are not to scale (adapted from Smith, 1966); (B) Examples of Epigravettian projectile points recovered from Grotta di Paina. Scale bar is 1 cm (adapted from Palma di Cesnola, 2001).

2004). It is available for download at <http://www.lifemapper.org/desktopgarp/>.

GARP requires as input the geographic coordinates where the target species has been observed and raster GIS data layers summarizing environmental variables that may be involved in limiting the geographic distribution of the species. In our application, the occurrence data were the geographic coordinates of radiometrically dated and culturally attributed archaeological sites. These archaeological data were obtained from a database, compiled by FdE and MV, that contains the geographic coordinates, recorded stratigraphic levels, associated cultural affiliations, and >6000 radiometric ages from ca. 1300 archaeological sites in Europe.

The raster GIS data consisted of landscape attributes and high-resolution climatic simulations for the LGM. The landscape variables included slope, aspect, elevation, and compound topographic index (a measure of tendency to pool water) from the Hydro-1K data set (U.S. Geological Survey's Center for Earth Resources Observation and Science – <http://edc.usgs.gov/products/elevation/gtopo30/hydro/index.html>).

Typically, climatic simulations for specific periods of time are produced by forcing general circulation models (GCMs),

which reconstruct past, present, and future climates globally typically at resolutions where grid squares measure 100–200 km on a side. For instance, the LGM and the mid-Holocene have been the focus of coordinated experiments in the framework of the Paleoclimate Modelling Intercomparison Project (Harrison et al., 2002; Jousaume and Taylor, 1995; PMIP, 2000). In an effort to use climatic data that approach the same scale of resolution as our geographic data, we use in the present study a regional climatic simulation with a grid box size over Europe of ~ 60 km on a side, which was run at the Laboratoire des Sciences du Climat et de l'Environnement, Gif-sur-Yvette, France.

This high-resolution LGM atmospheric simulation followed the PMIP1 protocol (<http://www-lsce.cea.fr/pmip>), with sea-surface temperatures and sea ice cover as prescribed from the CLIMAP (1981) data set and the ice-sheets from the Peltier (1994) ICE-4G reconstruction. Atmospheric CO₂ concentration was lowered to 200 ppmv according to the ice-core record (Raynaud et al., 1993) and orbital parameters adjusted to 21,000 cal BP values (Berger, 1978). The results of this simulation have been compared to pollen-based climatic reconstructions, with fairly close agreement for summer and annual mean temperatures but some underestimation of winter cooling and drying over Western Europe and the Mediterranean (Jost et al., 2005). From this simulation, we derived the following variables for input into GARP: warmest month temperature, coldest month temperature, mean annual temperature, and mean annual precipitation (Fig. 2). The values of warmest and coldest months refer to the warmest/coldest month in a climatic cycle averaged over 10 yr of simulation.

In GARP, geographic locations of archaeological sites are resampled randomly by the algorithm to create training and test data sets. An iterative process of rule selection is then performed within the program's functioning, in which an inferential tool is chosen from a suite of possibilities (e.g., logistic regression and bioclimatic rules) and applied to the training data to develop specific rules (Stockwell, 1999). These rules maximize predictivity by using independent data to evaluate them. Predictive accuracy is evaluated based on the known presence data and a set of pseudoabsence points (i.e., points sampled randomly from among points across the region of study where the species has not yet been detected) (Stockwell, 1999). This evaluation process is used to develop a rule-set that defines the distribution of a species in ecological space (i.e., an ecological niche) (Soberón and Peterson, 2005), which can be projected onto the landscape to predict a potential geographic distribution (Peterson, 2003: p. 421; Stockwell, 1999; Stockwell and Peters, 1999). GARP has undergone extensive improvement and testing in recent years, including detailed sensitivity analyses (Peterson and Cohoon, 1999; Stockwell and Peterson, 2002a,b; Anderson et al., 2002).

We applied GARP to archaeological sites dated by AMS to the LGM, in an effort to minimize the possibility of incorporating sites for which radiometric determinations are underestimates of true ages, as has been shown to be common for older Upper Paleolithic technocomplexes that date to the temporal limits of radiocarbon methods (d'Errico and

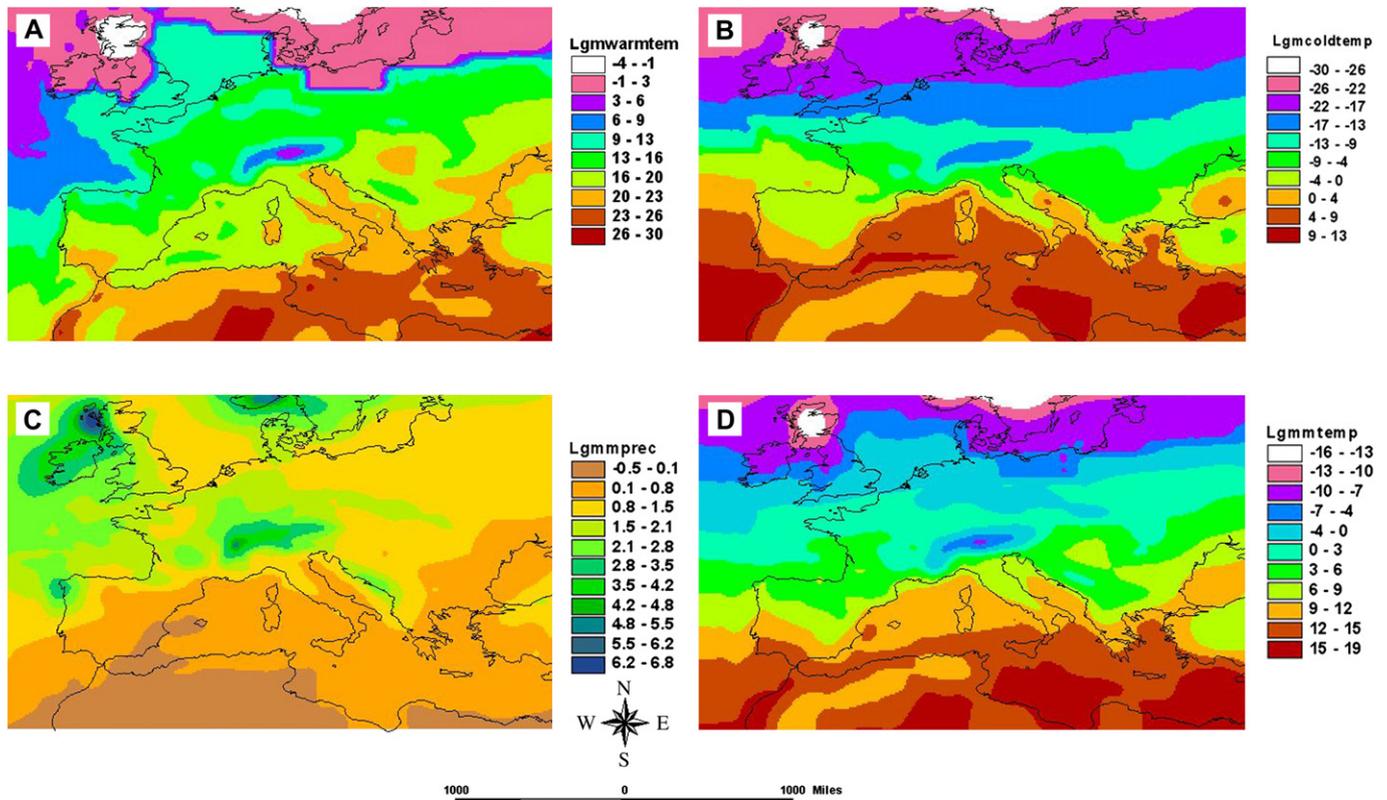


Fig. 2. High-resolution temperature and precipitation simulations for the Last Glacial Maximum (LGM) used in the GARP analyses: (A) warmest month temperature ($^{\circ}\text{C}$), (B) coldest month temperature ($^{\circ}\text{C}$), (C) mean annual precipitation ($\text{mm} \times 100$), (D) mean annual temperature ($^{\circ}\text{C}$). The values of warmest and coldest months refer to the warmest/coldest month in a climatic cycle averaged over 10 yrs of simulation.

Sánchez-Goni, 2003; Van der Plicht, 1999; Zilhão and d'Erco, 1999). The lack of agreement between conventional and AMS ages has been attributed by these authors to ineffective sample treatments, and the application of conventional ^{14}C counting methods to samples that fall near the limits of this dating method. While these factors should have a lesser impact concerning sites dated to the LGM, they still may be a source of error considering this period's relatively narrow time window. Fig. 3, presenting distributions of conventional and AMS ages from sites attributed to the Solutrean, indicates that such sources of error are present for ages during the LGM: conventional ages are slightly younger relative to AMS ages, suggesting that some underestimate the true age of their sites.

For this reason, the site samples used to create our Solutrean and Epigravettian ECNMs are composed primarily of sites radiometrically dated by AMS to the height of the LGM (defined here as 21 ± 1 kyr cal BP), and that contain diagnostic material assemblages associated with these technocomplexes (Table 1). AMS ages for sites assigned to the two technocomplexes of interest were calibrated using CALIB 5.0.2 html (Reimer et al., 2004; Stuiver et al., 2005). The geographic coordinates of those sites that fell within our targeted time frame were used as occurrence points. We included five undated sites in Italy reliably attributed to the early Epigravettian of the LGM based on their stratigraphic contexts and diagnostic material assemblages to increase sample size for this technocomplex.

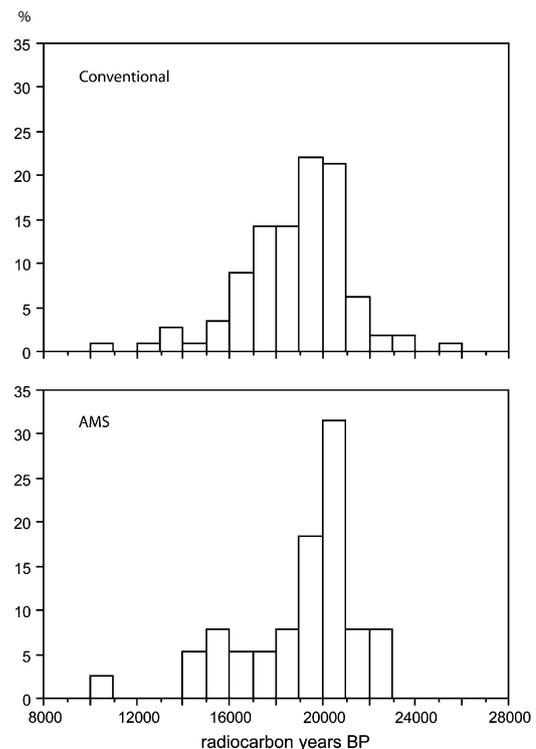


Fig. 3. Histograms of the percentages of uncalibrated conventional and AMS radiocarbon age determinations for the Solutrean technocomplex.

Table 1
Epigravettian and Solutrean sites used to produce eco-cultural niche models

Site	Culture	Long.	Lat.	Country	Code	Date	SD	Calib.	Type
Asprochaliko	Epigrav	20.75	39.19	Greece	OxA-775	18,000	300	21,365	AMS
Barma Grande	Epigrav	7.53	44.34	Italy	GifA-5072	17,200	180	20,333	AMS
Covolo Fortificato di Trene	Epigrav	11.55	45.44	Italy	UtC-2691	17,640	140	20,822	AMS
Riparo del Broion	Epigrav	11.6	45.48	Italy	UtC-10506	17,830	100	21,059	AMS
Ponte di Pietra	Epigrav	12.96	43.5	Italy	CRG-1019	18,515	618	21,959	AMS
Fosso Mergaoni	Epigrav	13.02	43.45	Italy	UtC-11551	18,160	240	21,583	AMS
Grotta dei Fanciulli	Epigrav	7.5	43.86	Italy	Diagnostics	LGM			n/a
Grotta della Cala	Epigrav	15.37	40.18	Italy	Diagnostics	LGM			n/a
Rip. Maurizio	Epigrav	13.65	42.01	Italy	Diagnostics	LGM			n/a
Grotta Tronci	Epigrav	13.65	42.05	Italy	Diagnostics	LGM			n/a
Rip. Del Sambuco	Epigrav	12.45	42.34	Italy	Diagnostics	LGM			n/a
Altamira	Solutrean	-4.12	43.38	Spain	GifA-90045	18,540	320	20,048	AMS
Caldeirao	Solutrean	-8.42	39.65	Portugal	OxA-2510	18,840	200	20,436	AMS
Combe Suaniere	Solutrean	0.16	45.14	France	OxA-488	17,700	290	20,940	AMS
Jean Blancs	Solutrean	0.49	44.86	France	GifA-97147	17,650	200	20,844	AMS
Grotte XVI	Solutrean	1.2	44.8	France	AA-2668	20,070	330	22,068	AMS
Buraca Escura	Solutrean	-8.73	39.98	Portugal	Gif-4585	18,040	230	21,421	Conv.
Placard	Solutrean	-0.03	45.8	France	GifA-91184	19,970	250	21,948	AMS
Solutre	Solutrean	4.31	46.38	France	CAMS-36630	19,720	70	21,676	AMS
Vale Almoinha	Solutrean	-9.4	39.08	Portugal	OxA-5676	19,940	180	21,932	AMS

The other exception to our site selection protocol is the Solutrean site of Buraca Escura. The conventional age from this site (Gif-4585) is very similar to the AMS ages from nearby Solutrean sites that, when calibrated, fall just outside the LGM time frame. In all, geographic coordinates for 11 Epigravettian and 9 Solutrean sites were used as input to produce the GARP models.

We used the following specifications in GARP. Given the random walk nature of the method, we ran 1000 replicate runs, with a convergence limit of 0.01. Given the small size of the samples, we used ca. 80% of occurrence points for developing training rules in each analysis and reserved one point for model selection and one for evaluating model predictive ability. We then followed a protocol for selecting among the resulting models (Anderson et al., 2003), with omission error (i.e., failure to predict a known presence) measured based on the single reserved model selection point (see above), and models retained only when they were able to predict that single point (i.e., hard omission threshold of 0%). Commission error, conversely, is a measure of areas of absence that are incorrectly predicted present (Anderson et al., 2003: p. 213). We followed recommendations of removing from consideration those 50% of models that show extreme values of proportional area predicted present. The resulting final ‘best-subset’ models ($N = 10$ for each technocomplex) were then summed to produce a best estimate of the potential geographic distribution for each technocomplex. This same procedure was used with all sites combined, regardless of cultural affiliation, to predict potential human range during the LGM.

Predictive models such as ECNMs are just that – predictions. As such, ECNMs must be tested for predictive accuracy before they can be interpreted. Given low occurrence data samples, we tested model predictions using the jackknife manipulation proposed by Pearson et al. (2007), which is the only robust test for evaluating models based on small samples.

Here, we used the single point set aside for evaluating model predictivity: if N occurrence points are available, $N - 1$ points are used to develop N jackknifed models. The success of each replicate model in predicting the single point that was omitted, relative to the proportional area predicted present, is then calculated using an extension to the cumulative binomial probability distribution (Pearson et al., 2007).

To evaluate whether the two technocomplexes reflect adaptations to different ecological regimes, we compared their respective ecological niches. First, we performed a Principal Component Analysis using *Statistica* 7.1 on the climatic and geographic variables’ values for the grid squares with a predicted presence for all 10 GARP best-subset models. Based on the results, described below, the values for mean annual precipitation, mean annual temperature, coldest month temperature, and warmest month temperature of these best-subset grid squares were plotted against all the available climatic data of the LGM simulation.

3. Results

The model produced using both Solutrean and Epigravettian sites identifies a clear northern boundary for potential human range during the LGM (Fig. 4), which is also reproduced in the models for each separate technocomplex (Fig. 5). This boundary follows the Loire valley in France, excludes the Massif Central, includes the Mediterranean regions of France, follows the southern limit of the Alps, and the northern limits of the Carpathian range (Fig. 4).

The territories predicted for the Solutrean and the Epigravettian are presented individually in Fig. 5. The Solutrean model predicts potential presence of human groups associated with this culture in southwestern and southern France, northwestern portions of the Iberian Peninsula, the Ebro valley, and in disjunct areas of Cantabria, northwestern Italy, and

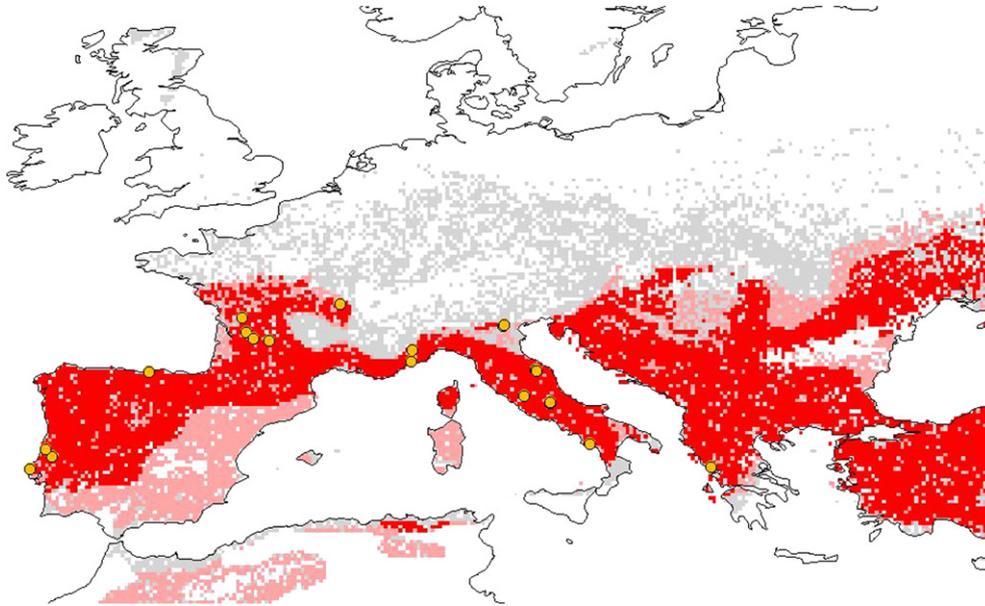


Fig. 4. GARP prediction based on both Solutrean and Epigravettian sites dated to 21 ± 1 kyr cal BP. Grid squares with 1–5 of 10 models predicting the presence of an eco-cultural niche are indicated in grey, grid squares with 6–9 models in agreement are depicted in pink, and squares with all 10 models in agreement are indicated in red. Archaeological site locations (i.e. GARP occurrence points) are indicated by yellow circles.

the Balkans. The model for the Epigravettian predicts a potential presence of this culture in the Balkans, the Italian Peninsula excluding the most southerly regions, the Mediterranean regions of France as well as the Aude and Garonne corridors, and the Iberian Peninsula excluding its southern regions. That these models have high predictive power regarding potential human distributions is shown by the accuracy observed in the jackknife manipulations. The independent test point was correctly predicted in 7 of the 9 jackknife models for the Solutrean and in all 11 models for the Epigravettian, with associated probabilities of $P = 0.00005$ and $P < 0.00001$, respectively.

Although potential distributions predicted for these two technocomplexes show only minimal overlap geographically, conclusions of ecological differentiation are complex. These models are geographic projections of ecological niches defined by multiple environmental variables, so small differences between ecological niches can result in different potential geographic distributions when ecological differences correspond to environmental conditions present over large regions.

A Principal Component Analysis of the environmental variables indicated that overall environmental variability in the study area is satisfactorily explained (85%) by the first two components, which are most influenced by the different temperature variables associated with each technocomplex's predicted distribution. Plotting the climatic variables' values of the grid squares where all best-subset models predicted potential presence against all of the available climatic data (Fig. 6) showed that the ecological niches occupied by the two technocomplexes overlap broadly, with only slight differences on the edges of their predicted niches. These differences indicate that the Solutrean technocomplex had the potential to occupy somewhat cooler and more humid environments than the Epigravettian. *T*-tests performed on these data matrices to compare the two technocomplexes were

uniformly significant ($p \ll 0.05$), indicating that the Solutrean and Epigravettian niches are not drawn from the same population.

4. Discussion

The northern limits of the human range predicted by ECNM for the LGM (Fig. 4) are arguably accurate. These limits are consistent with the known distribution of archaeological sites for this period (Bocquet-Appel et al., 2005; Demars, 1996; Soffer and Gamble, 1990). The only radiometrically dated site for our temporal range that seemingly contradicts our results is that of Wiesbaden-Igstadt (Street and Terberger, 1999), which has yielded seven AMS ages from a single occupation level ranging from 19,320 to 17,210 BP. Street and Terberger (1999: p. 267) think that these ages collectively represent the true age of the site but acknowledge, however, that uncertainties (e.g., contamination) could exist. When calibrated, two of these dates (UZ-3768 and OxA-7500) fall within our LGM window, but they are appreciably younger than the other calibrated dates from the same level suggesting that they underestimate the true age of the occupation. This interpretation is supported by the fact that when these two ages are averaged ($t_{\text{ave}} = 17,356 \pm 118$ BP) using the method described by Long and Rippeteau (1974), and compared to the next youngest age (OxA-7501), the null hypothesis of no difference is rejected ($t = 4.0143$, $P < 0.001$). Because the younger and older ages from Wiesbaden-Igstadt cannot be considered to be drawn from the same statistical population, and the older ages fall before the LGM when calibrated, we hesitate to accept that this site represents an LGM human occupation of the Central Rhineland. Wiesbaden-Igstadt probably dates to Dansgaard–Oeschger Interstadial 2 to which Shackleton et al. (2004: p. 1515) assign an age of 19.62 ± 0.21 kyr BP.

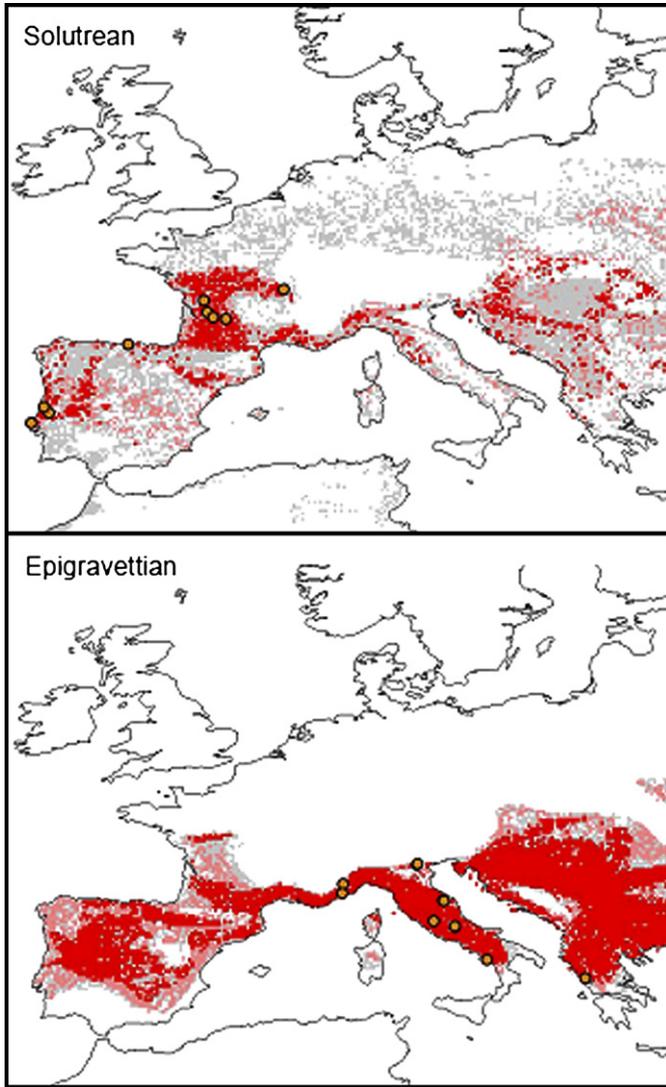


Fig. 5. Eco-cultural niche models for the Solutrean and Epigravettian technocomplexes at the Last Glacial Maximum. For each technocomplex, grid squares with 1–5 of 10 models predicting the presence of an eco-cultural niche are indicated in grey, grid squares with 6–9 models in agreement are depicted in pink, and squares with all 10 models in agreement are indicated in red. Archaeological site locations (i.e. GARP occurrence points on which the models were based) are indicated by yellow circles.

One might argue that the site samples used in our study are not representative of human population distributions, especially with respect to northern limits, during the LGM. In other words, some regions may have been only sporadically occupied leaving undetectable archaeological signatures. Such an argument is contradicted by statistical analyses (Bocquet-Appel et al., 2005) that convincingly show that the frequencies and distributions of recorded archaeological sites in Europe are representative, when considered with an appropriate taphonomic perspective, of prehistoric population distributions. Considering these arguments, the northern latitudinal limits of human occupation during the LGM indicated by our ECNM predictions represent accurate estimates of the areas occupied by hunter-gatherers during this period.

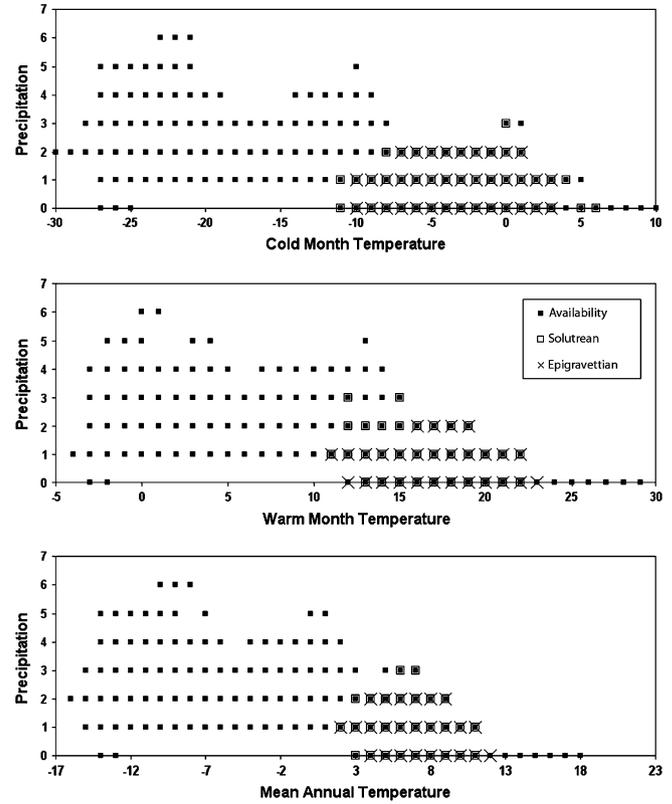


Fig. 6. Plots of Solutrean and Epigravettian ecological niches based on simulated LGM coldest month temperature (°C), warmest month temperature (°C), mean annual temperature (°C), and mean annual precipitation (mm × 100).

Interestingly, the northern range of the GARP predictions corresponds to the southern boundaries of periglacial environments in Western and Central Europe (Huijzer and Vandenberghe, 1998; Lautridou and Sommé, 1981). The GARP limits in France follow closely those that separated regions characterized by continuous deep permafrost [depths of 50–600 m (van Vliet-Lanoë, 2005: p. 94)] and continuous permafrost (Fig. 7) (van Vliet-Lanoë et al., 2004). The limits predicted by the ECNM for southern France, Iberia, and Italy generally follow the boundary between continuous and discontinuous permafrost (Texier, 1996; van Vliet-Lanoë, 1996). Such correspondence strengthens arguments for the predictive power of our modeling approach since periglacial environments have low biomass, which may have prevented systematic utilization by prehistoric human groups.

The geographic distributions predicted by the ECNMs for the Solutrean and Epigravettian show only minimal overlap (Fig. 5), suggesting that the populations associated with these two technocomplexes were to some degree adapted to different environments. Reconstructions of their ecological niches indicate that they overlap broadly, but that Solutrean populations were able to exploit colder and more humid areas, corresponding to areas with permanent permafrost during the LGM. In contrast, Epigravettian populations seem to have been more adapted to areas dominated by discontinuous permafrost and seasonal freezing. Neither technocomplex is associated with

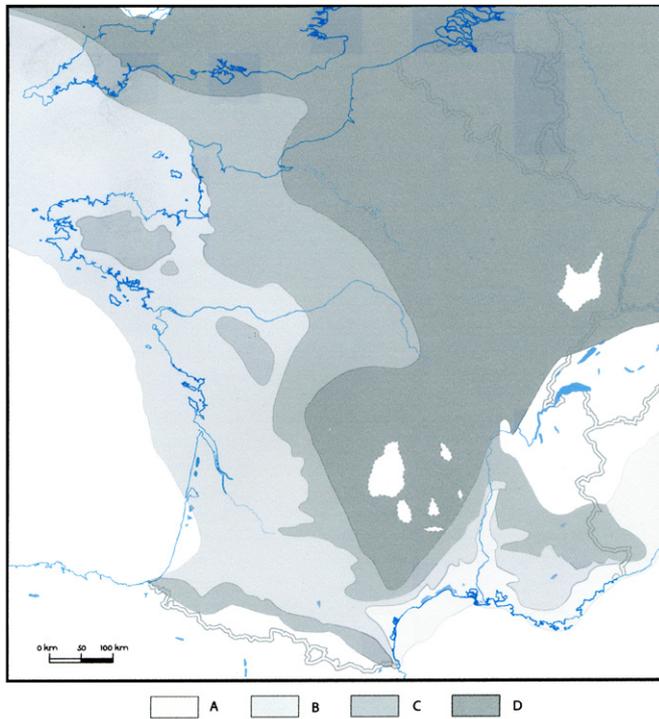


Fig. 7. Reconstructed limits of continuous and discontinuous permafrost conditions in France during the LGM (adapted from van Vliet-Lanoë et al., 2004: p. 105): (A) deep seasonally frozen, (B) discontinuous permafrost, (C) continuous permafrost, (D) continuous deep permafrost.

the more southerly, dry, and relatively warmer Mediterranean environments during the LGM.

It is important to point out that GARP identifies the potential ecological niche for a population and not necessarily the actual distribution as determined by cultural and historical contingencies. With respect to the correspondence between predicted and actual geographic ranges, the relatively restricted potential geographic distribution for the Solutrean corresponds well to this technocomplex's archaeological distribution. In contrast, the Epigravettian ECNM prediction exhibits a potential range across southern France and Spain that is not corroborated archaeologically. This phenomenon is common (Peterson, 2003) when species' predicted ecological niches are projected across broad geographic areas: habitable areas are frequently predicted outside their observed range. Four factors are generally cited to account for such discordances: (1) limited dispersal, (2) speciation, (3) extinction on regional scales, and (4) competitive exclusion (Peterson, 2003: pp. 422–423). Limited dispersal refers to the inability of a species to occupy other regions due to physical mobility constraints, which does not seem to apply to the Epigravettian populations since coastal corridors were open and habitable during the LGM and would have allowed them to colonize western territories. Speciation also is not a factor since human populations that occupied Europe at the end of OIS 3 and during OIS 2 arguably belonged to the same species. Likewise, regional extinction is not applicable, as it implies that Epigravettian populations were present in those regions before the

LGM, but went extinct before its onset. The archaeological record demonstrates that such is not the case.

Of the factors proposed by Peterson (2003), competition may explain the discordance between actual and predicted Epigravettian distributions since GARP only models the potential niche of one population at a time. The competition hypothesis implies that Epigravettian populations could not occupy suitable regions of Western Europe, such as the northern Iberian Peninsula, because it would have been necessary to cross large areas occupied by competing human groups bearing a different cultural tradition, the Solutrean. This idea raises the question of why such competition would create a boundary between human groups, instead of resulting in occupation of the entire potentially exploitable geographic area by only one of them.

In the case of a biological species, the reasons that create a boundary between competing species are mainly ecological (MacArthur, 1972; Hutchinson, 1978). With humans, other factors can play roles in creating boundaries between groups. Contrary to most animal species, the carrying capacity of a human population is directly linked to its ability to maintain and transmit between generations not only a suitable technical system, but also a complex and dynamic set of social rules, cultural and religious values, systems of symbols, language, and ethnic identity. The geographic extent over which this heritage can be maintained may vary according to the nature of each human culture but is also highly dependent, particularly for hunter-gatherers, on ecological constraints. Nettle (1998) demonstrated convincingly that the geographic extent of linguistic entities increases in regions of high ecological risk, where ecological risk is defined as the amount of variation which people face in their food supply over time (seasonally or inter-annually). Collard and Foley (2002) argued that cultural diversity decreases towards higher latitudes. Both studies attribute this pattern to the need to create long-distance social networks to increase the ability of human groups to survive in hostile environments. Limits to the expansion of such cultural and linguistic entities are thus arguably dictated by the need to maintain a degree of cultural and linguistic cohesiveness over these large ranges. The reconstructed ecological niches and their geographic projections for the two technocomplexes suggest that they occupied regions associated with different levels of ecological risk. Solutrean populations principally exploited regions characterized by colder and more humid conditions than those occupied by Epigravettian groups.

Good agreement exists between the predicted eco-cultural range for the Solutrean technocomplex and its actual archaeological distribution. We contend that Solutrean populations faced relatively high levels of ecological risk and consequently occupied as much of the potential geographic distribution allowed by their cultural adaptation as possible. Geographical barriers such as the Pyrenees and the Cantabrian range apparently were not obstacles to the occupation of their entire niche. In contrast, Epigravettian populations showed marked differences between potential and actual distributional areas. We suggest that Epigravettian groups faced lower levels of ecological risk and thus did not need to extend spatially as broadly.

Additionally, the potential geographic range predicted by the ECNM for the Epigravettian technocomplex during the LGM is restricted to a latitudinal band determined by geographic barriers (western Alps and Pyrenees) – given the narrowness of the European Mediterranean coastline, corridors between areas suitable for Epigravettian groups would have been restricted. Such irregular potential distributional areas would certainly have constituted major obstacles to maintenance of viable cultural and linguistic networks across these regions. These restrictions were probably more effective between the Italian and Iberian Peninsulas than between the Italian Peninsula and the Balkans owing to the broad Adriatic plain created by low sea levels during the LGM (Antonioli et al., 2004; Lambeck et al., 2004). This difference certainly facilitated exchange between populations of the Italian Peninsula and southeastern Europe, as supported by Epigravettian affinities to LGM industries of the Balkans (Montet-White, 1996: pp. 121–122).

5. Conclusions

ECNM is an effective approach by which to characterize and quantify eco-cultural niches associated with specific technocomplexes, and better understand how environmental factors influenced distributions of prehistoric human populations. Future research must focus on methods that can be used to evaluate more precisely the roles of competition and cultural cohesiveness in producing discords between predicted and actual ranges. The role of geography in constraining niches and creating cultural boundaries must be specifically targeted. Comparisons between the extent and location of niches occupied by populations associated with specific technocomplexes under similar climatic and environmental conditions may allow us to better disentangle the influences of environmental and cultural factors. It also would be useful to apply these techniques to animal species of the LGM and other climatic episodes to evaluate whether or not their predicted ecological niches were associated with those of humans. Finally, the application of ECNM to historically documented hunter-gatherers, for which detailed cultural and environmental data are available and cultural dynamics have been directly observed, would be instrumental in interpreting predictions based on archaeological and paleoclimatic data.

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Neanderthal Extinction by Competitive Exclusion

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Abstract

Background: Despite a long history of investigation, considerable debate revolves around whether Neanderthals became extinct because of climate change or competition with anatomically modern humans (AMH).

Methodology/Principal Findings: We apply a new methodology integrating archaeological and chronological data with high-resolution paleoclimatic simulations to define eco-cultural niches associated with Neanderthal and AMH adaptive systems during alternating cold and mild phases of Marine Isotope Stage 3. Our results indicate that Neanderthals and AMH exploited similar niches, and may have continued to do so in the absence of contact.

Conclusions/Significance: The southerly contraction of Neanderthal range in southwestern Europe during Greenland Interstadial 8 was not due to climate change or a change in adaptation, but rather concurrent AMH geographic expansion appears to have produced competition that led to Neanderthal extinction.

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Introduction

Climate changes unquestionably influenced Paleolithic hunter-gatherer adaptations, and particular attention has been paid to possible climatic influences on Neanderthal extinction and colonization of Europe by anatomically modern humans (AMH) [1–4]. Reasons behind Neanderthal extinction, however, are still debated intensively. Two competing hypotheses contend either that Neanderthals were unable to adapt to climatic changes towards the end of Marine Isotope Stage 3 (MIS3) or that competition with AMH was the driving factor in their extinction.

MIS3 (60–30 kyr cal BP), marked by many of the largest and quickest temperature excursions of the last glacial period [5], was characterized by an ice sheet of intermediate size and intermediate atmospheric CO₂ concentrations. MIS3 was punctuated by periods, called Heinrich events [6], during which massive discharges of icebergs into the Northern Atlantic Ocean resulted in near shut-down of the Atlantic Meridional Overturning Circulation [7]. Associated decreases in mid-latitude North Atlantic sea surface temperatures had marked rapid impacts on continental climate and vegetation. Greenland Interstadials (GI; mild phases) were characterized in Western Europe by open forest landscapes, while herbaceous-dominated landscapes existed during Greenland Stadials (cold phases) [8]. The environmental conditions associated with such phases, and the rapid and marked transitions between them, likely affected the distributions and adaptations of human populations.

Considerable discussion has surrounded the disappearance of Neanderthals and the spread of AMH, with debate focused on a number of specific issues: (a) relationships between particular stone tool technologies, or archaeologically-defined cultures (termed technocomplexes), and the human populations who made them (i.e., Neanderthals or AMH); (b) possible cultural interactions between these two human populations; (c) mechanisms behind Neanderthal extinction; and (d) timing of this population event.

With respect to the authorship of archaeological assemblages dated to ~43–35k calibrated (calendar) years ago (kyr cal BP), consensus exists that, in Europe, Mousterian technocomplexes were solely manufactured by Neanderthals [cf. 9, 10]. Most agree that the Châtelperronian, the only 'transitional technocomplex' associated with diagnostic human remains was also made by Neanderthals [11–13] —we assume this to be the case for the Bohunician [14] —, and that the typical Aurignacian technocomplex should be attributed to AMH [cf. 2, 15].

Intense debate has focused on possible cultural interactions between Neanderthal and AMH populations. Reappraisals of key sites have challenged the existence of a diagnostic Aurignacian older than ~41 kyr cal BP in Western Europe [16,17] and have shown that the Châtelperronian, previously interpreted as representing acculturation of Neanderthals by AMH immigrants, is almost certainly older than the first Aurignacian [18,19]. This assertion is consistent with the fact that the most recent reliably dated Mousterian sites in France are not younger than ~40.5 kyr cal BP [20] and that the Châtelperronian does not post-date

~40.5–39 kyr cal BP [19]. Although this timeline is now supported widely [21,22], some still consider the evidence ambiguous [23,24], and others support the idea of an early colonization of Europe by AMH at ~43 kyr cal BP, with subsequent acculturation of late Neanderthal populations prior to their extinction [4,9,25–28]. Some have also suggested the possibility of Neanderthal biological input, albeit undetected by genetic studies [29–32], to the first wave of AMH colonizers [2,33,34].

Considerable research links Neanderthal decline and extinction with MIS3 environmental variability, in particular regarding population dynamics during specific Dansgaard-Oeschger (D-O) climatic phases. Consensus exists that Neanderthal populations persisted in southern Europe, particularly in southern Iberia, well after they had disappeared from northern latitudes, and that environmental conditions briefly created a geographic barrier between them and AMH called the Ebro Frontier [35].

Diverse methodological approaches have been used to integrate paleoclimatic, chronological, and archaeological datasets [36,37] in efforts to understand human population dynamics during this period, and discussions have also focused on limitations of radiocarbon dating [24,38–41]. By correlating palynological data from deep sea cores with archaeological data, it has been proposed that AMH were present in Western Europe and northern Iberia just prior to Heinrich event 4, that conditions during Heinrich event 4 delayed their colonization of southern Iberia, and that subsequent competition with AMH drove Neanderthal extinction after this climatic episode [20]. A very late (~32 kyr cal BP) survival of Neanderthals in southern refugia, based on dates from Gorham's Cave, Gibraltar, has been proposed [42], and an even later disappearance (22.5–25.5 kyr cal BP) has been suggested recently [43]. This last proposal contends that D-O variability did not have a significant impact on this region, but rather that the long-term trend towards less favorable environmental conditions stressed Neanderthals to extinction, with little or no impact of competition with AMH. Such an idea, however, is contradicted by high-resolution climatic and vegetation simulations for Heinrich event 4 [44], which suggest development of semi-desert conditions in central and southern Iberia that impacted Neanderthal populations and delayed AMH settlement and consequent competition.

Creating a consensual chronological framework for the Middle-to-Upper Paleolithic transition is complicated by limitations of radiocarbon dating, uncertainties in radiocarbon comparison curves, and fluctuations in ^{14}C levels [38,39]. Recent dating methods have shown that ages from many previously dated samples underestimate true ages [40,41], and disagreements exist on cultural attributions assigned to archaeological levels at key sites. These discussions are complicated by the fact that correlating cultural and climatic events during MIS3 is difficult because the former are in radiocarbon years while some of the latter are in calendar years and often span relatively short periods of time (~1500 yr). Only recently have systematic efforts been made to overcome these limitations, either by correlating archaeological data directly with long, radiocarbon-dated climatic sequences [20,36] or by using comparison curves to 'calibrate' radiocarbon ages before correlating them with paleoclimatic sequences [26,45].

Here, we apply a new method that incorporates a variety of diverse data sets to reflect on this important population event to evaluate the climate versus competition hypotheses for Neanderthal extinction. Recent advances in biodiversity studies [46] have developed tools for estimating ecological niches of species and predicting responses to environmental changes. These tools were originally developed to estimate ecological niches of species and

predict responses to environmental changes. It has been recently shown that they have considerable potential for reconstructing eco-cultural niches of past human populations [47], defined as the potential range of environmental conditions within which a human adaptive system can exist without having to undergo significant change. Our assumption is that human adaptive systems, defined here as the range of technological and settlement systems shared and transmitted by a culturally cohesive population within a specific paleoenvironmental framework, can be considered to operate as a 'species' with respect to their interaction with the environment. This does not imply, however, that human adaptive systems necessarily remained stable over time, as might be the case with animal species occupying narrow and stable niches. Humans can change their adaptive systems rapidly through technical and social innovations in response to environmental change. We know, however, that this was not the case during the late Middle and Upper Paleolithic, periods during which specific human adaptive systems spanned a number of climatic events. Thus, the method described in this study is particularly relevant for addressing issues of human adaptive system stability and eco-cultural niche stability. Another advantage of this methodology is that it can help identify mechanisms (i.e. niche conservatism, niche contraction, etc.) behind changes occurring across time and space in the relationship between adaptive systems and environments by projecting a reconstructed human eco-cultural niche into a different paleoenvironmental framework.

We focus on the three climatic phases during which the bulk of AMH colonization of Europe and Neanderthal contraction (if not extinction) occurred: Greenland Interstadials 9–11 (pre-H4; 43.3–40.2 kyr cal BP, see [48]), Heinrich event 4 (H4; 40.2–38.6 kyr cal BP), and Greenland Interstadial 8 (GI8; 38.6–36.5 kyr cal BP). GI9–11 were three short-term mild events separated by two brief periods of cooling. They were marked by relatively wet conditions in Atlantic regions of Europe and comparatively drier conditions in western Mediterranean regions. H4 was marked in the western Mediterranean by extremely cold and dry conditions resulting in semi-desert vegetation, but was not so arid farther north with a consequent expansion of grasslands. GI8 was a relatively long phase with mild, moist conditions along Atlantic margins, which led to a weak development of deciduous forests. In western Mediterranean regions, warm, dry summers and moist winters created an open Mediterranean forest [8].

Here, we apply the approach termed eco-cultural niche modeling (ECNM; see *Materials and Methods* below) [49], to late Neanderthal and early AMH adaptive systems to define and characterize eco-cultural niches associated with these populations for each relevant climatic event, evaluate whether these niches changed during the Middle-to-Upper Paleolithic transition, and evaluate whether climate change or competition with AMH caused Neanderthal extinction.

Results

The ECNM for the pre-H4 Neanderthal adaptive system (Figure 1A) shows a potential distribution across ~40°–~50°N latitude, excepting the Alps and the Po and terminal Danube River plains. Suitability in Mediterranean regions is generally estimated as lower. Climatically, the predicted niche occupies a mean annual temperature range of -1° – $+12^{\circ}\text{C}$ and precipitation of <1095 mm/yr. The pre-H4 niche for AMH (Figure 1B) does not extend as far north as that of Neanderthals (Figure 1A), includes a tongue of potential distributional area extending into southeastern Iberia, and lacks suitable areas in southwestern

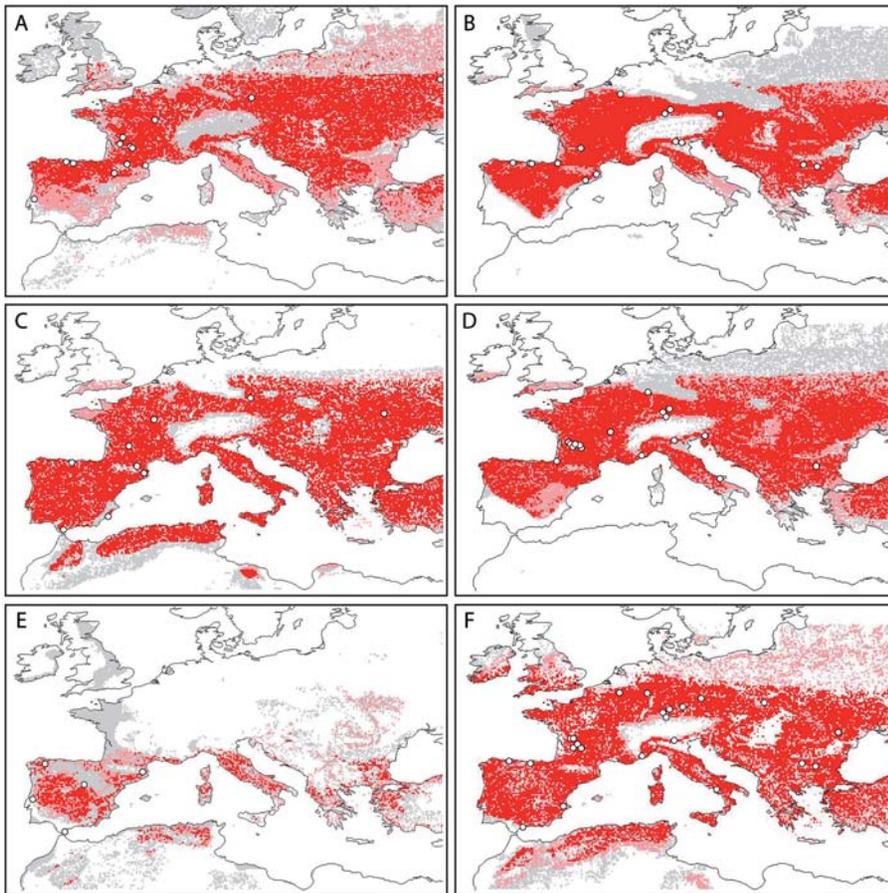


Figure 1. Maps of geographic projections of conditions identified as suitable by eco-cultural niche models for Neanderthals (A – pre-H4, C – H4, E – GI8) and AMH (B – pre-H4, D – H4, F – GI8). Grid squares with 1–5 of 10 models predicting presence of suitable conditions are indicated in grey, grid squares with 6–9 models in agreement are depicted in pink, and squares with all 10 models in agreement are indicated in red. Archaeological site locations are indicated with circles.
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Iberia. The pre-H4 AMH niche occupies a slightly narrower temperature range, but with precipitation values virtually identical to those of Neanderthals. The H4 Neanderthal potential distribution (Figure 1C) is reconstructed as occupying the entire Iberian, Italian, and Balkan peninsulas, with sharply defined northern limits, covering mean annual temperatures of 0–10°C and precipitation <730 mm/yr. The H4 AMH distribution (Figure 1D) again did not include southwestern Iberia, but has northern range limits and environmental ranges similar to those of the H4 Neanderthal adaptive system. The Neanderthal GI8 model, however, indicates a dramatically reduced potential distributional area, restricted to Mediterranean regions (Figure 1E). This niche occupies a mean annual temperature of 6–14°C with precipitation of <730 mm/yr. In contrast, the AMH GI8 model (Figure 1F) covers most of central and southern Europe, including a broader temperature (0–15°C) and precipitation (<1095 mm/yr) range than the contemporaneous Neanderthal niche. Principal component analyses performed on all the environmental variables associated with each of the six ECNMs all indicated that temperature variables were the most important in defining ranges of both adaptive systems. Almost all models showed significant predictive ability based on jackknife manipulations within time periods (all $P < 0.05$, except for H4 and GI8 Neanderthals, the periods with smallest sample size and most restricted distributions).

Neanderthal ECNM niche projections were able to predict the distribution of this adaptive system from pre-H4 to H4 and H4 to GI8 (Table 1) better than random expectations ($P < 0.05$). This result suggests that Neanderthals exploited the same eco-cultural niche across the three climatic phases, or at least that the niche had not shifted dramatically. For AMH as well, inter-period projections were statistically significantly interpredictive (Table 1). Niche breadth is similar between the two adaptive systems for pre-H4 and H4; however, during GI8, AMH niche breadth increases markedly but Neanderthal niche breadth decreases considerably (Figure 2).

Discussion

Our results highlight a reduction of potential Neanderthal range from pre-H4 through GI8, in terms of both ecology and geography. Two contrasting explanations were discussed above: (1) a contracting geographic footprint of the same niche in response to changing climate, versus (2) competition with expanding AMH populations. The first hypothesis implies that Neanderthals exploited the same ecological niche throughout the three climatic phases but had reduced geographic potential as the spatial manifestation of that niche contracted due to climate change. This scenario, however, can be rejected because the H4 to GI8 projection shows that the climatic shift to warmer and wetter

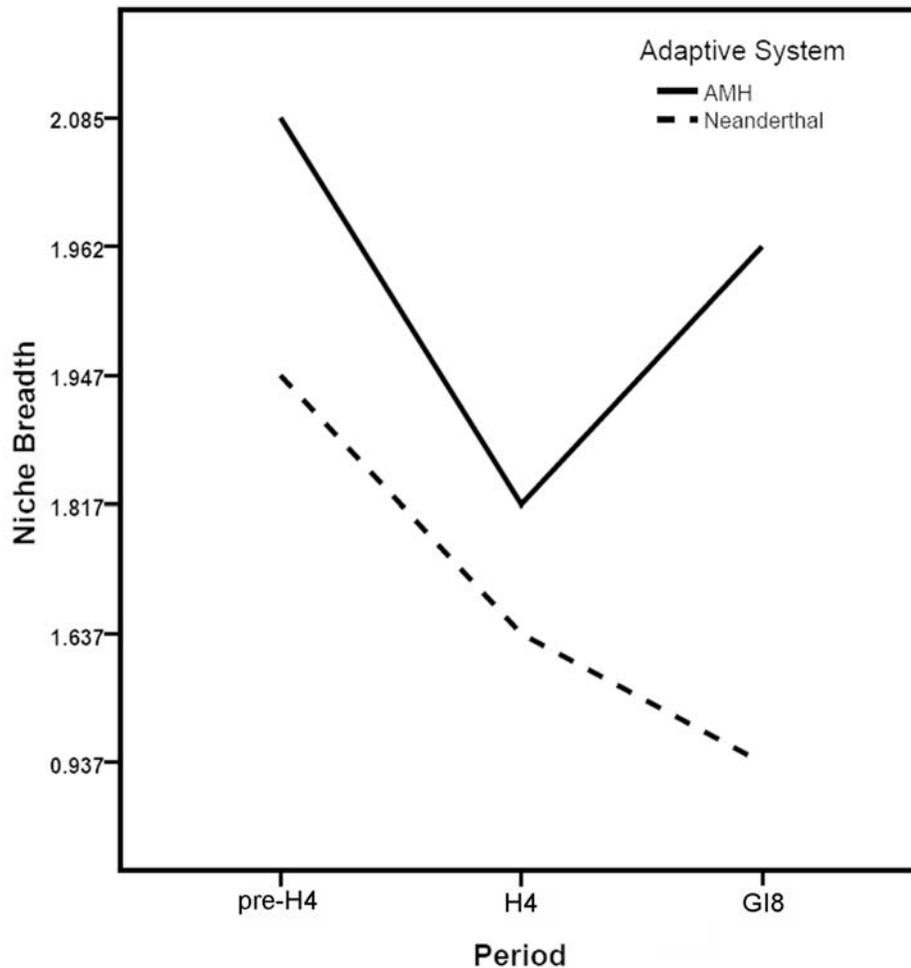


Figure 2. Summary of niche breadth measures for Neanderthal and AMH adaptive systems during each of the three climatic phases examined.

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conditions during GI8 anticipated a broader distributional area (Figure 3). This result indicates that only a small part of Neanderthal potential range was exploited during GI8, and that this reduced range was not a result of a contracting suitable climatic footprint, contradicting recent proposals that Early Upper Paleolithic populations reduced their niche due to environmental stress [50].

Our results indicate instead that competition with AMH represents a more cogent explanation for the situation. Predicted niches and potential geographic distributions for Neanderthal and AMH adaptive systems overlap broadly during pre-H4 and H4, except that southern Iberia was not within the distributional potential of AMH, lending support to the notion that the Ebro Frontier resulted from ecological causes. During GI8, however,

Table 1. Results of tests of predictivity among three climatic phases for Neanderthal and AMH eco-cultural niche model projections.

Comparison	All models predict			Most models predict			Any model predicts		
	Proportional Area	Success	<i>P</i>	Proportional Area	Success	<i>P</i>	Proportional Area	Success	<i>P</i>
Neanderthal pre-H4 predicts H4	0.2303	1/9	0.6499	0.3798	4/9	0.2259	0.584	8/9	0.0079
Neanderthal H4 predicts GI8	0.4599	3/5	0.1415	0.5651	4/5	0.0576	0.6452	4/5	0.1118
AMH pre-H4 predicts H4	0.2498	11/17	0.0001	0.3463	12/17	0.0005	0.432	13/17	0.0011
AMH H4 predicts GI8	0.3616	15/24	0.0023	0.4637	20/24	0.00003	0.6003	21/24	0.0007

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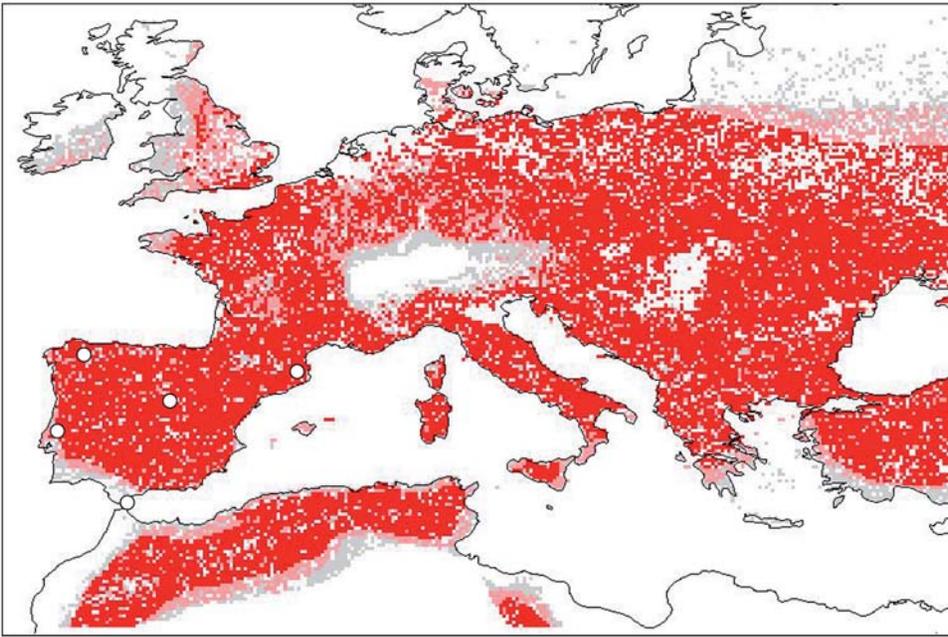


Figure 3. Projection of the H4 Neanderthal model onto GI8 climatic conditions. Grid squares with 1–5 of 10 models predicting presence of suitable conditions are indicated in grey, grid squares with 6–9 models in agreement are depicted in pink, and squares with all 10 models in agreement are indicated in red. Neanderthal sites dated to GI8 are indicated with circles.
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AMH niche breadth and potential distribution broadened, permitting AMH exploitation of the last Neanderthal refugium. The AMH expansion and Neanderthal contraction of niche characteristics were concurrent, and we suspect causally related. It follows that there was certainly contact between the two populations, which may have permitted both cultural and genetic exchanges. Our findings clearly contradict the idea that Neanderthal demise was mostly or uniquely due to climate change [51] and looks towards AMH expansion as the principal factor. Hence, we contend that AMH expansion resulted in competition with which the Neanderthal adaptive system was unable to cope.

Materials and Methods

To reconstruct eco-cultural niches, we used the Genetic Algorithm for Rule-Set Prediction (GARP) [52], which has been applied to topics as diverse as habitat conservation, the effects of climate change on species' distributions, the geographic potential of species' invasions, and the geography of emerging disease transmission risk [53–57]. It is available for free download at <http://www.nhm.ku.edu/desktopgarp/>. For data inputs, GARP requires the geographic coordinates where the target species has been observed and raster GIS data layers summarizing landscape and climatic dimensions potentially relevant to shaping the distribution of the species.

In this case, the 'species' is a technological adaptive system. Here, the occurrence data are the geographic coordinates of radiometrically dated and culturally attributed archaeological sites. These archaeological data were obtained from a database [58] containing the geographic coordinates, recorded stratigraphic levels, and cultural affiliations associated with ~6000 radiometric ages from ~1300 archaeological sites across Europe. The late Middle Paleolithic and early Upper Paleolithic technocomplexes date to the temporal limits of radiocarbon methods, making their ^{14}C determinations particularly sensitive to contamination by more recent carbon sources, resulting in frequent underestimation

of true ages of samples [16,20,40,59,60]. For this reason, we restricted the site samples used to create our pre-H4, H4, and GI8 ECNMs to sites dated by accelerator mass spectrometry (AMS) and containing diagnostic archaeological assemblages from stratified contexts, with a single exception (Table S1). Some AMS ages have relatively large associated errors such that it is difficult, if not impossible, to be sure that they date an occupation during a specific climatic event. Such ages were eliminated from consideration for this study. Also, it has been shown that a number of ages come from archaeological levels that have likely been disturbed by post-depositional site formation processes and it is unclear if the dated material was originally associated with the archaeological level from which it was recovered [see 45]. In these instances as well, the AMS ages in question were not used in this analysis. These quality-control steps minimize the possibility of incorporating sites for which radiometric determinations are minimum ages, and increase the likelihood that dates reflect a human presence during a specific climatic event. We employed CalPal [61] (using the recent Greenland-Hulu comparison curve [62]) to calibrate the age determinations and assign them to specific climatic phases.

It has been proposed [24] that any use of radiocarbon ages for this time period should be considered provisional see also [63]. We do not think, however, that a careful and consistent selection of dates will necessarily result in erroneous or misleading conclusions. Additionally, our method of testing model predictivity (see below) allows us to identify sites inconsistent with the remainder of the sample attributed to a particular climatic phase. In short, we need to test the pertinence of new methodological approaches on the available archaeological and chronological datasets so that heuristic tools will be in place as new data emerge.

The environmental data sets consisted of topographic/landscape attributes (assumed to have remained constant) and high-resolution climatic simulations for the three climatic phases considered here. Landscape variables included slope, aspect, and

compound topographic index (a measure of tendency to pool water) from the Hydro-1K dataset (U.S. Geological Survey's Center for Earth Resources Observation and Science - <http://edc.usgs.gov/products/elevation/gtopo30/hydro/index.html>).

The climatic simulations were created using the LMDZ3.3 Atmospheric General Circulation Model [64], in a high-resolution version (144 cells in longitude \times 108 in latitude), with further refinement over Europe (final resolution \sim 50 km) obtained by use of a stretched grid. Three simulations were performed with boundary conditions representing the three typical climatic situations of interest here: pre-H4 (baseline), interstadial, and Heinrich event, with mid-size ice-sheets compared to the full Last Glacial Maximum. Common to all simulations are the ice-sheets imposed as boundary conditions for which we used the Peltier [65] ICE-4G reconstructions for 14 kyr cal BP, a time at which sea-level was similar to that of Marine Isotope Stage 3 for which no global reconstructions exist. Orbital parameters and greenhouse gas concentrations were set to their 40 kyr cal BP values [44].

The only difference between the three simulations concerned sea surface temperatures (SSTs) and sea-ice extent in the North Atlantic. For the baseline configuration, we used the GLAMAP reconstruction [66]. For the Heinrich event configuration, we subtracted from the reference SSTs an anomaly of 2°C in the mid-latitude North Atlantic and Mediterranean Sea. The interstadial configuration added an anomaly of 2°C to the reference SSTs in the mid-latitude North Atlantic and Mediterranean Sea. For both states, sea-ice cover is imposed if SSTs are lower than -1.8°C . The model was then run with these boundary conditions for 21 years, the last 20 of which were used to compute atmospheric circulation and surface climate in balance with our defined boundary conditions. European climate proves quite sensitive to these changes in boundary conditions: continental temperatures and precipitation decrease from the interstadial to the stadial and finally the Heinrich event simulations, in a fashion similar to results described elsewhere [44]. From these climate simulations, temperature (the coldest and the warmest months as well as mean annual temperature) and precipitation values were extracted for use in GARP. The baseline simulation was used as a proxy for conditions during the period covering Greenland Interstadials 9–11 (pre-H4). The Heinrich event simulation is used to represent conditions during Heinrich event 4 (H4), and the interstadial simulation represents Greenland Interstadial 8 (GI8).

This experiment set-up is designed to be as realistic as possible for MIS3, given the available global data sets needed to perform atmosphere-only experiments. We used more recent SST/sea-ice reconstructions for our baseline experiment compared to previous simulations for the same climatic events [44]. In particular, these reconstructions are warmer over the North Atlantic than the CLIMAP [67] reconstruction and thus more relevant for the MIS3 baseline simulation. Therefore, the climate simulations used in the present study are unique for several reasons: they use updated SST reconstructions, mid-size ice-sheets, greenhouse gas levels, and orbital parameters appropriate for the periods that bracket Heinrich event 4. The resulting climate is obviously dependent on the hypotheses built up in the boundary conditions we used, and on the climate model itself, but we do not know of any equivalent experiments, with an equivalent model, that have high resolution over Europe.

In GARP, occurrence data are resampled randomly by the algorithm to create training 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 possibilities (e.g., logistic regression, bioclimatic rules) and applied to the training data to develop specific rules [52]. These rules are then “evolved” to

maximize predictivity by using a number of methods (e.g. crossing over among rules), mimicking chromosomal evolution. Predictive accuracy is evaluated based on the presence data and a set of points sampled randomly from regions where the species has not been detected. The resulting rule-set defines the distribution of the subject in ecological space (i.e., an ecological niche) [68] and can be projected onto the landscape to predict a potential geographic distribution [69].

We used the following specifications in GARP. Given the random-walk nature of the method, we ran 1000 replicate runs, with a convergence limit of 0.01. Given the small sample sizes (N), we used $N - 2$ occurrence points to develop models in each analysis, reserving one point for model selection and one for evaluating model predictive ability. We followed a modification of a protocol for selecting among resulting models [70], with omission error (i.e., failure to predict a known presence) measured based on the single reserved model-selection point, and models retained only when they were able to predict that single point (i.e., hard omission threshold of 0%). Commission error, conversely, is a measure of areas of absence that are incorrectly predicted present; we followed recommendations of removing from consideration those 50% of models that show extreme values of proportional area predicted present. The resulting 10 final ‘best subset’ models were then summed pixel by pixel to produce a best estimate of an adaptive system’s potential geographic distribution. This conservative approach is ideal when working with small sample sizes, and helps to maximize the robustness of the prediction.

Predictive models such as ECNMs are just that—predictions that must be tested for predictive accuracy before they can be interpreted. Given low occurrence data samples, we tested model predictions using the jackknife manipulation proposed by Pearson et al. [71], the only robust test for evaluating models based on small samples: $N-1$ points are used to develop N jackknifed models. The success of each replicate model in predicting the single omitted point, relative to the proportional area predicted present, is then calculated using an extension to the cumulative binomial probability distribution.

To determine if the Neanderthal and AMH adaptive systems exploited different environmental regimes, their predicted ecological niches, plotted in ecological space against available climatic data, were reviewed for each climatic phase. To determine which environmental variables most influenced the reconstructed niches, principal component analyses (PCA) were performed on these same data (climatic and geographic variables) for each period using *SPSS* 16.0.

We employed the GARP capability to project the ecological niche predicted for a climatic phase onto the environmental conditions of a subsequent period to evaluate if an adaptive system exploited the same ecological niche across different climatic phases (i.e., niche conservation). The resulting projection is compared to the locations of known occurrences for the latter period to see whether or not the model successfully predicts their spatial distribution. The degree of predictivity (i.e., niche stability) was evaluated statistically by determining the proportional area predicted present by the projected model at each predictive threshold (i.e., 10 out of 10 best subset models in agreement, 9 out of 10 in agreement, etc.) along with the number of occurrence points correctly predicted at each threshold. A cumulative binomial statistic is applied to these values to determine whether the coincidence between projected predictions and independent test points is significantly better than random expectations (Table 1). In other words, this approach evaluates whether the two distributions are more similar to one another than one would expect by chance.

To further examine variability within and between eco-cultural niches, we calculated a measure of niche breadth as the sum of the variances along independent factor axes [72,73]. First, predictions for each adaptive system and each climatic phase were projected with GARP onto the climatic variables associated with GI8. We performed a PCA on the GI8 climatic variables, and retained sufficient factors to explain 99% of the overall variance ($N=3$). Then, the variance of the factor loadings associated with areas predicted present by all 10 best subset models was calculated along each principal component and then summed across them. This sum is a robust measure of niche breadth, defined as the diversity of abiotic conditions under which a species can maintain a population [72,74].

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Supporting Information

Table S1 Archaeological sites with radiometrically dated components attributed to Neanderthals (Mousterian, Châtelperronian, Bohunician) or AMH (Aurignacian) for the pre-H4, H4, and GI8 climatic phases.
Found at: doi:10.1371/journal.pone.0003972.s001 (0.18 MB DOC)

Author Contributions

Conceived and designed the experiments: WEB. Performed the experiments: WEB. Analyzed the data: WEB Fd ATP. Contributed reagents/materials/analysis tools: MK AS MFSG. Wrote the paper: WEB Fd ATP MK MFSG.

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Reconstructing ecological niches and geographic distributions of caribou (*Rangifer tarandus*) and red deer (*Cervus elaphus*) during the Last Glacial Maximum

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ABSTRACT

A variety of approaches have been used to reconstruct glacial distributions of species, identify their environmental characteristics, and understand their influence on subsequent population expansions. Traditional methods, however, provide only rough estimates of past distributions, and are often unable to identify the ecological and geographic processes that shaped them. Recently, ecological niche modeling (ENM) methodologies have been applied to these questions in an effort to overcome such limitations. We apply ENM to the European faunal record of the Last Glacial Maximum (LGM) to reconstruct ecological niches and potential ranges for caribou (*Rangifer tarandus*) and red deer (*Cervus elaphus*), and evaluate whether their LGM distributions resulted from tracking the geographic footprint of their ecological niches (niche conservatism) or if ecological niche shifts between the LGM and present might be implicated. Results indicate that the LGM geographic ranges of both species represent distributions characterized by niche conservatism, expressed through geographic contraction of the geographic footprints of their respective ecological niches.

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1. Introduction

The term “refugia” generally refers to regions where temperate plant and animal species survived glacial periods with both reduced populations and restricted geographic distributions (e.g. Hewitt, 2000; Bennett and Provan, this issue). As such, refugial distributions during glacial episodes might be achieved in one of two ways. First, climate change during a glacial episode may produce a geographic contraction of the footprint of the ecological niche of a species. In this scenario, the species' geographic range contracts because it tracks the same ecological niche (i.e., niche conservatism) as its footprint contracts.

In the second scenario, the ecological niche itself may expand or contract in the face of environmental change: the refugial range is then the result of niche expansion or contraction and is larger or smaller, respectively, as a consequence of the niche having changed. Distinguishing between these scenarios is not always

straightforward when using paleontological and genetic data sets, but ecological niche modeling permits clear tests (Martinez-Meyer et al., 2004) because an important dimension of niche-based analysis and thinking is that of the constancy of the ecological conditions that a species or population inhabits. That is, if a species or population is found under consistent and predictable ecological circumstances through time and across space, then its potential distribution can be predicted (Peterson, 2003).

Also important is the debate surrounding the relevance of the glacial refugium concept when it comes to species adapted to northern latitudes (Pruett and Winker, 2008; Stewart and Dalén, 2008). It has been suggested that cold-adapted species occupy restricted ranges (i.e., refugia) during temperate climate events (interstadials) and broader geographic ranges during stadial episodes (e.g., Stewart and Lister, 2001).

The question, then, is what refugium concepts do we apply, to what data, and for which species? Perhaps more appropriate would be to shift to the simple view that species' distributional ranges are dynamic. Some species move among potential distributional areas in response to changing environmental conditions, while others fail to do so (e.g., Dalén et al., 2007). By applying the appropriate

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methods to the relevant data sets, we may quantify, accurately and consistently, and evaluate these distributional shifts for particular species during and between distinct climatic events.

The climatic conditions of the Last Glacial Maximum (LGM) affected geographic ranges of European temperate plant and animal species by forcing them southward into what have been termed refugia (Hewitt, 2000). These refugia were the source areas from which populations recolonized northern Europe at the end of the glacial period. Attempts have been made to characterize their location and extent (e.g., Petit et al., 2003; Sommer and Nadachowski, 2006; Garzón et al., 2007), determine the timing and routes of expansion during subsequent climatic amelioration (Taberlet et al., 1998; Valdiosera et al., 2007; Sommer et al., 2008), and understand the impacts that refugial bottleneck events may have had on later genetic variability (Hewitt, 2000; Flagstad and Røed, 2003; Petit et al., 2003; Sommer and Nadachowski, 2006; Knowles et al., 2007; Sommer et al., 2008).

Some of these attempts have relied solely on inferences from present-day genetic variability, while others have integrated information from fossil data sets. The latter data offer the advantage of testing predictions proposed solely on the basis of genetic data. While the paleontological record can provide information concerning distributions of past populations, such distributions may not accurately or completely reflect the past range of a species. Rather, extrapolations of ranges between and beyond observed occurrences depend on subjective knowledge of the species and the region of study, and usually overestimate species' distributions; on the other hand, simply plotting known occurrence localities on a map depicts a species' range too conservatively (Anderson et al., 2002). Additionally, simple plotting of occurrences cannot characterize a species' ecological requirements. Hence, traditional approaches allow crude characterization of distributions, but only incorporation of additional ecological and environmental data can provide an understanding of the ecological and geographic processes that shaped them.

Recent advances in biodiversity studies (Guisan and Zimmermann, 2000; Soberón and Peterson, 2005) have developed tools for estimating ecological niches of species and predicting responses to environmental changes, where an ecological niche is defined as the range of combinations of all relevant environmental variables under which a species or population can persist without migrational subsidy (Grinnell, 1924; Hutchinson, 1957). This approach has been termed "ecological niche modeling" (ENM; Peterson et al., 2002). These tools have been coupled with phylogenetic data (Knowles et al., 2007) and modern land cover data (Garzón et al., 2007), but these applications have assumed that niches remain stable over time, which is not always the case. Martínez-Meyer et al. (2004) and Martínez-Meyer and Peterson (2006) used ENM to reconstruct ecological niches of numerous mammal and plant species in North America since the LGM and evaluated temporal stability in niche characteristics. Peterson and Nyári (2007) and Waltari et al. (2007) developed these ideas still further, focusing on characterization and identification of Pleistocene distributions based on present-day ecological niche dimensions; this approach has also been used to identify human potential ranges and explore environmental influences on cultural geography in Europe during the LGM (Banks et al., 2008).

ENM tools have yet to be applied to the European faunal record of the Last Glacial Maximum. We argue that this methodological approach can help us to understand better the geographic range of a particular species, either temperate- or cold-adapted, during specific climatic events, and evaluate how it reacted to environmental changes. As such, the first goal of this study is to use ENM to reconstruct the ecological niches and potential ranges for caribou (*Rangifer tarandus*) and red deer (*Cervus elaphus*) during the LGM. The second goal is to evaluate whether shifts between LGM and

present-day distributions were the result of niche conservatism or whether ecological niche shifts are implicated.

2. Materials and methods

We used the Genetic Algorithm for Rule-Set Prediction (GARP; Stockwell and Peters, 1999) to estimate ecological niches. For data inputs, GARP requires the geographic coordinates of sites where the target species has been observed and raster GIS data layers summarizing environmental dimensions potentially relevant to shaping the distribution of the species.

2.1. Occurrence data

We developed occurrence data sets for the two species in the present-day and the LGM. For the LGM, we used the geographic coordinates of archaeological sites dated to this period from which caribou or red deer remains have been recovered. Even though hunter-gatherers often transport animal carcasses, or portions of them, between their kill locations and subsequent processing and consumption localities, the scale of such movement is typically below our grid resolution of ~60 km. Therefore, we assume that these data reflect past occurrences of the species. Our faunal database covers Marine Isotope Stages 2 and 3, and contains the geographic coordinates, stratigraphic provenance, taxonomic information (family, genus, and, when possible, species designations), and radiometric age determinations, when available, for faunal remains recovered from ~2000 individual archaeological levels at ~500 sites. Because faunal data are not presented consistently in the published literature, we quantified them in our database as presence/absence, number of identified specimens (NISP), or minimum number of individuals (MNI). We used CALIB 5.0.2 (Reimer et al., 2004; Stuiver et al., 2005) to calibrate radiocarbon ages and to determine whether they fell within our defined time frame for the LGM. To have sufficient site samples for the modeling procedure, we used sites with calibrated dates between ~23 kyr cal BP and ~19 kyr cal BP. Because the sample of sites for which both faunal data and radiocarbon age determinations exist is small, we also included sites for which faunal data were associated with components with cultural attributions that reliably place them in the LGM (Tables 1 and 2).

For present-day occurrence information, we consulted the Mammal Networked Information System (MaNIS; <http://manisnet.org>), a consortium of 17 North American mammal collections. Taxonomic and geographic information associated with mammal specimens in these institutions' collections are available through the system. A portion of the modern occurrence data for caribou and red deer was obtained from records in the following institutions and accessed through a MaNIS data portal on 11 December, 2007: Utah Museum of Natural History and the University of Michigan Museum of Zoology. Occurrence data were also provided by the Natural History Museum of Rotterdam, the Paleobiology Database, the Biological Records Centre (UK), the Highland Biological Recording Group (UK), the European Environmental Agency, and the Yale University Peabody Museum (accessed through GBIF data portal, <http://www.gbif.net>, accessed 11 December, 2007). These present-day occurrences represent specimens collected from the 19th century to the present-day, and we assume that they accurately reflect the species' distributions.

2.2. Environmental data

The raster GIS data used in this study include landscape attributes (assumed to remain constant) and high-resolution climatic

Table 1
Sites with cultural levels assigned to the Last Glacial Maximum that contain caribou remains.

Site	Longitude	Latitude	Country	Culture	Lab code	Median cal BP
Altamira	-4.12	43.38	Spain	Solutrean	GifA-90045	21,980
Amalda	-2.20	43.23	Spain	Solutrean	I-11355	20,910
C. Mina	1.17	43.43	Spain	Solutrean	Ua-3586	23,110
Combe Sauniere	0.16	45.14	France	Solutrean	OxA-488	20,990
El Ruso	-3.88	43.44	Spain	Solutrean	Beta-70810	19,580
Ermittia	-2.36	43.28	Spain	Solutrean	no date	LGM
Gandil	1.10	44.40	France	Lower Magdalenian	GifA-96307	20,440
Grotte des Cottiers	4.01	45.21	France	Badegoulian	Ly-720	25,330 ^a
Grotte d'Oullins	4.47	44.35	France	Lower Magdalenian	Gif-6017	19,770
Grubgraben	15.72	48.47	Austria	Epigravettian	Ly-1821	20,840
Isturitz	-1.2	43.37	France	Solutrean	no date	LGM
La Salpetriere	4.54	43.95	France	Solutrean	Ly-940	21,270
L'Abreda	2.75	42.17	Spain	Solutrean	Gif-6419	21,010
Lassac	2.40	43.29	France	Badegoulian	Gif-2981	19,890
Laugerie-Haute Est	0.38	44.90	France	Solutrean	no date	LGM
Lezetxiki	0.83	42.75	Spain	Solutrean	I-6144	23,110
Pegourie	0.90	45.20	France	Badegoulian	Ly-1394	20,830
Solutre	4.31	46.38	France	Solutrean	Ly-1534	20,770
Urtiaga	-2.32	43.28	Spain	Lower Magdalenian	GrN-5817	20,180

^a Date/calibration likely too old, but cultural affiliation warrants inclusion in the LGM sample.

simulations for the LGM and present day. Landscape variables included slope, aspect, and compound topographic index (a measure of tendency to pool water) from the Hydro-1K data set (U.S. Geological Survey, Center for Earth Resources Observation

and Science; <http://edc.usgs.gov/products/elevation/gtopo30/hydro/europe.html>).

The Last Glacial period was marked by dramatic climatic variability (Johnsen et al., 1992; Dansgaard et al., 1993), with the LGM

Table 2
Sites with cultural levels assigned to the Last Glacial Maximum that contain red deer remains.

Site	Longitude	Latitude	Country	Culture	Lab code	Median cal BP
Aitzbitzarte	-1.90	43.26	Spain	Solutrean	GrN-5993	21,260
Altamira	-4.12	43.38	Spain	Solutrean	GifA-90045	21,980
Amalda	-2.20	43.23	Spain	Solutrean	I-11355	20,910
Ambrosio	-2.24	37.52	Spain	Solutrean	Gif-7277	19,870
Arene Candide	8.33	44.17	Italy	Epigravettian	R-2550	21,630
Beneito	-0.47	38.70	Spain	Solutrean	no date	LGM
Bolinkoba	1.05	43.13	Spain	Solutrean	no date	LGM
Buxu	-5.12	43.35	Spain	Solutrean	GrN-19386	19,920
C. Mina	1.17	43.43	Spain	Solutrean	Ua-3586	23,110
Caldas	2.23	43.34	Spain	Solutrean	Ly-2423	21,720
Caldeirao	-8.42	39.65	Portugal	Solutrean	OxA-2510	22,400
Castillo	-3.97	43.29	Spain	Solutrean	OxA-971	19,970
Chufin	-4.46	43.29	Spain	Solutrean	CSIC-258	20,600
Combe Sauniere	0.16	45.14	France	Solutrean	OxA-488	20,990
Cosauti	28.27	48.21	Moldavia	Epigravettian	GIN-4146	20,380
Cova Rosa	1.44	43.44	Spain	Solutrean	no date	LGM
Clemente Tronci	13.37	42.37	Italy	Epigravettian	no date	LGM
Grotta dei Fanciulli	7.52	43.83	Italy	Epigravettian	no date	LGM
Grotta delle Veneri	18.10	40.07	Italy	Epigravettian	no date	LGM
Grotta di Paina	11.52	45.43	Italy	Epigravettian	UtC-2043	23,120
Grotta Parabita	18.10	40.07	Italy	Epigravettian	no date	LGM
H. Peña	0.34	43.26	Spain	Solutrean	BM-1882R	24,200 ^a
Klithi	20.67	39.67	Greece	Epigravettian	OxA-2971	19,790
Le Piage	0.95	45.10	France	Solutrean	Gif-5026	22,530
La Salpetriere	4.54	43.95	France	Solutrean	Ly-940	21,270
L'Arbreda	2.75	42.17	Spain	Solutrean	Gif-6419	21,010
Lezetxiki	0.83	42.75	Spain	Solutrean	I-6144	23,110
Lluera	2.25	43.34	Spain	Solutrean	no date	LGM
Morin	-3.86	43.32	Spain	Solutrean	no date	LGM
Palidoro	12.18	41.95	Italy	Epigravettian	no code	19,140
Parpalló	-0.18	38.97	Spain	Solutrean	BM-861	21,480
Pasiega	0.28	43.29	Spain	Solutrean	no date	LGM
Pegourie	0.90	45.20	France	Badegoulian	Ly-1394	20,830
Peña Candamo	-6.08	43.45	Spain	Solutrean	no date	LGM
Rascaño	-3.71	43.29	Spain	lower Magdalenian	BM-1455	19,630
Riera	-4.86	43.42	Spain	Solutrean	UCR-1272A	20,430
Ripara Maurizio	13.75	42.25	Italy	Epigravettian	no date	LGM
Riparo Mochi	7.53	43.84	Italy	Epigravettian	no date	LGM
Santimamiñe	1.05	43.35	Spain	Solutrean	no date	LGM
Taurisano	18.22	39.95	Italy	Epigravettian	no code	19,200
Urtiaga	-2.32	43.28	Spain	initial Magdalenian	GrN-5817	20,180
Zupanov Spodmol	14.22	45.78	Slovakia	Epigravettian	GrN-5288	19,890

^a Date/calibration likely too old, but cultural affiliation warrants inclusion in the LGM sample.

representing a unique suite of environmental conditions (Ditlevsen et al., 1996; Peyron et al., 1998). This period, centered on 21 kyr-cal BP, was the last period of maximum global ice-sheet volume, along with cold and generally arid conditions in northern and Western Europe. To capture the climatic impact of LGM conditions, we used an atmospheric general circulation model with a refined grid over Europe (resolution of ~60 km over Western Europe), run at the Laboratoire des Sciences du Climat et de l'Environnement, Gif-sur-Yvette, France. This high-resolution LGM atmospheric simulation follows the protocol proposed by the PMIP2 project (Braconnot et al., 2007, <http://pmip2.lsce.ipsl.fr>), with orbital parameters and atmospheric greenhouse gas concentrations set to their 21,000 cal BP values (Berger, 1978; Raynaud et al., 1993) and ice-sheet height and extent prescribed according to the Peltier (2004) ICE-5G reconstructions. The PMIP2 protocol is designed for coupled ocean-atmosphere models, whereas an atmosphere-only model was used in the present study. Therefore, a prescription of the sea-surface characteristics (temperatures and sea-ice extent) was necessary and we used the most recent reconstructions, i.e. the GLAMAP data set (Paul and Schäfer-Neth, 2003; Sarthain et al., 2003). The results of this simulation have been compared to pollen-based climatic reconstructions, with fairly close agreement for summer and annual mean temperatures, but some underestimation of winter cooling and drying over Western Europe and the Mediterranean. From this simulation, we derived the following variables for input into the ENM: warmest month temperature, coldest month temperature, mean annual temperature, and mean annual precipitation. The values of warmest and coldest months refer to the warmest or coldest month as determined from 10 yr averages of simulation results.

While there are many simulations of the LGM climate (e.g., those performed in the first and second phases of the Paleoclimate Modeling Intercomparison Project), there are few high-resolution simulations. Jost et al. (2005) compared three of these simulations. All of them are driven with the CLIMAP (1981) sea-surface temperature and sea-ice reconstructions for the LGM. In this work, we use a more up-to-date surface ocean forcing data set and to our knowledge, there are no other high-resolution simulations using this data set yet. It would be interesting, in an extension to this study, to examine the sensitivity of the resulting ecological niche models to the climate forcing.

For parallel present-day climates, we used simulated modern-day climate derived from the same model. In this case, atmospheric CO₂ concentration was set at 348 ppmv and orbital parameters were taken from modern conditions. Sea-surface conditions were set based on averages from the AMIP2 data set for 1979–1989 (<http://www-pcmdi.llnl.gov/projects/amip/AMIP2EXPDSN/BCS/amip2bcs.php>). This arrangement means that, for every year of the simulation, the same annual SST and sea-ice cover cycle parameters were prescribed to the model. This present-day simulation was run with these boundary conditions for 11 yr, with the last 10 yr used to compute the climatic characteristics simulated for the modern climate, as was done for the LGM run.

It would have been possible to first drive the ecological niche models with a present-day observation data set and then use the LGM-present-day difference simulated by our climate model to build an LGM forcing for the ecological models. This “perturbative method” is often used, especially when the present-day simulation from the climate model is too biased to produce a satisfactory output from the forced model (i.e., in our case, an ecological niche model). For this study, even though our climate simulation is not perfect (cf. Jost et al., 2005), the ecological models, forced by the climate model present-day output, provided satisfactory results, and therefore it was not necessary to apply the perturbative method. The ecological niche models were consistently

driven by the same model output, both for the present-day and the LGM.

In GARP, occurrence data are resampled randomly by the algorithm to create training 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 possibilities (e.g., logistic regression, bioclimatic rules) and applied to the training data to develop specific rules (Stockwell and Peters, 1999). These rules evolve to maximize predictivity by using a number of methods (e.g., crossing over among rules) mimicking chromosomal evolution. Predictive accuracy is then evaluated based on an independent subsample of the presence data and a set of points sampled randomly from regions where the species has not been detected. The resulting rule-set defines the distribution of the subject in ecological space (i.e., the ecological niche; Soberón and Peterson, 2005), and can be projected onto the landscape to predict a potential geographic distribution (Peterson, 2003).

We used the following specifications in GARP. Given the random-walk nature of the method, we ran 1000 replicate runs, with a convergence limit of 0.01. Given the very small sample sizes (N), we used $N - 2$ occurrence points to develop models in each analysis, reserving one point for model selection and one for evaluating model predictive ability (Pearson et al., 2006). We followed a modification of a recent protocol for selecting among resulting models (Anderson et al., 2003), with omission error (i.e., failure to predict a point of known presence) measured based on the single reserved model-selection point, and models retained only when they were able to predict that single point (i.e., hard omission threshold of 0%). Commission error, conversely, is a measure of areas of absence that are incorrectly predicted as potentially present; we followed recommendations of removing from consideration the 50% of models that show the most extreme values of proportional area predicted present. The resulting final ‘best subset’ of 10 models was then summed, pixel by pixel, to produce a best estimate of the species’ potential geographic distribution. This conservative approach is ideal when working with small sample sizes, and helps to maximize the robustness of the prediction.

To evaluate whether caribou and red deer exploit today the same niche as during LGM (i.e., niche conservatism), we projected the ecological niche model developed for one climatic phase onto the environmental conditions of a different climatic phase. The resulting projection was compared to the locations of known occurrences for the “other” period to test whether or not the projection of the model successfully predicts the known distribution. The degree of predictivity (i.e., niche stability) was evaluated statistically by determining the proportional area predicted present by the projected model at each predictive threshold (i.e., 10 out of 10 best subset models in agreement, 9 out of 10 in agreement, etc.), along with the number of occurrence points correctly predicted at each threshold. A cumulative binomial statistic was applied to these values to determine whether the coincidence between projected predictions and independent test points is significantly better than random expectations. In other words, the approach evaluates whether the two distributions are more similar to one another than one would expect by chance. For this study, GARP predictions for the LGM were projected onto the modern-day climatic simulation, and modern-day predictions projected onto the LGM climatic simulation.

To examine further temporal variability in ecological niches, we calculated a measure of niche breadth as the sum of the variances along independent factor axes (Rotenberry and Wiens, 1980; Carnes and Slade, 1982). First, LGM and modern-day ENMs were both projected with GARP onto the modern-day climate simulation. We performed a principal component analysis on the modern-day climatic variables, and retained sufficient factors to explain 99% of the overall variance ($N = 3$). Then, the variance of the factor loadings associated with areas predicted present by all 10 of the best

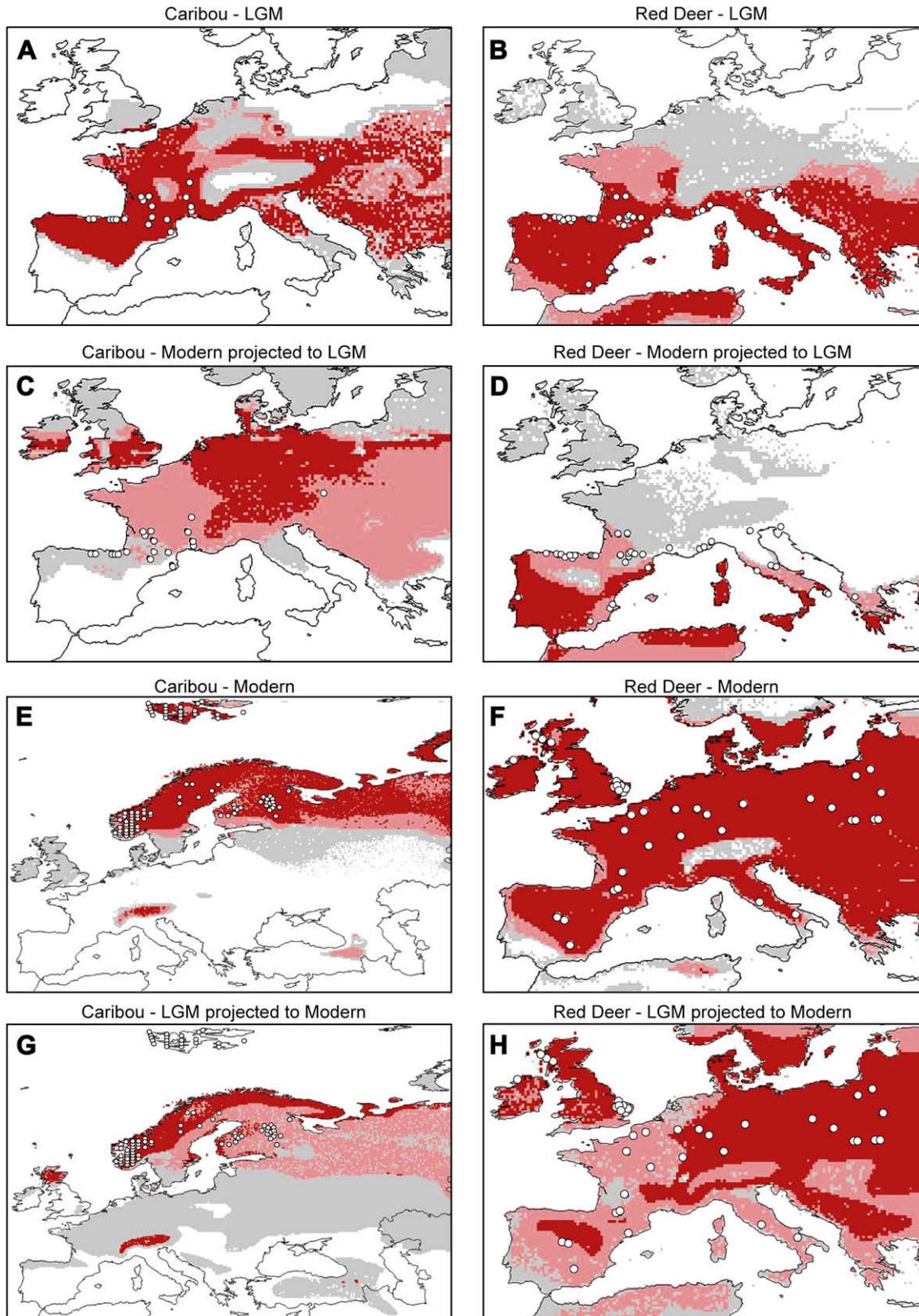


Fig. 1. Caribou and red deer ecological niche predictions. For each model, grid squares with 1–5 of 10 models predicting the presence of suitable conditions are indicated in grey, grid squares with 6–9 models in agreement are depicted in pink, and squares with all 10 models in agreement are indicated in red. (For interpretation of the references to colour in this figure legend the reader is referred to the web version of this article.)

subset models was calculated along each principal component, and then summed across them. This sum is a robust measure of niche breadth, defined as the diversity of abiotic conditions under which the species' can maintain populations (Carnes and Slade, 1982;

Soberón, 2007). Reduced niche breadth may not necessarily reflect changes in niche dimensions but rather may reflect poor representation of the species' niche conditions within the study area under one set of environmental conditions.

3. Results

3.1. Period-specific ENMs

The predicted geographic range for caribou during the LGM covers all of the middle latitude areas in Europe, with the exception of the Massif Central, the Alps, the Vosges, the Ardennes, and the northern European plain (Fig. 1A). For Eastern Europe and western Eurasia, the predicted range is more diffuse than in Western Europe. These ecological niche conditions cover a mean annual temperature range of -13 to $+7$ °C and a mean annual precipitation range of 0–1100 mm. The present-day ecological niche prediction for caribou shows a potential geographic range across Scandinavia and extreme northern Asia, excluding southern Sweden and Finland (Fig. 1E). Mean annual temperature values are -9 to $+4$ °C, and mean annual precipitation of 365–2500 mm.

The predicted LGM range for red deer completely covers southern mid-latitudes, excluding the extreme southwestern portion of the Iberian Peninsula, extending northward into southwestern France and the Rhône and Saône valleys (Fig. 1B). This ecological niche covers mean annual temperatures of 0–12 °C and mean annual precipitation of 0–1100 mm. The present-day prediction of the geographic range for red deer covers all of Europe and western Eurasia, including extreme southern Sweden, and excluding the southwestern Iberian Peninsula, the extreme southern portions of the Italian and Balkan Peninsulas, and the Alps (Fig. 1F). The mean annual temperature and precipitation ranges for this reconstructed ecological niche are 5–15 °C and 0–2500 mm, respectively.

3.2. Niche projections between time periods

The projection of the present-day ecological niche prediction for caribou back onto LGM conditions predicted a geographic range covering the central northern European Plain, the Alps, and the northern Rhône River valley (Fig. 1C). Most of these areas are not predicted in the LGM model: rather, all of the LGM caribou occurrences are only predicted successfully at the low ($P < 0.014$) and intermediate ($P < 0.011$) thresholds in the projected model. Nevertheless, while the ecological niche predictions for the LGM and for the present-day projected to LGM differ in their geographic expressions, statistically they are interpredictive, except at the most restrictive threshold (Table 3).

Projecting the LGM caribou ecological niche model onto present-day climatic conditions predicts a modern range that is more or less coincident with the prediction based on modern occurrence data and climatic conditions, excluding eastern Sweden, Finland, and the Arctic Russian coast (Fig. 1G). Because this projected model duplicates most of the present-day prediction and only failed to predict the northern and easternmost modern occurrences, the two are highly interpredictive at all prediction levels (all $P < 1.114 \times 10^{-5}$; Table 3).

The modern-day ecological niche prediction for red deer projected onto LGM conditions predicts a geographic range restricted to the southern and western Iberian Peninsula and the extreme

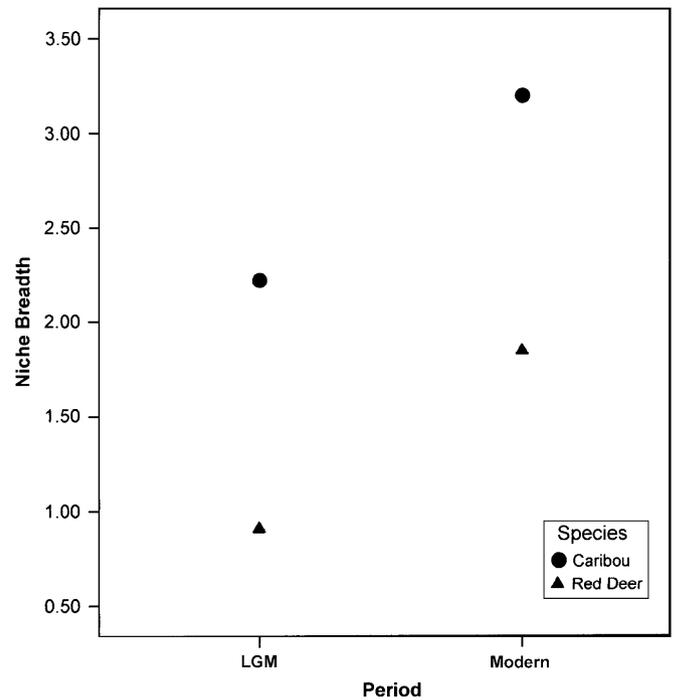


Fig. 2. Summary of Last Glacial Maximum and modern-day niche breadth measures for caribou and red deer.

southern parts of the Italian and Balkan peninsulas (Fig. 1D). These regions represent only a portion of the regions predicted by the LGM model and most of the LGM occurrence data are only predicted at intermediate thresholds. Despite these differences, however, this projected niche prediction and the LGM model are highly interpredictive, except at the most restrictive predictive threshold (Table 3).

Projecting the LGM red deer model onto modern conditions, the resulting prediction included only the eastern half of its modern range, with the exception of the British Isles and the northern Iberian Meseta (Fig. 1H) and some modern occurrences are only predicted at intermediate thresholds. The red deer LGM and present-day models are highly interpredictive at all prediction levels ($P < 1.867 \times 10^{-6}$; Table 3).

In both time periods, caribou are seen to have a broader niche than red deer (Fig. 2). Additionally, although the LGM and present-day projections for both species are interpredictive, reconstructed niche breadth expanded for both species between the LGM and the present day.

4. Discussion

Predictive models are just that – predictions – and before they are interpreted, one must be sure that they are accurate and robust. Our sample sizes for the LGM and present-day occurrences are sufficient to avoid the need for manipulations commonly used for

Table 3

Results of predictivity tests between LGM and modern climatic conditions for caribou and red deer ecological niche projections.

Comparison	All models predict			Most models predict			Any model predicts		
	Prop. area	Success	P	Prop. area	Success	P	Prop. area	Success	P
Caribou LGM predicts modern	0.0665	48/111	2.442×10^{-15}	0.2231	79/111	2.442×10^{-15}	0.5988	87/111	1.114×10^{-5}
Caribou modern predicts LGM	0.0576	0/19	0.6758	0.3494	11/19	0.0113	0.6419	16/19	0.0142
Red deer LGM predicts modern	0.1479	22/49	9.007×10^{-8}	0.6165	44/49	1.867×10^{-6}	0.9531	49/49	0
Red deer Modern predicts LGM	0.1222	6/42	0.2485	0.26068	27/42	4.141×10^{-8}	0.4002	35/42	1.308×10^{-9}

small samples (Pearson et al., 2007). Stockwell and Peterson (2002) demonstrated that GARP consistently produces accurate and robust predictive models when occurrence samples are ≥ 20 . Previous modeling exercises have shown excellent predictive abilities of ENMs regarding distributional patterns of species (Illoldi-Rangel et al., 2004; Martínez-Meyer et al., 2004). Therefore, we assume that the models described above capture the essence of the species' ecological niches and associated geographic ranges.

The binomial tests comparing projections among time periods indicate that caribou followed a consistent ecological niche between the LGM and the present (Table 3). As a consequence, the caribou ENM identifies a glacial distribution that is the result of tracking a geographic contraction of the ecological niche footprint. This geographic contraction at the LGM is evident in both the LGM to modern and modern to LGM projections. Because in the former case the projected niche occupies only a subset of the modern geographic range, and because the species was found in a narrower resource space during the LGM (Fig. 2), we surmise that the ecological amplitude seen in European caribou populations has expanded since the LGM. Thus, whether caribou can be considered to have occupied a glacial refugium during the LGM, or, as a cold-adapted species, inversely are occupying a refugium today is irrelevant. With ENM and statistical evaluations of the resultant predictions, one can understand the dynamics behind the changes in their distribution, which in essence is the goal, whether one examines glacial refugia or cryptic northern refugia.

At first glance, it would appear contradictory to have LGM and present-day niches that are statistically interpredictive, but niche breadth expanding markedly. However, even if niche breadth varies between two periods, if the core of a species' ecological niche does not shift, then projections between periods will remain interpredictive. More importantly, if environmental conditions are such that only a limited portion of habitable conditions for a species is represented in a particular bounded study area, ENMs may reconstruct a smaller niche envelope. Such is the pattern observed for caribou and red deer between the LGM and the present, suggesting that LGM conditions saw only a very limited representation of suitable conditions for these species. This result leads to the testable hypothesis that a similar analysis farther east in Asia or in North America, where a southern boundary (i.e., the Mediterranean Sea) is not present, would not encounter a reduced LGM potential range for these species.

The GARP prediction for red deer during the LGM (Fig. 1B) corresponds well to this species' known range during that period (Sommer et al., 2008), and corresponds to regions characterized by discontinuous permafrost and seasonal freezing (van Vliet-Lanoë et al., 2004). The hypothesis of a red deer "Carpathian" LGM refugium (Sommer and Nadachowski, 2006; Sommer et al., 2008), however, is not supported by our LGM prediction. This lack of support, though, may be due to the fact that our predictions consider a narrower temporal range. Results indicate that red deer had a conserved ecological niche, and tracked a climatically induced geographic contraction. This Mediterranean range during the LGM reflects a refugium where only the colder and drier portions of their present-day ecological niche were expressed. The present-day prediction for red deer projected onto LGM climatic conditions identifies as suitable only the extreme southern portions of their reconstructed LGM range and also extends into southern latitudes beyond the LGM range. When the red deer ecological niche for the LGM is projected onto present-day climatic conditions, the resulting model corresponds only to the eastern half of their present-day geographic range, representing continental environmental conditions. Like caribou, red deer niche breadth increases between the LGM and the present. Rather than reflecting a change in behavior or adaptation, again it is likely that the red deer niche was simply poorly represented in the study area at LGM. In other words, red deer

populations were presented with a narrower and geographically constrained ecological range during the LGM.

The fact that the niche breadth ratios for both species are very similar between the LGM and present day confirms the idea that the presence of the Mediterranean Sea resulted in a narrower exploitable resource range being present for each species during the LGM. The similarity in their ratios also suggests that, despite their distinct ecological requirements, the two species reacted in a similar way to the subsequent trend of climatic amelioration.

5. Conclusions

Taken together, the LGM predictions, the projections of ecological niches between periods, and the calculated measures of niche breadth indicate that the LGM geographic ranges of both caribou and red deer represent distributions characterized by geographic contraction of the footprints of their respective ecological niches, and that the cores of these species' LGM ecological niches do not differ from those of the present. We have demonstrated that radiometrically dated fossil data and bio-computational architectures can be used to identify past ranges of a species, but more importantly that such approaches can accurately reconstruct the ecological niches of fossil populations and allow us to understand the ecological dynamics involved in the formation of glacial distributions. Such results would be difficult, if not impossible, to achieve using distributional data alone.

This approach also has implications for studies of prehistoric hunter-gatherer subsistence economies and adaptations. Middle-range research, the practice of constructing frames of reference within which to interpret the archaeological record (Binford, 1982), has included study of historical hunter-gatherer exploitation of particular species (e.g., Binford, 1978) to infer how variability in animal distributions and behavior may have influenced prehistoric hunter-gatherer subsistence and settlement strategies and their archaeological signatures. To increase the relevance of such modern analogs to interpretations of the archaeological record, reconstructions of the prehistoric ecological niches of prey mammal populations are critical, so that appropriate modern environmental contexts can be identified as a focus of study in order to construct the most relevant inferential frames of reference.

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Investigating links between ecology and bifacial tool types in Western Europe during the Last Glacial Maximum

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ABSTRACT

We apply Eco-Cultural Niche Modeling (ECNM), using the Genetic Algorithm for Rule-Set Prediction, to reconstruct the ecological niches exploited by Middle Solutrean and Upper Solutrean populations during the latter stages of Heinrich Event 2 and the early part of the Last Glacial Maximum, respectively. We focus on the Upper Solutrean technocomplex and its regionally distinct styles of hunting weaponry to investigate whether regional cultural variability reflects a link between material culture and ecology. Our analytical approach uses archaeological and geographic data in conjunction with high-resolution paleoclimatic simulations and vegetation reconstructions for the two climatic phases in question. Our results indicate that cultural choices behind the production of specific projectile point types have at some level an ecological basis and are linked to particular environments. We also find that the identified pattern of Upper Solutrean territoriality has an ecological foundation, but that its stylistic expression in the variation of diagnostic armature types is likely a byproduct of cultural drift. We argue that ECNM is an effective means with which to evaluate the paleoecological pertinence of archaeologically defined artifact types and to identify the ecological and cultural mechanisms underlying material culture variability.

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1. Introduction

Recent years have seen a multitude of studies aimed at understanding how prehistoric hunter-gatherer populations responded to climatic and environmental variability. Using a variety of analytical methodologies, these research endeavors have combined archaeological, radiometric, and paleoenvironmental data sets to study a diverse range of topics such as population movements (Field et al., 2007), resettlement episodes (Gamble et al., 2004; Straus et al., 2000), demography (Bocquet-Appel et al., 2005), human adaptive tolerances related to environmental variability (Binford, 2001; Van Andel and Davies, 2003), and population replacements (d'Errico and Sánchez-Goñi, 2003; Sepulchre et al., 2007). Such research has been conducted with the idea that studies of prehistoric hunter-gatherer cultures should consider the environmental contexts within which those cultures operated. One must keep in mind that archaeological cultures, or

technocomplexes (defined here as the structured combination of technological systems shared and transmitted by a culturally cohesive population), can encompass a range of settlement-subsistence systems across their geographic distribution and be extremely flexible and diverse. In other words, a technocomplex is not necessarily the direct technological “expression” of a specific culture/environment relationship or “adaptation” (sensu Binford, 1962). Despite such flexibility, the lifeways of hunter-gatherers, in prehistoric times as much as in the present, must have been constrained to some degree by the environmental parameters within which they operated. Thus, one goal of many prehistoric hunter-gatherer studies has been to describe and interpret, against an environmental backdrop, the range of adaptive solutions preserved in the archaeological record and thereby better understand prehistoric human/environment interactions.

Recently, Eco-Cultural Niche Modeling (ECNM; Banks et al., 2006) has been proposed as a means to explore the complex interactions between cultural and natural systems, understand how these influenced the adaptations and movements of archaeological populations, and tackle hurdles encountered by previous

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approaches. ECNM integrates archaeological, radiometric, geographic, and paleoclimatic data sets via a biocomputational architecture, derived from biodiversity studies (Guisan and Zimmermann, 2000; Soberón and Peterson, 2005), in order to reconstruct the ecological niches exploited by past human populations and identify the mechanisms that shaped these niches. An eco-cultural niche can be defined as the potential range of environmental conditions within which a human adaptive system can persist without immigrational subsidy (Banks et al., 2008a). This analytical approach has been used to reconstruct eco-cultural niches, identify potential human ranges, and explore the environmental influences on cultural geography in Europe during the Last Glacial Maximum (LGM; Banks et al., 2008a) and Neanderthal/modern human interaction during the latter stages of Marine Isotope Stage 3 (Banks et al., 2008b).

To date, applications of ECNM have focused on examining eco-cultural niche variability between different human species (or subspecies) and different technocomplexes, both synchronically and diachronically. It should be possible to identify and evaluate potential internal eco-cultural niche variability within a single technocomplex provided that its material culture is diverse enough to identify cohesive variants within the broader technocomplex. Such an application of ECNM could investigate whether regional cultural variability, and more specifically hunting technology, reflects a link between the material culture and a given environmental framework.

This paper targets the Upper Solutrean technocomplex of Western Europe during the temporal frame (ca. 19–20 kyr ^{14}C BP) immediately preceding the height of the LGM, to investigate whether its recognized diversity of lithic projectile point types reflects adaptations to specific environments (i.e. ecological niches) or the expression of cultural geography unrelated to environmental conditions. In the former case, one would expect a distinct armature type's predicted ecological niche to correspond closely to its actual geographic distribution, with little or no overlap between the different lithic types' eco-cultural niches. For the latter case, we would expect 1) each reconstructed niche to have a geographical expression much larger than that of its associated armature type and 2) a high degree of coincidence between the different reconstructed eco-cultural niches. The Upper Solutrean is an ideal case for testing these different scenarios because it represents the first well-documented instance in human prehistory of a wide range of distinct hunting armatures in a context that is well-constrained chronologically, climatically, and geographically.

2. The Solutrean phenomenon

As the height of the LGM approached, human groups in France and the Iberian Peninsula developed a suite of novel technologies characterized by a variety of diagnostic bifacial projectile points and knives, which are used to define the Solutrean (Mortillet, 1872; Smith, 1966). It has been proposed that these specialized technologies and associated subsistence systems reflect a response to harsher environmental conditions that caused a contraction of the human range and, as a consequence, increased demographic pressure in the southwestern European refugium—"The Original Arms Race" (Straus, 1990, 2005). This hypothesis, however, was originally proposed when our understanding of climatic and environmental conditions for the LGM and preceding periods was less detailed than at present. The recognition of millennial-scale climatic variability (Dansgaard-Oeschger variability and Heinrich Events; Dansgaard et al., 1993; Heinrich, 1988; Hemming, 2004) and its impact on terrestrial environments has greatly improved our understanding of the environmental conditions in which Upper Paleolithic hunter-gatherers operated. We know now, for example,

that the climatic phase that preceded the LGM, called Heinrich Event 2 (HE2), was characterized by conditions in many respects harsher than those of the LGM (see below). Thus, the increase in Solutrean projectile point variability following HE2 cannot be linked to extreme climatic conditions alone.

An alternative view is that the purported higher population density linked to climatic deterioration is a product of archaeological visibility and preservation factors (Zilhão, 1997, *in press*; Zilhão and Almeida, 2002). For instance, the distinctive nature of Solutrean armatures enables isolated finds to be mapped as "sites", thereby biasing site counts in favor of the Solutrean and against other Upper Paleolithic technocomplexes. Moreover, in parts of Iberia (e.g., Portugal), the number of known Gravettian sites is on the same order of magnitude as that of the Solutrean, and, in terms of size, weight, hafting and propelling technology, there is no apparent difference between Gravettian (e.g., the French *fléchettes* and the Portuguese Casal do Felipe points) and Solutrean spear/javelin/sagaie stone points (e.g., the shouldered points of the Upper Solutrean). In this view, the Solutrean could be interpreted as a phenomenon of cultural drift, the emergence of its distinctive lithic technology representing a change that, although essentially neutral in terms of adaptation, carries significant information on the social geography of the LGM, highlighting a disruption of the pan-European information and exchange networks of the earlier Upper Paleolithic. Such a rupture would have isolated human groups in southwestern Europe from those in Italy and central and Eastern Europe where we see the maintenance of the Gravettian lithic technological tradition during this period.

2.1. Middle and Upper Solutrean armature types, chronology, and geography

Although challenged in the 1970s and the 1980s on the basis of its inconsistency with radiocarbon dating results, Smith's classical tripartite subdivision of the Solutrean (into Lower, Middle and Upper stages defined by the successive appearance of new projectile point types) has since been validated by the taphonomic evaluation of anomalous dates, the excavation of new sites, and the revision of classical stratigraphic sequences (e.g., Aubry et al., 1995; Corchón, 1999; Rasilla, 1989, 1994; Renard, 2008; Tiffagom, 2006; Utrilla and Mazo, 1994; Zilhão, 1997; Zilhão and Almeida, 2002; Zilhão and Aubry, 1995; Zilhão et al., 1999). On the basis of these results, the cultural-stratigraphic succession of the Solutrean between ~ 21.0 ^{14}C (~ 25.0 cal) kyr BP and ~ 19.0 ^{14}C (~ 23.0 cal) kyr BP, can be summarized as follows:

- Protosolutrean – characterized by bone/wood projectile points armed with unretouched and marginally retouched bladelets or small flakes, and by stone projectile tips obtained via minimal modification of large, hard hammer-extracted, triangular blanks with dorsally thinned bases — Vale Comprido points.
- Lower Solutrean – defined by the first use of invasive, flat retouch to extensively modify/shape the dorsal side of Vale Comprido blanks, sometimes with minimal ventral retouch of the bases, thus creating a new index fossil, the *pointe à face plane*.
- Middle Solutrean – characterized by the introduction, alongside the *pointe à face plane*, of the period's iconic, fully bifacial laurel-leaf point/knife.
- Upper Solutrean – characterized by the emergence, alongside laurel-leaf bifaces, of the shouldered point, most likely representing a functional replacement of the *pointe à face plane*, which disappears from lithic inventories during this period.

After ~ 19.0 ^{14}C (~ 23.0 cal) kyr BP, the Solutrean world breaks up. In France, the Solutrean technology based on the extensive

modification of blanks through flat, invasive retouch disappears altogether in the succeeding Badegoulian technocomplex, which emphasizes bone/antler points in combination with backed bladelets, foreshadowing the Magdalenian of the Tardiglacial period. In Iberia, the Upper Solutrean seems to have lasted until ~ 18.0 ^{14}C (~ 21.5 cal) kyr BP. In Cantabrian Spain, however, the end of the period is poorly known, due to a pattern of major erosion affecting the caves and rockshelters of the region after ~ 19 kyr ^{14}C BP, which created hiatuses and/or significant disturbances in the upper part of all known Solutrean stratigraphic sequences. In Mediterranean Spain (and with indications that the same holds true in Portugal), however, an epigonic Solutrean, the Solutreogravettian, in which flat retouch almost entirely disappears, seems to have persisted until ~ 17.0 ^{14}C (~ 20.0 cal) kyr BP.

This break-up is rooted in the marked regional differentiation already apparent in the Upper Solutrean, long recognized by all students of the phenomenon. Although the “shouldered point” principle and the persistence of laurel-leaves inherited from the preceding Middle Solutrean provide a measure of unity that justifies the treatment of all its manifestations as part of a single technocomplex, the Upper Solutrean is also characterized by the tight geographical clustering of certain lithic types that appear alongside the shouldered point (Fig. 1). Two classical examples are the concave-based point, almost exclusively found in the Cantabrian strip, with a few examples spreading eastward into the foothills of the central Pyrenees (Straus, 1977), and the barbed-and-tanged or Parpallò point (Fullola, 1985; Pericot, 1942), whose distribution is exclusive to south-central Portugal, western

Andalucia, and the Mediterranean littoral south of Valencia, with a few examples in the central Iberian Meseta. To these we can add two other subtypes with a restricted distribution within France: 1) Plisson and Geneste’s (1989) subtype A of shouldered points (large, fully bifacial, with straight edges, the overall shape fitting that of an elongated triangle), which is essentially exclusive to the Dordogne basin, but with isolated occurrences in the Pyrenees to the south and the Charente region to the north; and 2) the very large laurel-leaf bifaces best exemplified by the specimens from the famous Volgu cache (subtype J of Smith, 1966), whose core area corresponds to a latitudinal band extending westward from Burgundy to the Paris basin and the Indre and Loire valleys, and whose Upper Solutrean chronology is demonstrated by their association with shouldered points and backed bladelets at the production site of Les Maîtresaux (Aubry et al., 2007a, 2007b).

At an intermediate level of hierarchical characterization, the territory of southwestern Europe encompassed by the Upper Solutrean can also be subdivided into two macroregions on the basis of the mode of retouch used in shaping the shouldered points: 1) Franco-Cantabrian, where flat, invasive, often fully bifacial retouch is used, with abrupt retouch limited to the notching operation required to detach the lateral tang; and 2) Mediterranean, where flat retouch is absent, the shoulder is always on the right and the opposite side is fully backed from the tip of the point to the base of the tang. The actual distributions of these two concepts of the shouldered point are completely separate, although areas of overlap exist at both ends of the Solutrean, most clearly in south-central Portugal, where the Mediterranean and the Atlantic worlds also merge in terms of both geography and ecology (Ribeiro, 1987).

2.2. Possible links between technology and environment

The Middle Solutrean (~ 20.5 – 20.0 ^{14}C or ~ 24.5 – 24.0 cal kyr BP) roughly corresponds to the latter part of HE2, and the Upper Solutrean (~ 20.0 – 19.0 ^{14}C or ~ 24.0 – 23.0 cal kyr BP) is associated with the earliest stages of the LGM. Paleoenvironmental records indicate that during the Middle Solutrean environmental conditions in Western Europe were slightly colder and drier than those associated with the Upper Solutrean (Fletcher and Sánchez Goñi, 2008; Sánchez Goñi et al., 2008). During Heinrich Events, the landscape of western France was dominated by steppic plants (principally *Artemisia*) associated with heaths and sedges, northern Iberia was characterized by grass and heathlands, and southern Iberia was characterized by semi-desert conditions with landscapes dominated by *Artemisia*, *Chenopodiaceae* and *Ephedra*. (Sánchez Goñi et al., 2008). The slightly warmer and wetter conditions of the early stages of the LGM allowed for expansions of Mediterranean forest, composed of deciduous and evergreen *Quercus* species, in southern Iberia and slight development of deciduous *Quercus*–*Pinus* forest in northern Iberia (Fletcher and Sánchez Goñi, 2008).

Thus, the trend towards climatic amelioration from the Middle to the Upper Solutrean coincides with the pattern of geographical diversification of projectile point types. This raises two important questions: Diachronically, did the improvement in climatic conditions cause a significant change in the ecological niche exploited by Upper Solutrean populations with respect to their Middle Solutrean predecessors? If this was the case, one would expect to see either an expansion or a contraction of the ecological niche they exploited, in other words an absence of niche conservatism. Synchronically, is the regional diversification of Upper Solutrean projectile point types a reflection of the exploitation of distinct ecological niches by regionally differentiated human populations? As mentioned earlier, if this were to hold true, one would expect the predicted ecological niche for each armature type to closely correspond to that type’s actual geographic distribution, with little or no overlap between the

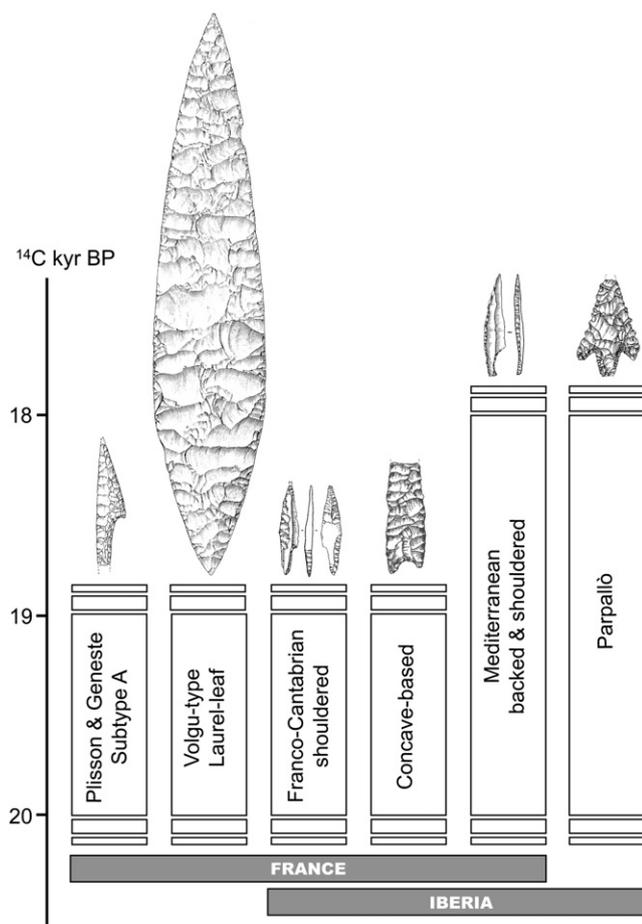


Fig. 1. Upper Solutrean index fossils and their generalized chronological and geographic distributions.

eco-cultural niches. The opposite would result in geographically broad and largely overlapping eco-cultural niche reconstructions.

3. Materials and methods

To address these questions, we used the Genetic Algorithm for Rule-Set Prediction (GARP; Stockwell and Peters, 1999) to estimate eco-cultural niches. GARP has been applied to a diverse set of topics, including habitat conservation, the effects of climate change on species' distributions, the geographic potential of species' invasions, and the geography of emerging disease transmission risk (Adjemian et al., 2006; Martínez-Meyer et al., 2004; Peterson et al., 2004; Soberón and Peterson, 2004). For data inputs, GARP requires the geographic coordinates where the species of interest has been observed and raster GIS data layers summarizing environmental dimensions potentially relevant in shaping the geographic distribution of the species.

3.1. Occurrence data

For this study, the 'species' is, according to the question being addressed, either a technocomplex in its entirety (i.e., Middle Solutrean or Upper Solutrean) or distinct projectile point types. The occurrence data are the geographic coordinates of radiometrically dated or culturally attributed archaeological sites. A review of the literature was conducted to collate archaeological sites with cultural levels that contain the diagnostic armature types described above for the Middle and Upper Solutrean and that can be placed into the 20.5–20.0 or 20.0–19.0 ¹⁴C kyr BP temporal ranges,

respectively, based on either radiometric age determinations, stratigraphic data, or a combination of both (Tables 1 and 2). The geographic coordinates of these sites were input into GARP to reconstruct armature-specific eco-cultural niches.

The use of non-radiometrically dated sites is justified by the pattern of succession of the different index fossils of the period, which follows the same order and proceeds at about the same time in the different regions where the Solutrean was present. This recurrence allows those diagnostics to be used as chronological markers as precise as radiocarbon ages, which, after calibration, yield 95.4% probability intervals typically as large as five to ten centuries. Coverage of Upper Solutrean geography that is both extensive and representative of the technocomplex's actual territory is thus obtained. This has not been possible for the Middle Solutrean because laurel-leaf projectile points can occur in both Middle and Upper Solutrean assemblages. This often makes it impossible, in the absence of radiometric evidence, to determine whether the absence of shouldered points in small assemblages or isolated finds implies a "Middle Solutrean" occurrence or an "Upper Solutrean" one for which that absence relates to functional or sampling factors. Therefore, in assembling the Middle Solutrean occurrence data set, we retained only those sites for which either assemblage size was sufficiently large to warrant this cultural designation or a secure chronology could be derived from the stratigraphic context.

3.2. Environmental data

The raster GIS data used in this study include landscape attributes (assumed to remain constant) and high-resolution climatic

Table 1
Middle Solutrean sites used to reconstruct eco-cultural niches.

Site	Country	Province	Longitude	Latitude	Reference(s)
Caldeirão	Portugal	Santarém	−8.42	39.64	Zilhão, 1997
Lagar Velho	Portugal	Leiria	−8.73	39.76	Zilhão and Trinkaus, 2002
Casal do Cepo	Portugal	Santarém	−8.56	39.43	Zilhão, 1997
Vale Almoinha	Portugal	Lisboa	−9.40	39.08	Zilhão, 1997
Monte da Fainha	Portugal	Évora	−7.69	38.76	Zilhão, 1997
Mallaetes	Spain	Valencia	−0.30 ^a	39.00 ^a	Fortea and Jordá, 1976
Parpalló	Spain	Valencia	−0.27	39.00	Villaverde and Peña, 1981
Ambrosio	Spain	Almeria	−2.10	37.83	Cortés et al., 1996
Nerja	Spain	Málaga	−3.85	36.76	Cortés et al., 1996
Bajondillo	Spain	Málaga	−4.59 ^a	36.62 ^a	Cortés et al., 1996
El Sotillo	Spain	Madrid	−3.70 ^a	40.39 ^a	Martínez de Merlo, 1984
Arenero Martínez	Spain	Madrid	−3.70 ^a	40.39 ^a	Conde et al., 2000
Fuente de las Pocillas	Spain	Valladolid	−4.77	41.74	Iglesias, 1987
La Viña	Spain	Oviedo	−5.83 ^a	43.31 ^a	Fortea, 1990
Las Caldas	Spain	Oviedo	−5.92	43.33	Straus, 1983; Corchón, 1999
Cueto de la Mina	Spain	Oviedo	−4.87	43.42	Straus, 1983; Rasilla, 1988
Hornos de la Peña	Spain	Santander	−4.43	43.27	Straus, 1983
El Castillo	Spain	Santander	−3.97	43.30	Straus, 1983
L'Arbreda	Spain	Girona	2.75	42.16	Canal and Carbonell, 1989
Azkonzilo	France	Pyrénées-Atlantiques	−1.23	43.26	Renard, 2008
Saussaye (aka Tercis)	France	Landes	−1.10	43.67	Smith, 1966
Coustaret	France	Hautes-Pyrénées	0.09	43.16	Foucher et al., 2002
Roquecoubère	France	Ariège	1.01	43.09	Smith, 1966
Montaut	France	Landes	0.63	43.71	Smith, 1966
Espasols 91	France	Pyrénées-Orientales	2.76 ^a	42.85 ^a	Sacchi, 1990
La Salpêtrière	France	Gard	4.56	43.94	Smith, 1966
Grotte du Figuier	France	Ardèche	4.57	44.30	Smith, 1966
Solutré	France	Saône-et-Loire	4.72	46.30	Smith, 1966
Grotte Mayenne	France	Mayenne	−0.36	48.00	Pigeaud et al., 2003
Le Placard	France	Charente	0.03	45.08	Smith, 1966
Abri Casserole	France	Dordogne	1.01	44.93	Aubry et al., 1995
Laugerie-Haute	France	Dordogne	1.01	44.93	Smith, 1966
Le Ruth	France	Dordogne	1.04	44.97	Smith, 1966
Abri Pataud	France	Dordogne	1.01	44.93	Smith, 1966
Badegoule	France	Dordogne	1.22	45.13	Smith, 1966
Pré-Aubert	France	Corrèze	1.53	45.16	Smith, 1966

^a Approximate coordinate.

Table 2

Upper Solutrean sites and diagnostic armature type presence (×)/absence (–) used to reconstruct eco-cultural niche models.

Site	Country	Province	Longitude	Latitude	Concave-based	Subtype A	Franco-Cantabrian shouldered	Mediterranean backed and shouldered	Parpallò	Volgu-type	Reference(s) ^(b)
Almonda	Portugal	Santarém	–8.61	39.51	–	–	–	×	–	–	Zilhão 1997
Baío	Portugal	Lisboa	–9.38 ^a	39.08	–	–	×	×	–	–	Zilhão, 1997
Caldeirão	Portugal	Santarém	–8.42	39.64	–	–	×	×	×	–	Zilhão, 1997
Casa da Moura	Portugal	Lisboa	–9.25	39.33	–	–	–	–	×	–	Zilhão, 1997
Correio-Mor	Portugal	Lisboa	–9.19	38.83	–	–	×	–	–	–	Corchón and Cardoso, 2005
Olga Grande 4	Portugal	Guarda	–7.05	41.00	–	–	×	–	–	–	Zilhão, 1997
Olival da Carneira	Portugal	Santarém	–8.93	39.35	–	–	×	×	–	–	Zilhão, 1997
Ourão	Portugal	Leiria	–8.74	40.02	–	–	×	–	–	–	Zilhão, 1997
Passal	Portugal	Santarém	–8.84	39.32	–	–	–	–	×	–	Zilhão, 1997
Poço Velho	Portugal	Lisboa	–9.39 ^a	38.70	–	–	–	–	×	–	Zilhão, 1997
Porto Dinheiro	Portugal	Lisboa	–9.34	39.15	–	–	×	–	–	–	Zilhão, 1997
Quintal da Fonte	Portugal	Santarém	–8.84	39.32	–	–	×	–	–	–	Zilhão, 1997
Salemas	Portugal	Lisboa	–9.20	38.88	–	–	×	×	×	–	Zilhão, 1997
Vale Boi	Portugal	Faro	–8.81	37.09	–	–	×	×	×	–	Gibaja and Bicho, 2006
Rua de Campolide	Portugal	Lisboa	–9.16	38.73	–	–	–	–	×	–	Zilhão, 1997
Sewell's Cave	Gibraltar	Gibraltar	–5.41	36.41 ^a	–	–	–	×	×	–	Cortés et al., 1996
Balmori	Spain	Oviedo	–4.83	43.43	–	–	×	–	–	–	Straus, 1983
Coberizas	Spain	Oviedo	–4.87	43.42	×	–	–	–	–	–	Straus, 1983
Cova Rosa	Spain	Oviedo	–5.11	43.44	×	–	×	–	–	–	Straus, 1983
Cueto de la Mina	Spain	Oviedo	–4.87	43.42	×	–	×	–	–	–	Straus, 1983
Cueva Oscura	Spain	Oviedo	–5.11	43.42 ^a	×	–	×	–	–	–	Straus, 1983
El Buxu	Spain	Oviedo	–5.09	43.36	–	–	×	–	–	–	Straus, 1983
El Cierro	Spain	Oviedo	–3.95	43.31	×	–	–	–	–	–	Straus, 1983
La Lluera	Spain	Oviedo	–5.84	43.36	–	–	×	–	–	–	Rodríguez-Asensio, 1990
La Riera	Spain	Oviedo	–4.87	43.42	×	–	×	–	–	–	Straus, 1983
La Viña	Spain	Oviedo	–5.83	43.31	×	–	×	–	–	–	Fortea, 1990
Las Caldas	Spain	Oviedo	–5.92	43.33	×	–	×	–	–	–	Straus, 1983
Tres Calabres	Spain	Oviedo	–4.87	43.42	–	–	×	–	–	–	Straus, 1983
Altamira	Spain	Santander	–4.11	43.29	×	–	×	–	–	–	Straus, 1983
Cueva Chuffin	Spain	Santander	–4.45	43.28	×	–	×	–	–	–	Straus, 1983
Cueva Morin	Spain	Santander	–3.86	43.31	–	–	×	–	–	–	Straus, 1983
El Mazo de Camargo	Spain	Santander	–3.86	43.30	×	–	–	–	–	–	Straus, 1983
El Mirón	Spain	Santander	–3.46	43.26	×	–	×	–	–	–	Straus, 1983; Straus and González-Morales, 2003
El Pendo	Spain	Santander	–3.92 ^a	43.32 ^a	×	–	×	–	–	–	Straus, 1983
La Pasiiega	Spain	Santander	–3.86	43.30	×	–	–	–	–	–	Straus, 1983
Aitzbitarte IV	Spain	Guipúzcoa	–1.89	43.31	×	–	×	–	–	–	Straus, 1983; Chauchat, 1990
Atxuri	Spain	Vizcaya	–2.66	43.14	×	–	×	–	–	–	Straus, 1983
Ermittia	Spain	Guipúzcoa	–2.37	43.27	–	–	×	–	–	–	Straus, 1983
Abauntz	Spain	Navarra	–2.04	43.02	–	–	×	–	–	–	Montes and Utrilla, 2008
Ambrosio	Spain	Almeria	–2.10	37.83	–	–	–	×	×	–	Cortés et al., 1996
Los Morceguillos	Spain	Almeria	–2.05	37.22	–	–	–	×	×	–	Cortés et al., 1996
Serrón	Spain	Almeria	–1.92	37.25	–	–	–	×	×	–	Cortés et al., 1996
Los Ojos	Spain	Granada	–3.59	36.99	–	–	–	–	×	–	Cortés et al., 1996; Toro and Almohalla, 1985
Higuerón	Spain	Málaga	–4.30	36.75	–	–	–	×	×	–	Cortés et al., 1996
Tajo del Jorox	Spain	Málaga	–4.86	36.73	–	–	–	×	–	–	Cortés et al., 1996
Boquete de Zafarraya	Spain	Málaga	–4.13	36.95	–	–	–	×	–	–	Cortés et al. 1996
Abrigo 6 del Humo	Spain	Málaga	–4.32	36.74 ^a	–	–	–	–	×	–	Cortés et al., 1996
Cubeta de la Paja	Spain	Cádiz	–5.81	36.34	–	–	–	–	×	–	Giles-Pacheco et al., 1998
Cuevas de Levante	Spain	Cádiz	–5.81	36.34	–	–	–	×	×	–	Giles-Pacheco et al., 1998
Higueral (Cerro de Motillas)	Spain	Cádiz	–5.59	36.55	–	–	–	–	×	–	Giles-Pacheco et al., 1998
La Fontanilla I	Spain	Cádiz	–6.07 ^a	36.28	–	–	–	×	×	–	Ramos et al., 1995
El Pirulejo	Spain	Córdoba	–4.13	37.41	–	–	–	–	×	–	Cortés et al., 1998
Peña de la Grieta	Spain	Jaén	–4.18	37.87	–	–	–	–	×	–	Arteaga et al., 1998
Cau de les Goges	Spain	Girona	2.85	42.03	–	–	×	–	–	–	Canal and Carbonell 1989
L'Arbreda	Spain	Girona	2.75	42.16	–	–	×	–	–	–	Canal and Carbonell, 1989
Reclau Viver	Spain	Girona	2.75	42.16	–	–	×	–	–	–	Canal and Carbonell, 1989
Davant Pau	Spain	Girona	2.75	42.16	–	–	×	–	–	–	Canal and Carbonell, 1989
Parpallò	Spain	Valencia	–0.27	39.00	–	–	–	×	×	–	Villaverde and Peña, 1981
Barranc Blanc	Spain	Valencia	–0.26	38.93	–	–	–	×	×	–	Villaverde and Peña, 1981
Cova dels Porcs	Spain	Valencia	–0.18	38.97	–	–	–	×	×	–	Villaverde and Peña, 1981
Cejo del Pantano	Spain	Murcia	–1.54	37.75	–	–	–	×	×	–	Cacho, 1980
Finca Doña Martina	Spain	Murcia	–1.49	38.04	–	–	–	×	×	–	Unpublished (ongoing excavations by Zilhão & Villaverde)
Abrigo del Palomar	Spain	Albacete	–2.32	38.36	–	–	–	×	×	–	Córdoba and Vega, 1988

(continued on next page)

Table 2 (continued)

Site	Country	Province	Longitude	Latitude	Concave-based	Subtype A	Franco-Cantabrian shouldered	Mediterranean backed and shouldered	Parpallò	Volgu-type	Reference(s) ^(b)
Arenero de Vidal	Spain	Madrid	-3.70	40.42	-	-	-	-	×	-	Pericot and Fullola, 1981
Abri Casserole	France	Dordogne	1.01	44.93	-	×	×	-	-	-	Aubry et al., 1995
Cantalouette II	France	Dordogne	0.57	44.86	-	-	-	-	-	×	Smith, 1966
Combe Saunière 1	France	Dordogne	0.16	45.14	-	×	×	-	-	-	Geneste and Plisson, 1990
Excideuil	France	Dordogne	1.05	45.34	-	×	-	-	-	-	Smith, 1966
Fourneau du Diable	France	Dordogne	0.59	45.32	-	×	×	-	-	-	Smith, 1966
Grotte des Eyzies	France	Dordogne	1.01	44.93	-	-	×	-	-	-	Smith, 1966
La Balutie	France	Dordogne	1.16	45.07	-	×	-	-	-	-	Smith, 1966
La Crouzette	France	Dordogne	1.02	44.93	-	-	-	-	-	×	Smith, 1966; Aubry et al., 2008
La Ferrassie	France	Dordogne	0.92	44.98	-	×	×	-	-	-	Smith, 1966
Lachaud	France	Dordogne	1.31	45.13	-	×	-	-	-	-	Smith, 1966
Laugerie Haute	France	Dordogne	1.01	44.93	-	×	×	-	-	×	Smith, 1966
Le Pouzet	France	Dordogne	1.31	45.13	-	-	×	-	-	-	Smith, 1966
Les Bernous	France	Dordogne	0.59	45.32	-	×	×	-	-	-	Smith, 1966
Les Jean-Blancs	France	Dordogne	0.77	44.81	-	×	×	-	-	-	Smith, 1966
Mazerat	France	Dordogne	0.73	44.80	-	-	×	-	-	-	Smith, 1966
Oreille d'Enfer	France	Dordogne	1.01	44.93	-	-	×	-	-	-	Smith, 1966
Pech de la Boissière	France	Dordogne	1.00	45.09	-	×	×	-	-	-	Smith, 1966
Roc de Combe-Capelle	France	Dordogne	0.82	44.77	-	×	-	-	-	-	Smith, 1966
Saint-Front-de-Cornac	France	Dordogne	0.66	45.53	-	-	×	-	-	-	Smith, 1966
Tourtoirac	France	Dordogne	1.05	45.34	-	-	×	-	-	-	Smith, 1966
Valojoulx	France	Dordogne	1.11	45.00	-	-	×	-	-	-	Smith, 1966
Ferrand	France	Gironde	-0.16	44.90	-	-	×	-	-	-	Lenoir, 1990
La Cabanne	France	Gironde	0.08	44.74	-	-	×	-	-	-	Lenoir, 1990
La Chapelle	France	Gironde	0.08	44.74	-	-	×	-	-	-	Lenoir, 1990
Les Queyrons	France	Gironde	-0.23	44.69	-	-	×	-	-	-	Lenoir, 1990
Les Vignes du Moulin	France	Gironde	0.16	44.74	-	-	×	-	-	-	Lenoir, 1990
Murlet	France	Gironde	-0.09	44.81	-	-	×	-	-	-	Lenoir, 1990
Pourteau	France	Gironde	-0.09	44.95	-	-	×	-	-	-	Lenoir, 1990
Grotte du Pape	France	Landes	-0.70	43.63	×	×	-	-	-	-	Smith, 1966
Vallon d'Escamat	France	Landes	-0.75	44.15	-	-	×	-	-	-	Lenoir, 1990
Azkonzilo	France	Pyrénées-atlantiques	-1.23	43.26	×	-	×	-	-	-	Chauchat, 1990
Haregi	France	Pyrénées-atlantiques	-0.93	43.15	×	-	×	-	-	-	Chauchat, 1990
Isturitz	France	Pyrénées-atlantiques	-1.20	43.37	×	-	-	-	-	-	Foucher and Normand, 2004
Volgu	France	Saône-et-Loire	4.06	46.51	-	-	-	-	-	×	Smith, 1966; Aubry et al., 2008
Abri Fritsch	France	Indre	1.25	46.71	-	-	×	-	-	×	Aubry et al., 2007a, 2007b
Fressignes	France	Indre	1.58	46.44	-	-	×	-	-	-	Aubry et al., 2007a, 2007b
Monthaud	France	Indre	1.20	46.54	-	-	×	-	-	×	Smith, 1966
Les Maitreaux	France	Indre-et-Loire	0.96	46.83	-	-	×	-	-	×	Aubry et al., 2007a, 2007b
Les Roches à Abilly	France	Indre-et-Loire	0.73	46.94	-	-	-	-	-	×	Smith, 1966; Aubry et al., 2008
St.-Sulpice-de-Favières	France	Essonne	2.18	48.54	-	-	-	-	-	×	Schmider, 1990
Grande Grotte de Bize	France	Aude	2.88	43.32	-	-	×	-	-	-	Sacchi, 1976; Sacchi 1990
Petite Grotte de Bize	France	Aude	2.88	43.32	-	-	×	×	-	-	Sacchi 1976; Sacchi, 1990
La Rouvière	France	Gard	4.24	43.93	-	-	×	×	-	-	Bazile, 1990
La Salpêtrière	France	Gard	4.56	43.94	-	-	×	×	-	-	Smith, 1966
Baume d'Oullins	France	Gard/Ardèche	4.40	44.35	-	-	×	×	-	-	Bazile, 1990
Chez Rose	France	Corrèze	1.53	45.16	-	-	×	-	-	-	Smith, 1966
Noailles	France	Corrèze	1.53	45.10	-	-	×	-	-	-	Smith, 1966
Pré-Aubert	France	Corrèze	1.52	45.13	-	×	-	-	-	-	Smith, 1966
Puy de Lacam	France	Corrèze	1.56	45.17	-	-	×	-	-	-	Smith, 1966
Grotte des Harpons	France	Haute-Garonne	0.67	43.23	×	-	×	-	-	-	Foucher and San Juan 2000a, 2000b
Grotte des Rideaux	France	Haute-Garonne	0.67	43.23	-	-	×	-	-	-	Foucher and San Juan 2000a, 2000b
Lacave	France	Lot	1.52	44.85	-	×	-	-	-	-	Smith, 1966
Le Cuzoul	France	Lot	1.55	44.48	-	-	×	-	-	-	Renard, 2008
Peyrugues	France	Lot	1.67	44.54	-	×	×	-	-	-	Renard, 2008
Reilhac	France	Lot	1.72	44.70	-	×	-	-	-	-	Smith, 1966
Grotte Rochefort	France	Mayenne	0.39	48.01	-	-	-	-	-	×	Smith, 1966
Gavechou	France	Charente	0.35	45.49	-	-	×	-	-	-	Smith, 1966
La Combe-à-Rolland	France	Charente	0.10	44.35	-	×	×	-	-	-	Smith, 1966
Le Placard	France	Charente	0.03	45.80	-	×	×	-	-	-	Smith, 1966
Les Vachons	France	Charente	0.12	45.52	-	-	×	-	-	-	Smith, 1966
Roc de Sers	France	Charente	0.32	43.60	-	-	×	-	-	-	Smith, 1966

Table 2 (continued)

Site	Country	Province	Longitude	Latitude	Concave-based	Subtype A	Franco-Cantabrian shouldered	Mediterranean backed and shouldered	Parpalló	Volgu-type	Reference(s) ^(b)
Le Rail	France	Charente-Maritime	-0.67	45.51	–	–	–	–	–	×	Smith, 1966
La Guitière	France	Vienne	0.84	46.68	–	–	–	–	–	×	Smith 1966; Aubry et al., 2008

^a Approximate coordinate

^b Because Smith (1966) subsumed under “*pointe à cran*” the form subsequently discriminated by Plisson and Geneste (1989) as “subtype A”, and because he sometimes counted as concave-based those laurel-leaf items whose basal morphology was, in fact, the byproduct of a break, not of intentional shaping, we used only the illustrated sites in his gazetteer to tabulate presence/absence of these diagnostics.

simulations for HE2 and the LGM. Landscape variables included slope, aspect, elevation, and compound topographic index (a measure of tendency to pool water) from the Hydro-1 K data set (U.S. Geological Survey, Center for Earth Resources Observation and Science).

In order to reconstruct Middle and Upper Solutrean eco-cultural niches, we used a high-resolution LGM “cold anomaly” simulation and a high-resolution LGM simulation, respectively. The former is used as a proxy for paleoclimatic conditions associated with HE2 between 21.0–20.0 kyr ¹⁴C BP, and the latter approximates the initial stages of the LGM between 20.0–19.0 kyr ¹⁴C BP. The last glacial period was marked by dramatic climatic variability (Dansgaard et al., 1993; Johnsen et al., 1992), with the LGM representing a unique suite of environmental conditions (Ditlevsen et al., 1996; Peyron et al., 1998). This period, centered on ~18.0 ¹⁴C (~21.5 kyr cal) BP, was the last period of maximum global ice sheet volume, along with cold and generally arid conditions in northern and western Europe. To capture the climatic impact of LGM conditions, we used an atmospheric general circulation model with a refined grid over Europe (resolution of ~60 km over western Europe), run at the Laboratoire des Sciences du Climat et de l'Environnement, Gif-sur-Yvette, France. This high-resolution LGM atmospheric simulation follows the protocol proposed by the PMIP2 project (Braconnot et al., 2007, <http://pmip2.lsce.ipsl.fr>), with orbital parameters and atmospheric greenhouse gases concentrations set to their 21,000 cal BP values (Berger, 1978; Raynaud et al., 1993) and ice-sheet height and extent prescribed according to the Peltier (2004) ICE-5G reconstructions. The PMIP2 protocol is designed for coupled ocean-atmosphere models, whereas an atmosphere-only model was used in the present study. Therefore, a prescription of the sea-surface characteristics (temperatures and sea-ice extent) was necessary and we used the most recent reconstructions, i.e. the GLAMAP data set (Paul and Schäfer-Neth, 2003; Sarnthein et al., 2003). The results of this simulation, over our area of interest, have been compared to pollen-based climatic reconstructions (Wu et al., 2007). They are in close agreement with the pollen data for summer and annual mean temperatures, as well as mean annual precipitation, but display some underestimation (of up to 2 °C) of winter cooling over Western Europe and the Mediterranean.

Table 3

Vegetation types simulated with ORCHIDEE.

Vegetation type	Variable code
tropical broad leaf evergreen	tble
tropical broad leaf raingreen	tblr
temperate needle leaved evergreen	tnle
temperate broad leaved evergreen	tmple
temperate broad leaved summergreen	tbls
boreal needle leaved evergreen	bnle
boreal broad leaved summergreen	bbbs
boreal needle leaved summergreen	bnls
C3 grasses	c3 g
C4 grasses	c4 g

While there are many simulations of the LGM climate (e.g., those performed in the first and second phases of the Paleoclimate Modeling Intercomparison Project), there are few high-resolution simulations. Jost et al. (2005) compared three of these simulations, all of which were driven with the CLIMAP (1981) sea surface temperature and sea ice reconstructions for the LGM. In this work, we use a more up-to-date surface ocean forcing data set and to our knowledge, there are no other high-resolution simulations that have used this data set.

In order to effectively simulate climatic conditions immediately preceding the LGM, we modified the forcing component related to the surface conditions in the North Atlantic by applying zonal all-year-long sea surface temperature (SST) anomalies. Thus, this “LGM cold anomaly” simulation roughly approximates the conditions of HE2. The simulation was created by cooling the North-Atlantic surface by 2 °C between 40–55 °N, and by linearly decreasing values to 0 °C at 30°N to the south and at 63°N to the north. The choice of the 2 °C maximum cooling anomaly is based on the reconstructions by Cortijo et al. (1997) for the SST decrease between 40° and 60°N associated with HE4, the best identified Heinrich event in the numerous North-Atlantic cores they analyzed. Sea-ice cover consistent with the SSTs is obtained by imposing sea ice where the SST is lower than -1.8 °C. As all the other forcing components are kept the same, this HE simulation is a sensitivity experiment to changes in North-Atlantic surface conditions.

From these two simulations, we derived the following variables for input into GARP: warmest month temperature, coldest month temperature, mean annual temperature, and mean annual precipitation. The values of warmest and coldest months refer to the warmest or coldest month as determined from 10 yr averages of simulation results. In addition to these climatic variables, we used a dynamic vegetation model, ORCHIDEE (Krinner et al., 2005), to simulate vegetation cover offline. By forcing ORCHIDEE with the high-resolution climatic simulation output, data concerning 10 vegetation classes were compiled (Table 3). These climatic and vegetation data were incorporated into the GARP predictive modeling process. These simulations are available upon request.

3.3. Genetic algorithm for rule-set prediction

In GARP, occurrence data are resampled randomly by the algorithm to create training 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 possibilities (e.g., logistic regression, bioclimatic rules) and applied to the training data to develop specific rules (Stockwell and Peters, 1999). These rules evolve to maximize predictivity by using a number of methods (e.g., crossing over among rules) mimicking chromosomal evolution. Predictive accuracy is then evaluated based on an independent subsample of the presence data and a set of points sampled randomly from regions where the species has not been detected. The resulting rule-set defines the distribution of the subject in

ecological space (i.e., the ecological niche; Soberón and Peterson, 2005), and is projected onto the landscape to predict a potential geographic distribution (Peterson, 2003). The GARP specifications we used are the same as those detailed in previous ECNM studies (Banks et al., 2008a; Banks et al. 2008b; Banks et al. 2008c).

To evaluate whether human populations exploited the same ecological niche (i.e., niche conservatism) during HE2 and the early LGM, we projected the eco-cultural niche model developed for each period onto the climatic conditions of the other. Each projection was compared to the locations of known occurrences for the technocomplex associated with the climatic phase into which the model had been projected to test whether or not it successfully predicted the known distribution. For example, the Middle Solutrean eco-cultural niche projected onto LGM conditions was compared to the locations of the known Upper Solutrean sites. The degree of predictivity (i.e., niche stability) was evaluated statistically by determining the proportional area predicted present by the projected model at each predictive threshold (i.e., 10 out of 10 best-subset models in agreement, 9 out of 10 in agreement, etc.), along with the number of occurrence points correctly predicted at each threshold. A cumulative binomial statistic was applied to these values to determine whether the coincidence between projected predictions and independent test points was significantly better than random expectations. In other words, the approach evaluates whether the two distributions are more similar to one another than one would expect by chance [see Peterson and Nyári (2007) for a similar application of this methodology].

4. Results

4.1. Period-specific ECNMs

The predicted geographic range of the Middle Solutrean technocomplex (Fig. 2 A) covers central and western France, with

a northern limit corresponding roughly to the regions just north of the Loire River valley. The predicted range excludes the Massif Central and all of northeastern France. The range also extends well to the south to include most of the Iberian Peninsula, with the exception of its northwestern regions and the Pyrenees. This eco-cultural niche is also present across the Italian peninsula, although the Solutrean complex is known not to have extended into this part of Europe. This reconstructed ecological niche's mean annual temperature and precipitation and their ranges are contained in Table 4.

The geographic range of the reconstructed eco-cultural niche for the Upper Solutrean technocomplex (Fig. 2 B) is very similar to that of the Middle Solutrean, although the Upper Solutrean range additionally includes, in France, regions of Brittany, Normandy and the southern Paris Basin, as well as the extreme southern limits of the Iberian Peninsula. Similar to the Middle Solutrean, this niche also covers a broad mean annual temperature range, although it is warmer and wetter than the former (Table 4).

4.2. Armature-specific Upper Solutrean ECNMs

In France, the reconstructed eco-cultural niche for the Franco-Cantabrian shouldered point type (Fig. 3 A) is geographically restricted to the west, with a northern limit defined by the Loire River valley. This niche is not present in regions of northern and eastern France, nor the Massif Central. The niche's range covers southern France, including the foothills of the Pyrenees, northern Spain including Cantabria and the Ebro valley, central Spain, and central-littoral Portugal. This ecological niche is also expressed in the northern and central portions of the Italian Peninsula, although this Upper Solutrean technology does not extend that far to the east. The Franco-Cantabrian shouldered point niche is characterized by a slightly cooler mean annual temperature and higher mean annual precipitation than that of the Upper Solutrean technocomplex as a whole (Table 4).

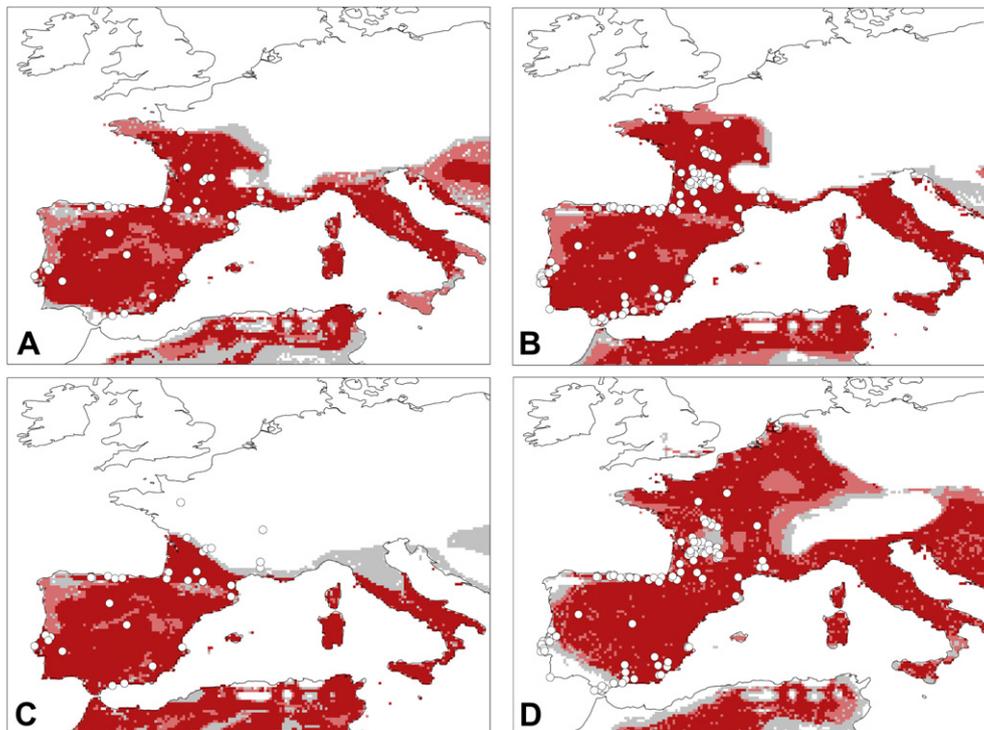


Fig. 2. Eco-cultural niche reconstructions: A) Middle Solutrean, B) Upper Solutrean, C) Projection of the Upper Solutrean eco-cultural niche model onto Heinrich Event 2 climatic conditions, D) Projection of the Middle Solutrean eco-cultural niche model onto LGM climatic conditions. For each model, grid squares with 1–5 of 10 models predicting the presence of suitable conditions are indicated in grey, grid squares with 6–9 models in agreement are depicted in pink, and squares with all 10 models in agreement are indicated in red.

Table 4

Reconstructed eco-cultural niche mean annual temperature and precipitation ranges and values.

Technocomplex or projectile point type	Mean annual temperature range (°C)	Mean annual temperature (°C)	Mean annual precipitation range (mm)	Mean annual precipitation (mm)
Middle Solutrean	0–12	4.62	< 1095	142.35
Upper Solutrean	1–14	7.24	< 1095	200.75
Shouldered point	2–14	6.23	< 1095	262.8
Backed/Shouldered point	2–14	7.03	< 730	102.2
Plisson & Geneste Type A	2–5	4.06	< 1095	704.45
Leaf point	1–5	3.15	365–1095	708.1
Concave base point	4–5	4.61	365–730	489.1
Parpallò point	6–14	9.07	< 365	32.85

The geographic expression of the Mediterranean backed and shouldered projectile point ecological niche (Fig. 3 B) is principally restricted to Mediterranean regions with notable exceptions in the southwestern and northwestern portions of the Iberian Peninsula. As with the Franco-Cantabrian shouldered point, this ecological niche is also expressed in the northern and central portions of the Italian Peninsula. This point type's climatic ranges are similar to

those of the Franco-Cantabrian shouldered point, with a slightly higher mean annual temperature and significantly reduced mean annual precipitation (Table 4).

The “subtype A” shouldered armature has one of the more restricted geographic expressions of the reconstructed eco-cultural niches (Fig. 3 C). Its limits are constrained by the Loire and Vienne Rivers and the northern Pyrenees, with a core centered on the

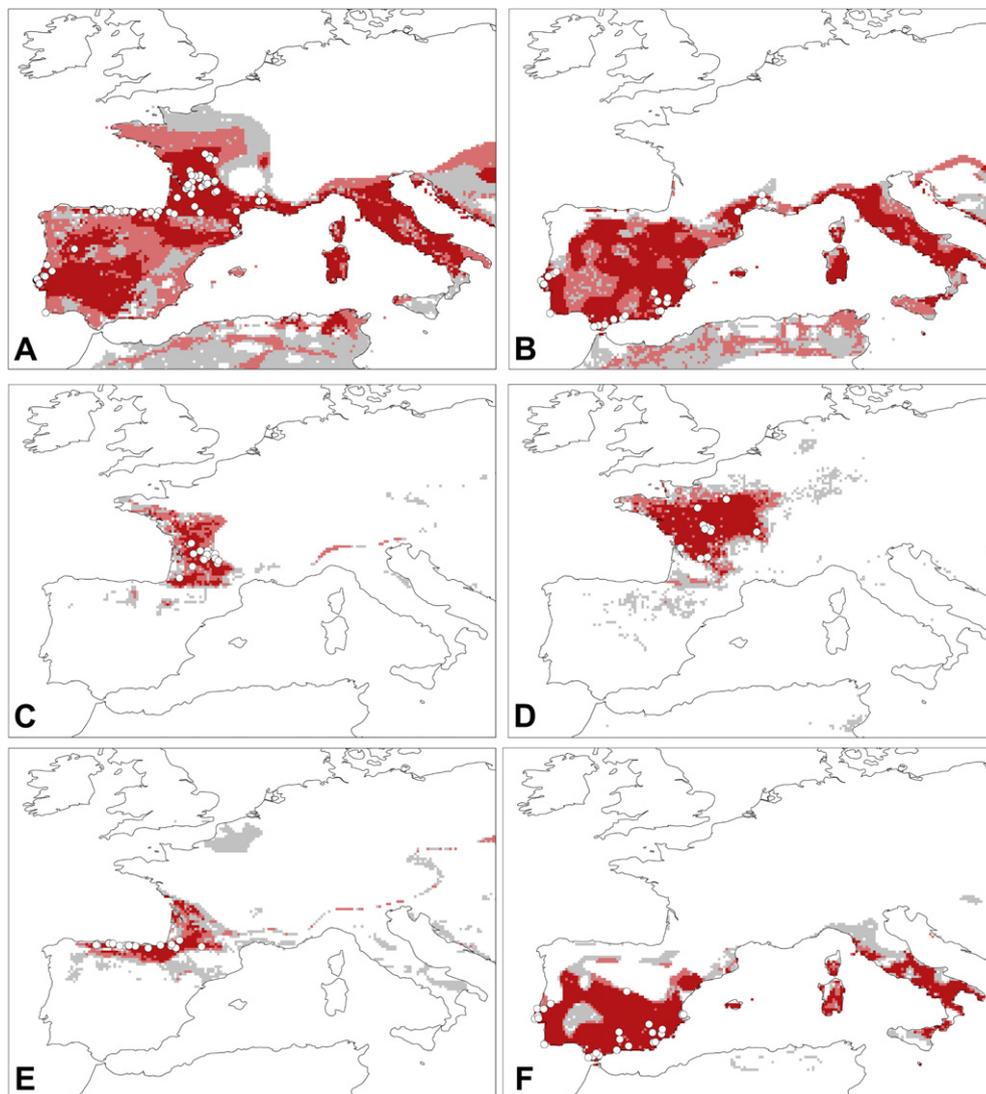


Fig. 3. Upper Solutrean eco-cultural niche reconstructions based on sites from which distinct armature types have been recovered: A) Franco-Cantabrian shouldered point, B) Mediterranean backed and shouldered point, C) Plisson and Geneste's subtype A shouldered point, D) Very large, Volgu-type laurel-leaf biface, E) Concave-based point, F) Parpallò point. For each model, grid squares with 1–5 of 10 models predicting the presence of suitable conditions are indicated in grey, grid squares with 6–9 models in agreement are depicted in pink, and squares with all 10 models in agreement are indicated in red. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Périgord region. This niche has a mean annual temperature range of 2–5 °C, with a mean towards the upper end of this range, and it has one of the highest mean annual precipitation values (Table 4).

The very large Volgu type leaf points are associated with an ecological niche that has a relatively broad and northerly distribution (Fig. 3 D). It extends from the Atlantic coast along the limits of the Loire River valley into the southern Paris Basin, south along the Seine and Yonne valleys, along the northern limits of the Massif Central and across the Périgord. Its ecological dimensions (Table 4) essentially overlap those associated with the subtype A shouldered point, although their core areas differ, with the Volgu type having a range extending well to the north and east compared to that of subtype A.

The reconstructed eco-cultural niche for the concave-based armature type has a limited geographic expression restricted to the Cantabrian region of northern Spain and the northern limits of the Pyrenees and their foothills in southwestern France (Fig. 3 E). There are some very restricted expressions of this ecological niche in regions immediately surrounding Bordeaux, but these are not associated with any recorded sites associated with this point type. The concave-based point's eco-cultural niche occupies a very restricted mean annual temperature range and has a relatively mid-range mean annual precipitation value (Table 4).

The Parpallò point type's ecological niche is geographically restricted to the southern half of the Iberian Peninsula, with a marked absence in the Huelva and Badajoz regions of Spain (Fig. 3 F). These same ecological conditions are also expressed in southern portions of the Italian peninsula. This eco-cultural niche covers the upper range of mean annual temperatures associated with the Upper Solutrean reconstructions, and it is associated with extremely dry conditions (Table 4).

4.3. Niche projections between Middle and Upper Solutrean

The projection of the Middle Solutrean eco-cultural niche onto the early LGM climatic conditions associated with the succeeding Upper Solutrean predicts a range (Fig. 2 D) that extends more into higher latitudes than the actual eco-cultural niche range reconstructed for the Upper Solutrean technocomplex (Fig. 2 B). Major dissimilarities consist of low predictive success in the present-day French departments of Dordogne and Limousin, the southwestern portion of the Iberian Peninsula, and the southern coastal regions of present-day Portugal. Despite the fact that the geographic range of the projected Middle Solutrean eco-cultural niche onto the LGM climatic conditions is broader than the Upper Solutrean site distribution, it and the Upper Solutrean eco-cultural niche are interpredictive at all thresholds (Table 5).

The projection of the Upper Solutrean eco-cultural niche reconstruction back onto the climatic conditions of late HE2 results in a predicted range (Fig. 2 C) that is restricted to more southerly latitudes than the actual distribution of Middle Solutrean sites. The projected ecological niche is expressed in extreme southwestern Iberia, a region where no presence is reconstructed in the Middle Solutrean eco-cultural niche. Despite the differences, the Middle Solutrean eco-cultural niche and that of the Upper Solutrean projected onto HE2 climatic conditions are interpredictive at all thresholds (Table 5).

5. Discussion

5.1. Accuracy and robusticity of the predictions

Before interpreting predictive models, it is important to establish that they are accurate and robust. Our sample sizes for each of the Upper Solutrean adaptive system subsamples are sufficient to avoid the need for jackknifing manipulations applied to small samples (Pearson et al., 2007). Stockwell and Peterson (2002) demonstrated that GARP consistently produces accurate and robust predictive models when occurrence samples are ≥ 20 . Previous modeling work has shown excellent predictive abilities for ecological niche models concerning distributional patterns of species (Iloldi-Rangel et al., 2004; Martínez-Meyer et al., 2004). On the basis of this work, we can assume that our models accurately represent the different adaptive systems' and subsystems' eco-cultural niches and associated geographic ranges. The inter-regional imbalance in research histories, however, biases occurrence patterns and implies that issues of coverage and sampling validity must be borne in mind when interpreting our results.

The lack of predicted presence in the Massif Central, the Pyrenees, and the highest Iberian mountains during both the Middle and the Upper Solutrean genuinely reflects past reality, as these regions correspond to glaciated terrain unavailable for human settlement. Given the 150-year-long history of intensive Upper Paleolithic research in France, the northward expansion of Upper Solutrean occurrences and of the corresponding eco-cultural niche is probably genuine too. An intriguing result of the niche projections is that French Middle Solutrean adaptive systems should be expected to have expanded into northern France, Belgium, the Netherlands, western Germany and eastern France under the slightly ameliorated climatic conditions of the Upper Solutrean (Fig. 2 D). It is most likely that such an expansion did not occur because these regions, characterized by periglacial environments with deep, continuous permafrost (van Vliet-Lanoë et al., 2004), may have remained uninhabitable. This discord between the actual distribution of Upper Solutrean sites and the projected Middle Solutrean model also reflects the fact that the Upper Solutrean ecological niche was slightly narrower than that of the Middle Solutrean, even though the two are not significantly different (Table 5). Therefore, Middle Solutrean populations occupied a broader range of ecological conditions during HE2. With the slight amelioration of conditions during the LGM, human populations did not need such ecologically and geographically extensive settlement and subsistence systems.

Concerning the slight northern expansion of the human range during the Upper Solutrean, we note that the pattern may well be stronger than indicated by our models since the validity of one of our Middle Solutrean occurrences, the site of Mayenne-Sciences (Porche de la Dérouine; Pigeaud et al., 2003), is open to question. Located in the same Saulges canyon, the nearby site of Grotte Rochefort has yielded an assemblage of laurel leaf bifaces dated to the Upper Solutrean. These data suggest that the absence of shouldered points at these sites may well be due to sampling factors or site function, and thus open the possibility that the Solutrean occupation of this northern region corresponds solely to the Upper, and not the Middle, Solutrean.

Table 5
Results of predictivity tests between LGM and post-LGM climatic conditions for Middle and Upper Solutrean eco-cultural niche projections. Site totals for each period are lower than those contained in Tables 1 and 2 because the projection calculations are based on spatially unique sites (i.e. some grid squares contain more than one archaeological site).

Comparison	All models predict			Most models predict			Any model predicts		
	Prop. Area	Success	P	Prop. Area	Success	P	Prop. Area	Success	P
Middle Solutrean predicts Upper Solutrean	0.31983	54/92	3.87×10^{-8}	0.47468	77/92	1.05×10^{-13}	0.5259	83/92	4.33×10^{-15}
Upper Solutrean predicts Middle Solutrean	0.19892	23/31	8.81×10^{-12}	0.24817	23/31	1.17×10^{-9}	0.32173	26/31	3.59×10^{-10}

The Upper Solutrean's apparent expansion into southernmost Iberia is in all likelihood an artifact of the current impossibility of validating as "Middle Solutrean" non-dated, small-sized assemblages or isolated finds of laurel-leaf bifaces, such as at the cave of Escoural, in the Portuguese Alentejo (Gomes et al., 1990). The lack of occurrence points must also explain why presences in the Galicia region of extreme northwestern Spain are not predicted for the Middle and Upper Solutrean eco-cultural niches. It is unlikely that this absence reflects a real settlement void. Instead, it is most certainly caused by the fact that the entire Upper Paleolithic of the region prior to the Magdalenian remains unknown as a result of a historical deficit in the study of the period in the region (Villar, 2008).

The other voids in some of the Iberian distributions are more difficult to evaluate. For instance, those corresponding to the Huelva and Badajoz provinces in both the Mediterranean backed and shouldered point and the Parpalló point eco-cultural niches (Figs. 3B, 3F) might be taken to indicate, in agreement with the pattern in Fig. 3A, that these areas are exclusively associated with the range of the Franco-Cantabrian shouldered point. An alternative possibility is that the area of overlap between the Mediterranean and Atlantic worlds seen in central Portugal extended eastward along the drainages of the Guadiana and the Guadalquivir rivers.

5.2. Period comparisons

The binomial tests comparing eco-cultural niche projections between the HE2 and early LGM climatic phases (Table 5) indicate that human populations associated with Solutrean material cultures occupied and exploited a consistent niche across these two periods. Thus, there is eco-cultural niche conservatism for the period $\sim 21.0\text{--}19.0$ ^{14}C ($\sim 25.0\text{--}23.0$ cal) kyr BP. While their ecological niches were not significantly different, we do see that the Upper Solutrean eco-cultural niche has a slightly broader geography incorporating higher latitudes. This is likely a product of the less severe climatic conditions of the period, which would have favored a northward extension of the human range, accompanied by permanent Upper Solutrean settlement of territories that might have been only of marginal and warmer season use during the preceding Middle Solutrean.

When the Upper Solutrean technocomplex is viewed as a whole, the geographic expression of its reconstructed eco-cultural niche is broad and essentially covers those portions of Europe that were habitable. This is in agreement with reconstructions of the human range in Western Europe under full LGM conditions (Banks et al. 2008a), and both ranges would not be expected to differ dramatically since differences between early LGM and full LGM environmental conditions would have been minor.

5.3. Significance of the armature-specific niches

When the reconstructed eco-cultural niches associated with distinct Upper Solutrean armature types are examined, it is apparent that several of the point types correspond to distinct suites of environmental conditions. The Franco-Cantabrian shouldered and the Mediterranean backed and shouldered point types occupy relatively broad ecological ranges. The subtype A, Volgu, concave-base, and Parpalló armature types, despite relatively slight differences between their respective climatic conditions (Table 4), are associated with geographically distinct eco-cultural niches that exhibit very little overlap. Therefore, by identifying the links between these occurrences and environmental conditions, the GARP models indicate that these cultural territories correspond to distinct suites of environmental factors, thus demonstrating that

there is a significant link between their cultural territories and ecology.

The eco-cultural niche projections indicate that the transition from the Middle to the Upper Solutrean is characterized by eco-cultural niche conservatism, so it cannot be argued, in the fashion of 'Arms Race' explanations for the Solutrean as a whole, that the diversification of point styles during the Upper Solutrean reflects cultural solutions to changing environmental conditions. In fact, with respect to settlement-subsistence, there is complete regional continuity between the Middle and the Upper Solutrean, with substantial differences existing (and being maintained) across this entire time interval only when the different regions encompassed by the phenomenon are compared with one another. For example, Middle and Upper Solutrean groups in SW France were subarctic reindeer hunters but open-pine-and-heathland red deer hunters in the littoral areas of central Portugal, where, as is also the case in the rest of southwestern Iberia, reindeer never existed.

In short, for the Middle Solutrean, a pattern of significant technological homogeneity overprinted a diverse range of environments. What is new in the Upper Solutrean is the rise of significant technological heterogeneity in the face of broadly similar environmental constraints. The most parsimonious explanation for these patterns is that, with the slight amelioration of climatic conditions following HE2, human populations of the early LGM were able to reduce not only the territories that they exploited with their settlement and subsistence systems, but also the geographically broad social networks that likely characterized the cultural landscape during the preceding period. One cultural adaptation that is beneficial in harsher environments (those characterized by higher levels of ecological risk; see Collard and Foley, 2002) is the establishment and maintenance of extensive social networks that allow human populations to manage periods marked by shortages in subsistence-related resources. Our hypothesis is that under the more benign conditions that followed HE2, the need for extensive social networks was reduced, thereby allowing populations to become more regionalized, meaning that cultural transmission between geographic regions diminished in frequency (Zilhão, *in press*). One result of such regionalization would be the development of culturally distinct armature types and the extraction of resources from regionally distinct and narrower ranges of ecological conditions.

While distinct Upper Solutrean projectile point types are associated with discrete ecological niches, it is difficult to identify the specific behavioral features within these adaptive systems that linked them to particular environments. These behavioral features may be directly linked to hunting activities and armature use, or the different projectile point styles may reflect differences in other aspects of subsistence systems. In the latter case, the stylistic differences in armatures indirectly signal subsistence differences that are difficult to detect archaeologically. Whatever the case, these different armature types reflect a trend towards regionalization which would have allowed for the development of cultural adaptations that were environmentally specific.

While it is unclear at present what lies behind this specificity, one thing is certain: Upper Solutrean armature type diversity cannot have been directly related to the hunting of specific prey animals, since 1) the different projectile point types are relatively consistent in their range of dimensions, and hafting and ballistic properties, 2) some of the diagnostics, namely the very large Volgu-type foliates, are clearly not projectiles and, although conceivably used in the processing of the kills, would have played no direct role in their acquisition (Aubry et al., 2007a, 2007b), and 3) the same point type (e.g., the Franco-Cantabrian shouldered point) was used in different regions to hunt different prey (e.g. reindeer in France and red deer in Portugal).

5.4. The different dimensions of Upper Solutrean territoriality

In concert with slight climatic amelioration and lowered levels of ecological risk, it is possible that specializations in specific subsistence activities unrelated to big-game hunting using lithic projectile points might have allowed for cultural drift that resulted in the regional diversification of projectile point styles. More likely, this diversification represents a process towards increased territoriality that, although ultimately linked to differences in adaptation, must also have expressed itself in the realms of social organization, ideology and non-material culture. In conjunction with a reduction in the size of interaction networks, this increase in territoriality could have resulted in levels of cultural drift sufficient to generate the regionally-specific technological idiosyncrasies that we see in the Upper Solutrean. In this regard, it is interesting to note that the distributions of the more restricted armature types (Volgu foliates, subtype A shouldered points, and concave-based points) define territories whose size, under population densities typical of subarctic conditions, broadly correspond to those to be expected for ethno-linguistic entities (Collard and Foley, 2002).

Accepting the notion that at least some of the regionally diagnostic Upper Solutrean types may indicate ethnicity at some level (whether passive or active is irrelevant here) raises the issue of the significance of isolated occurrences of such types outside the core areas indicated by their denser concentrations of occurrences. For instance, does the single concave-based point from the Grotte des Harpons (Lespugue, Haute-Garonne; Fig. 3E) represent an actual extension of this type's cultural territory into the northern foothills of the central Pyrenees? Or, does this far easterly occurrence reflect a presence outside this armature type's core eco-cultural niche as a result of trade or atypical group movement? The fact that the geographic area between the Grotte des Harpons and the cave of Haregi (Aussurucq, Pyrénées-atlantiques) is included in the eco-cultural niches reconstructed for both the Upper Solutrean and the concave-based armature indicates that the Grotte des Harpons may well represent this niche's eastern limit. However, additional occurrences of this point type are necessary to convincingly demonstrate this.

The same question can be raised concerning the fragments of Volgu-type foliates found at a few sites in the Dordogne basin, such as Laugerie-Haute and La Crouzette (Smith, 1966). In instances for which the raw-material has been identified and its source located, these exceptional foliates are invariably traced to the southern edge of the Paris basin (Aubry et al., 2007a, 2007b). Thus, one might postulate that the *entre-Loire-et-Dordogne* landscape was an integral part (perhaps a northern extension exploited during the warm season) of the cultural territory of the hunter-gatherer groups of the Périgord defined by the shouldered points of subtype A. The latter, however, has never been found north of the Charente region, even if, at the large sites of Le Placard and Fourneau du Diable in the Périgord, a significant number of these points are made on raw materials from the Cher and Claise River valleys located >150 km to the north (areas where the subtype itself is unknown; Aubry, personal communication, June 2009). A parsimonious reading of this evidence suggests 1) that the distribution of the Volgu-type foliates defines a distinct cultural territory, and 2) that the occasional presence of such foliates at sites located at or beyond the southern boundary of their core area represents trade, exchange, or movement of raw materials, material culture items, and individuals across that boundary.

The above examples illustrate the potential for refinement of the eco-cultural niche reconstructions presented here. Such refinement will be necessary to advance in the investigation of the differences in adaptive basis (settlement system, exploited resources, or acquisition strategies) that must underlie the marked expression of

territoriality seen in at least one aspect of the Upper Solutrean material culture, the lithic point types.

A key issue that we have not addressed here is if, and to what extent, the same level of territoriality evident in the Upper Solutrean already existed, but remains archaeologically invisible, in preceding Paleolithic periods. In fact, it has been suggested (Zilhão, 1997) that it is only thanks to the plasticity of Solutrean technology at the peak of its craftsmanship that a range of equivalent solutions to the same technical problem (arming a projectile with a stone tip of a certain size and weight) can be seen at this time in the realm of stone tools. This technical flexibility made it possible for cultural drift to generate patterns of territoriality with a level of resolution that lithic technologies characterized by a lower degree of freedom in blank transformation are not able to express. That this suggestion must be borne in mind is confirmed by indications that the apparent homogeneity of the Middle Solutrean across its entire geographical range is to a certain extent a byproduct of considering all laurel-leaf points as a single "type." In fact, while pointed-base, lozenge-shaped forms predominate in France, most Iberian laurel-leaf bifaces have convex bases and an overall lanceolate form, which suggests that elements of cultural territoriality of at least an intermediate level of hierarchical characterization (the same level that, in the Upper Solutrean, is expressed by the marked spatial segregation of Franco-Cantabrian shouldered points and Mediterranean backed and shouldered points) may also exist in the Middle Solutrean.

6. Conclusions

This study has demonstrated that Eco-Cultural Niche Modeling is an effective means with which to evaluate the paleoecological pertinence of archaeologically defined artifact types and to identify ecological and cultural mechanisms behind the variability observed in the archaeological record. For the Upper Solutrean, it is evident that the cultural choices (production technology, size, morphology, etc.) behind the production of specific point types have at some level an ecological basis and are linked to particular environments. Thus, Upper Solutrean armature types are not purely archaeological constructions in that they appear to reflect an eco-cultural reality.

We have argued that the ecological component of Upper Solutrean point-type variation is not necessarily embodied in the points themselves. As far as we can see no particular link exists between the specific combination of production technique, the overall morphological characteristics of each point-type, and the corresponding ecological niche: a Parpallò point probably would be as efficient in arming a missile for reindeer hunting in the Périgord as it must have been in arming a projectile for red deer hunting in southern Andalucía. In short, the pattern of Upper Solutrean territoriality has an ecological foundation, but its stylistic expression in the variation of diagnostic armature types is probably a byproduct of cultural drift. For the technocomplex as a whole, the role played by purely cultural factors in the explanation of the Upper Solutrean phenomenon is further highlighted by the fact that its actual (archaeological occurrences) and potential (reconstructed eco-cultural niche) geographical extensions differ markedly, as the latter includes vast regions of the Mediterranean basin far beyond the well-established boundaries of the Solutrean (Fig. 2B).

In a similar vein, are the patterns identified here for the Upper Solutrean unique from an archaeological standpoint, or might the same pattern hold true for preceding phases of the Solutrean and other archaeological cultures and time periods elsewhere? For example, did similar links between hunting technology and ecology exist during the Early Epigravettian of Central and Southern Europe? Likewise, might other aspects of material culture be strongly linked to the environments exploited by prehistoric

hunter-gatherer populations? Projectile points represent a direct link between human culture and ecology since they functioned in roles of resource extraction, but are there other aspects of a hunter-gatherer cultural system, less directly associated with subsistence, that show links to the exploitation of distinct suites of environmental conditions? Our results highlight the need to incorporate other aspects of material culture, such as personal ornaments and mobiliary art styles, into this methodological approach. The analysis of such types of artifacts could help to clarify the mechanisms at play between cultural adaptation and ecology. Such research also has the potential to further refine our understanding of hunter-gatherer territories as they relate to ecological parameters.

Addressing such questions is central to an improvement of our understanding of the nature of Upper Paleolithic cultural systems and of how they interacted with climatic and environmental conditions. Our results contradict the idea that cultural drift is independent from ecological parameters and only driven by purely cultural mechanisms. In particular, our findings seem to confirm the idea that cultural diversification will occur when environmental conditions result in a decrease in the levels of ecological risk, thereby allowing hunter-gatherers to develop new adaptive systems and cultural identities linked to more geographically restricted ecological settings. Our results, on the other hand, also contradict the idea that stylistic variability in stone tools, both synchronic and diachronic, is strictly determined by environmental parameters alone and can be fully explained under a “culture as adaptation” worldview. In short, our findings suggest that, in order to move forward in the productive reconstruction of prehistoric cultures, archaeologists need to develop and pursue new methodological approaches capable of focusing on the complex and space-time-specific interactions between human cultures and their environmental contexts.

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Eco-cultural niches of the Badegoulian: Unraveling links between cultural adaptation and ecology during the Last Glacial Maximum in France

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ABSTRACT

This study details an application of eco-cultural niche modeling (ECNM) using two modeling architectures—a genetic algorithm (GARP) and maximum entropy (Maxent)—aimed at examining the ecological context of sites with archaeological remains attributed to the culture termed the Badegoulian (ca. 22–20 k cal BP), which dates to the middle part of the Last Glacial Maximum (ca. 23–19 k cal BP). We reconstructed the ecological niche of the Badegoulian and assessed whether eco-cultural niche variability existed within this technocomplex. We identified two broad but distinct spatial entities in the distribution of Badegoulian sites based on lithic raw material sources and circulation, and found that these spatial units share a similar ecological niche. We discuss the implications of territorial differentiation within this niche in light of research on land use by culturally affiliated groups within a broad cultural entity. We propose that Badegoulian circulation networks reflect distinct social territories associated with particular conditions within a single ecological niche. This study illustrates the utility of combining ecological niche reconstructions with archaeological data to identify and evaluate diachronic trends in cultural continuity for situations where such patterns may be missed when the focus of study is restricted solely to lithic technology and typology.

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Introduction

Eco-cultural niche modeling (ECNM) has been proposed as an effective approach by which to explore interactions between cultural and natural systems, and to understand how ecological dynamics influenced adaptations and movements of prehistoric hunter–gatherer populations (Banks et al., 2008a, 2009). ECNM integrates archaeological, chronological, geographic, and paleoclimatic datasets via biocomputational architectures derived from biodiversity studies (Soberón and Peterson, 2004) to reconstruct ecological niches occupied by prehistoric hunter–gatherer populations and identify and characterize factors that shaped these niches.

An eco-cultural niche is defined as the range of environmental conditions within which a human adaptive system can persist without immigrational subsidy (Banks et al., 2008a). ECNM assumes that, at a basic level, a human adaptive system is compara-

ble to a 'species' that operates within a given environmental framework (i.e., its ecological niche). This approach allows one to identify and analyze possible links between human adaptive systems and the ecological niches they exploited. At the same time, one must keep in mind that a technocomplex—defined here as the structured combination of technological systems shared and transmitted by a culturally cohesive population—can show great flexibility with respect to environmental constraints, such that it may be difficult to establish consistent relationships between culture and environment. The utility of ECNM is that it provides the ability to assess such situations and evaluate quantitatively whether such links exist between a given adaptive system and ecological constraints, or if the characteristics and geographic distribution of a given technocomplex may have been influenced more by non-ecological (i.e., cultural) processes. ECNM has permitted reconstruction of eco-cultural niches, identification of potential human ranges, exploration of the environmental influences on cultural geography and lithic technology in Europe during the Last Glacial Maximum (LGM), as well as on Neanderthal/modern human interactions during the latter stages of Marine Isotope Stage 3 (Banks et al., 2008a,b, 2009).

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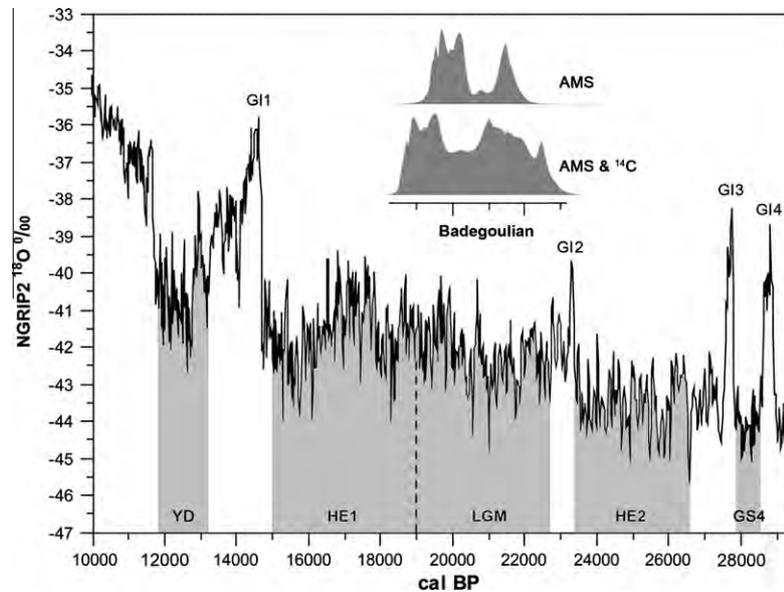


Fig. 1. Chronological and paleoclimatic context of the Badegoulian. Age distributions are based on radiometric age determinations from Badegoulian sites (AMS: $n = 14$; AMS and ^{14}C : $n = 57$) and were produced with the sum function of a uniform phase model in OxCal (see Bronk Ramsey, 2009) using the IntCal09 calibration curve (Reimer et al., 2009). Principal climatic phases are indicated with reference to the NGRIP2 oxygen isotope curve (Svensson et al., 2006, 2008). Temporal boundaries of cold phases (indicated in gray) are derived from Sanchez Goñi and Harrison (2010), Stanford et al. (2011) and Svensson et al. (2008). Abbreviations are as follows: YD – Younger Dryas; HE – Heinrich Event; GI – Greenland Interstadial; GS – Greenland Stadial; LGM – Last Glacial Maximum.

Recently applied to the Upper Solutrean, an archaeological culture dated to the early part of the LGM, ECNM was used to investigate whether lithic projectile point variability reflected adaptations to distinct ecological niches, or if this diversity of material culture was an expression of cultural geography independent of environment (Banks et al., 2009). The hypothesis was put forward that, while the regionalization of armature types had an ecological foundation, this stylistic variability was a by-product of cultural drift that occurred between different regional populations following a slight amelioration of climatic conditions between Heinrich Event 2 and the LGM.

The present study applies ECNM approaches to the Badegoulian, an archaeological culture dated to the middle part of the LGM (Fig. 1; see below for a discussion of Badegoulian chronology and its placement within the climatic framework of the Last Glacial period). The goal is to evaluate whether the Badegoulian was characterized by a continuity in the trend towards regionalization identified for the preceding Upper Solutrean, and if so, whether it had an ecological basis. Within the Badegoulian, it is not possible at present to identify regionally distinct technological markers as with the Upper Solutrean nor clear diachronic typo-technological changes (see below). Therefore, we reconstructed the overall Badegoulian eco-cultural niche, and evaluated whether significant ecological differences could be identified between two distinct geographic ranges defined on the basis of lithic raw material circulation networks.

The Badegoulian

The term ‘Proto-Magdalenian’ was proposed by Cheynier (1939) to define the ‘primitive Magdalenian’ at the site of Badegoule, with the idea of differentiating the earliest part of the Magdalenian from the rest of this archaeological culture. Cheynier (1951) later proposed three phases, with the oldest being characterized by ‘raclettes’ and transverse burins, which he used to link the archaeological levels containing these items at Badegoule to level I’ defined by Peyrony (1938) at Laugerie-Haute. Vignard (1965) proposed the term ‘Badegoulian’ to replace ‘Proto-Magdalenian’.

With the publication of the archaeological sequence at Abri Fritsch (lower Creuse Valley, central France), Allain and Fritsch (1967) relied on the absence of bladelet production and retouched bladelets in levels 6–3 to justify the use of the term ‘Badegoulian’ and define it as a distinct archaeological technocomplex. It thus was sandwiched between two archaeological cultures with retouched lithic tools made primarily on blade and bladelet blanks: the upper Solutrean in the lower part of the Abri Fritsch sequence (levels 10–7) and the Middle Magdalenian that J. Allain has investigated for over 20 years at the site of La Garenne, situated ~40 km up the same valley.

The separation of these industries from the Solutrean, which had been noted earlier by Breuil (1937, p. 40): “s’il est un fait certain en Préhistoire, c’est que les premiers Magdaléniens ne sont pas des Solutréens évolués: c’étaient bien de nouveaux venus dans ces endroits, aussi inhabiles dans l’art de tailler et de retoucher le silex que leurs prédécesseurs y excellaient” [if one thing is certain in prehistory, it is that the first Magdaléniens are not evolved Solutreans: they were certainly newcomers into these areas, and clumsy in knapping and retouching flint, tasks in which their predecessors excelled—our translation], was supported by de Sonneville-Bordes (1967). De Sonneville-Bordes pointed out, however, that while the Magdalenian 0 from Laugerie-Haute lacked backed bladelets, it did display the typological characteristics of the Magdalenian 1 levels stratigraphically above it where the raclettes are associated with retouched bladelets. Thus, two schools of thought emerged: one that recognized a Magdalenian 0 and a Magdalenian 1 as the beginning of the Magdalenian, which is defined by the presence of backed bladelets in variable amounts, and a second that considered the Badegoulian to be a standalone archaeological culture.

Subsequently, research in the Iberian Peninsula identified erosional events in stratigraphic sequences that made difficult the study of the transition between Upper Solutrean and initial Magdalenian industries bearing backed bladelets (Rasilla-Vives, 1994; Zilhão, 1994). Where no Badegoulian exists (Allain, 1983), the radiocarbon data indicate a persistence of the Solutrean, whose typological features are distinct with respect to the Solutreo-Gravettian of Mediterranean Spain (Fortéa et al., 1983) as well as

to the Solutrean-to-Magdalenian transitional industries of Cantabria (Corchón-Rodríguez, 1994; Rasilla-Vives, 1994). Therefore, the Badegoulian appears to be a geographically limited archaeological culture restricted to a large portion of present-day France (de Sonneville-Bordes, 1989).

The question of the Badegoulian came again to the forefront in the early 1990s. Technological study of the bone industry from Badegoulian levels at Abri Fritsch was used to support the idea of a techno-typological differentiation between the Badegoulian and the Magdalenian lithic industries proposed by Allain and Fritsch (1967). Blanks used to make spear points from reindeer antler were obtained by percussion, a technique markedly different from the grooving and splinter technique used during the Middle Magdalenian at La Garenne (Allain et al., 1974; Allain, 1983; Rigaud, 2004). Identifying this percussion technique as diagnostic of the Badegoulian was confirmed in other Badegoulian assemblages such as those from Abri Casserole (Bidart, 1991) and Cuzoul de Vers (Clottes et al., 1986). The discovery in levels 7 and 8 at Abri Fritsch of reindeer antler splinters produced by percussion was put forth cautiously by Rigaud as indicating a continuity between the Upper Solutrean and the Badegoulian. However, technological analyses of the entire sequence at Abri Fritsch, identification of refits between levels, studies of differential use of lithic raw material source areas, along with an absence of bifacial thinning flakes, together indicate that the series from levels 8B–7 are more similar to the Badegoulian levels 6–3 than to the Solutrean occupations evident in levels 10–8e (Aubry et al., 2007).

On the other hand, technological studies of assemblages from the Aquitaine region (Cretin, 1996, 2000; Cretin et al., 2007; Morala, 1993), the Paris Basin (Cretin and Le Licon, 1997), and the Massif Central (Bracco, 1992) have served to (a) confirm that a rupture exists between the lithic chaînes opératoires of the Upper Solutrean (Aubry et al., 2007; Renard, 2010) and the Badegoulian; (b) differentiate the Badegoulian from the Initial Magdalenian dated to ca. 17,500 ¹⁴C BP (Foureloubey, 1998; Langlais, 2007). New excavations and analyses of lithic assemblages from sites in the Paris Basin demonstrate that the schema of two phases within the Badegoulian (transverse burins to raclettes: Trotignon, 1984; Bosselin and Djindjian, 1988, 1999) does not hold up (Bodu et al., 2007), and that the absence of backed bladelets is not as pervasive or systematic as suggested from analyses of the Abri Fritsch sequence (Aubry et al., 2007). This hypothesis of two phases, however, merits further attention as new radiocarbon ages are obtained and additional technological studies are conducted. Furthermore, the presence of Mediterranean-style shouldered points, observed initially at Pégourié Cave (Séronie-Vivien, 1995), is confirmed in levels containing raclettes at Cuzoul de Vers (Ducasse, 2010). In each case, their presence is difficult to explain with arguments of post-depositional mixing, and rather seems to be characteristic of sites along the southern limits of the Badegoulian distribution.

With respect to lithic technology, Badegoulian series show an absence of the bifacial operative scheme systematically present in Upper Solutrean assemblages, as well as great diversity of production techniques (high frequencies of splintered piece-tools or -cores, and production of bladelets from carinated scrapers, flake edges, and Bertonne cores). This latter aspect contrasts with preceding Solutrean industries that have more homogenous chaînes opératoires, despite the existence of regionally distinct shouldered point types. Furthermore, the Badegoulian presents a simplified and relatively low-investment toolkit (see Straus and Clark, 2000). The raclette appears to be the sole tool type unique to the Badegoulian that is well constrained both temporally and spatially. Experimental work by Rigaud (2004) has shown that when they are hafted, raclettes are effective in shaping reindeer antler blanks, and that their use is directly linked to fabrication of tools from such blanks, and perhaps wood.

From a chronological standpoint, a degree of uncertainty exists regarding the time span of the Badegoulian owing to several conventional radiocarbon age determinations with large standard errors that do not always correspond with AMS age determinations from the same archaeological levels (d'Errico et al., 2011; but also see Cretin, 2007; Ducasse, 2010). However, the general tendency of the age determinations, excluding outliers and favoring AMS ages, indicates that the Badegoulian solidly occupies the time range of ca. 22–20 k cal BP (~18.2–16.5 k ¹⁴C BP), within the middle part of the LGM (Fig. 1). The term LGM can refer to differing time frames, depending on the definition used. Here, we use it to refer to the period between 23 k cal BP and 19 k cal BP, corresponding to the EPILOG group's chronozone level 1 (Mix et al., 2001), which refers to different marine proxies that indicate a period of high ice volume but relatively low climatic variability between Heinrich Events 2 and 1. Therefore, we are referring neither to climatic conditions over Greenland (Svensson et al., 2006) nor to estimations of ice sheet volume maxima that range between 26 k and 19 k cal BP (Clark et al., 2009). The termination of the LGM, as defined here, occurred at ca. 19 k cal BP (Clark et al., 2009; Peltier and Fairbanks, 2006; Yokoyama et al., 2000); after this period, Badegoulian industries disappear from the archaeological record.

As discussed earlier, the Badegoulian is restricted to what is present-day France (Fig. 2A), and suggestions that this technocomplex has a broader geographic distribution do not hold up. The designation as Badegoulian of lithic assemblages from archaeological levels in Cantabria described as Solutrean in the process of 'de-Solutreanization' was proposed by Bosselin and Djindjian (1999) on the basis of a typological analysis of materials from the site of La Riera. These arguments, however, were refuted by Straus and Clark (2000), based on the presence in those levels of typical Solutrean bifacial pieces shaped by percussion and pressure. Sites in southern Germany (Wiesbaden-Igstadt) and Switzerland (Kastelhöhle-Nord) have also been termed Badegoulian based on radiocarbon ages (see Terberger and Street, 2002), but the descriptions of the lithic assemblages, which lack diagnostic raclettes, do not support such a designation. Lithic assemblages from Parpalló, Spain, dated to ca. 16,000 ¹⁴C BP (Aura Tortosa, 2007), have also been interpreted as Badegoulian based on the presence of flakes with inverse retouch that are also present in assemblages for the earliest phase of the Lower Magdalenian in Portugal. However, they differ morphologically from the French raclettes and are too recent to be identified as Badegoulian (Zilhão, 1997). Thus, no data demonstrate convincingly the presence of Badegoulian industries in the Iberian Peninsula or central Europe.

Geographic differentiation within the Badegoulian

Contrary to the Upper Solutrean, in which one observes transportation over long distances of high quality flint used in the production of technologically complex tools (shouldered points, laurel leaf bifaces, blade tools) (Aubry, 1991; Aubry et al., 2009), the Badegoulian is characterized by a predominant use of local sources, usually located less than 30 km from sites. Blade tools made on flint from extremely distant sources are rare (Aubry, 1991): the only known case is in the Massif Central where evidence indicates use of flint from sources located in the lower Cher, Creuse, and Claise River Valleys, a distance of >200 km (Bracco, 1992).

Lithic raw material use was not exclusively local and, on the basis of raw material origin and circulation, it is possible to identify two distinct and mutually exclusive territories for the Badegoulian (Fig. 2B). In the northern territory, local lithic raw materials aside, flint comes from several formations: the lower Turonian (Berry), the upper Turonian (Touraine), the Infralias of the Vienne River valley, and the Senonian (s. lato) of the southeastern Paris Basin (Aubry, 1991; Aubry et al., 2007; Bodu and Senée, 2001). In the

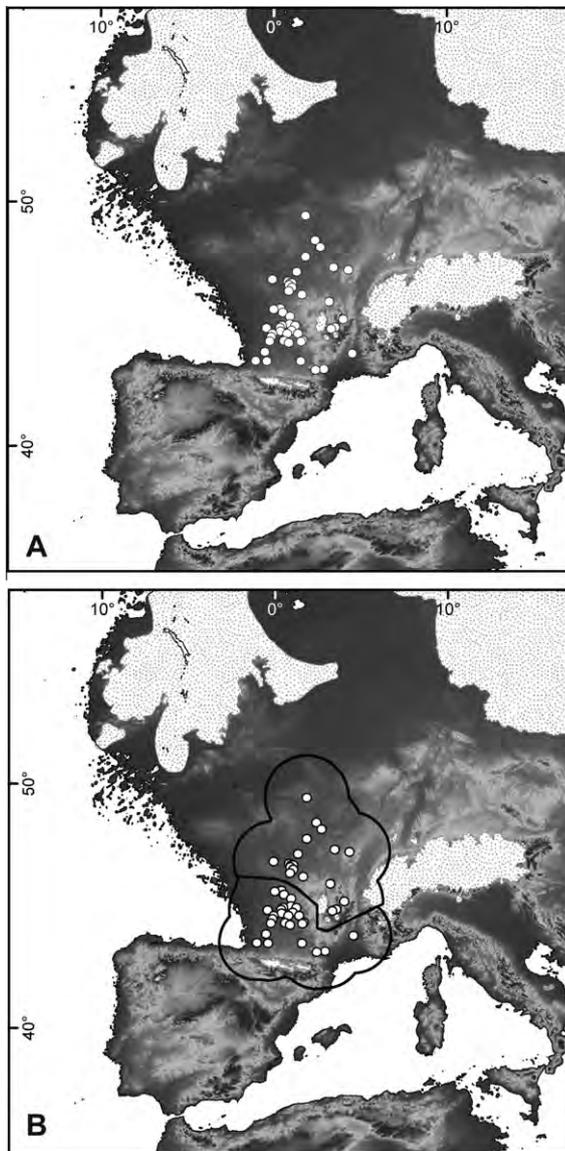


Fig. 2. (A) Physical map of Western Europe showing the locations of the Badegoulian sites listed in Table 1. (B) Approximate limits of the northern and southern Badegoulian territories based on observed differences in recovered lithic raw materials. These limits reflect our hypothesized background areas (M) estimated using a radius of 175 km centered on site clusters within each territory. Ice sheet and glacier limits after Ehlers and Gibbard (2004). LGM coastlines were obtained by lowering sea levels by 120 m (Lambeck and Chappell, 2001; Lambeck et al., 2002).

southern territory, exotic raw materials originate from a variety of formations: Senonian (s. lato), Maastrichtian of southern Aquitaine, Maastrichtian of Bergerac, and lower Turonian of Fumel (Cretin, 2000; Ducasse, 2010; Fourloubey, 1998; Morala, 1993). No circulation of lithic raw materials between these two territories is known (Fig. 3), despite the fact that research and joint analyses of relevant assemblages has been conducted at a dedicated meeting of researchers who work in the two areas (workshop of the *Société pré-historique française*, Toulouse, December 2006). Two blade fragments made from Bergerac flint have been identified at Le Silo (Level C), Grand-Pressigny (northern territory) by Primault (2003, p. 347). However, these artifacts were recovered from an exposure, and technological analysis suggests that they may be in fact Magdalenian artifacts, recognized at several sites in the region (Aubry, 1991). Moreover, the use of Senonian flint from sources in the Aquitaine region has been confirmed in several Middle Magdalenian occupation levels at La Garenne (Aubry, 2004).

Does this apparent territorial division relate to exploitation of distinct ecological niches? If such were the case, one would expect little to no interpredictivity between the eco-cultural niche reconstructions for each territory. Alternatively, if eco-cultural niches for the two territories overlap broadly, then no relationship likely exists between these territories and ecological conditions. The relationship between these territories and ecological factors has interesting implications, considering that they share a common lithic technological industry. Do these archaeological territories represent distinct social territories? If so, what social dynamics might lead to the creation and maintenance of distinct social territories that share a common lithic industry? Here, we use new randomization-based tools (Warren et al., 2008) to compare the eco-cultural niches estimated for the two territories, taking into account the use or non-use of conditions within the dispersal range of the human populations in question.

Materials and methods

To evaluate possible culture–environment links for the Badegoulian, we used genetic algorithm (GARP; Stockwell and Peters, 1999) and maximum entropy (Maxent; Phillips et al., 2004, 2006) techniques to estimate eco-cultural niches. GARP and Maxent have been applied to a diverse set of topics including reconstructing species' distributions, estimating effects of climate change on species' distributions, and forecasting the geographic potential of species' invasions (Araújo and Rahbek, 2006; DeVaney et al., 2009; Kozak and Wiens, 2006; Martínez-Meyer et al., 2004; Pearson et al., 2007; Peterson, 2003; Peterson et al., 2007). For data inputs, GARP and Maxent require the geographic coordinates where the species or population of interest has been observed, and a set of raster GIS data layers summarizing environmental dimensions potentially relevant to shaping the geographic distribution of the species.

Occurrence data

The occurrence data are the geographic coordinates of archaeological sites at which materials have been recovered that can be identified culturally as Badegoulian (Table 1). As discussed above, sites in Germany (Wiesbaden Igstadt), Switzerland (Kastelhöhle-Nord), and Spain (e.g., La Riera, Rascaño) that are contemporaneous with the Badegoulian but lack diagnostic tool types (i.e., raclettes and/or transverse burins) are excluded from this study. It should be noted that the designation as Badegoulian of two sites in our database (Les Battants, Rond du Barry) may be called into question, but we retained them, since their original designations as having Badegoulian archaeological components have not been refuted in the published literature. Our consideration of error probabilities in setting thresholds (see description below) minimized the possibility that their inclusion biased the reconstructed eco-cultural niches.

Environmental data

The raster GIS data sets used in this study summarize landscape attributes (assumed to have remained constant) and a high-resolution climatic simulation for the LGM. Landscape variables included slope, aspect, elevation, and topographic index (a measure of tendency to pool water). Elevation was obtained from the ETOPO1 dataset (Amante and Eakins, 2009), whereas the remaining landscape values were calculated from the ETOPO2 dataset (ETOPO2v2). We reconstructed approximate LGM coastlines for the European continent by lowering sea levels by 120 m (Lambeck and Chappell, 2001; Lambeck et al., 2002).

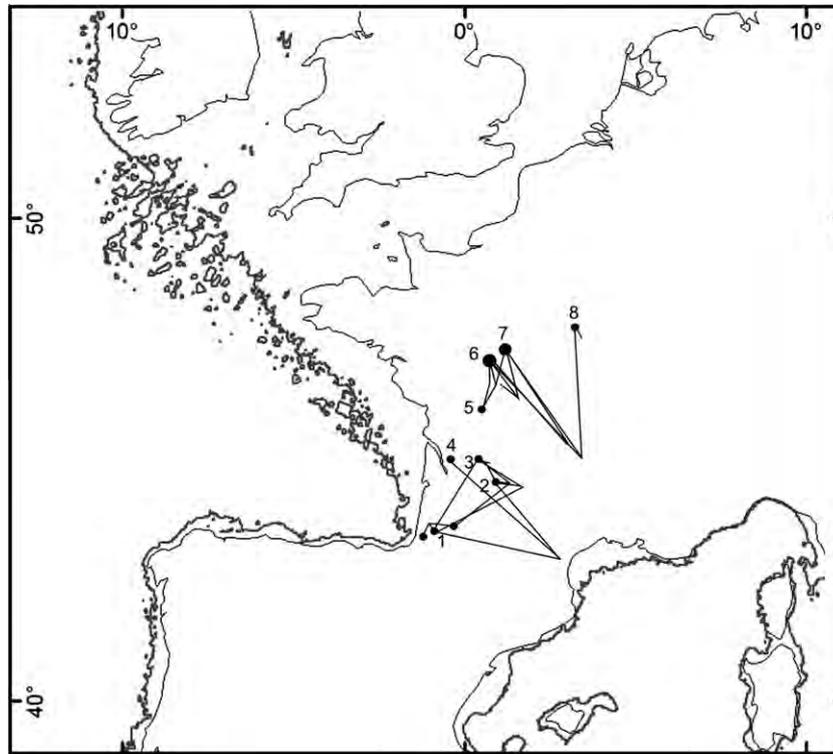


Fig. 3. Depiction of lithic raw material source areas and circulation. Source areas are indicated by solid black circles. Sources in the southern territory: (1) Senonian (s. lato), Maastrichtian of southern Aquitaine (Bidache, Tercis, Chalosse), (2) lower Turonian of Fumel, (3) Maastrichtian of Bergerac, (4) Senonian of Charente; Sources in the northern territory: (5) Infralias of the Vienne River valley, (6) upper Turonian (Touraine), (7) lower Turonian (Berry), (8) Senonian (s. lato) of the southeastern Paris Basin. Lines indicate the direction and distance of lithic raw material circulation. Present-day coastlines are depicted in black. LGM coastlines are depicted in bold grey and were obtained by lowering sea levels by 120 m (Lambeck and Chappell, 2001; Lambeck et al., 2002).

To reconstruct Badegoulian eco-cultural niches, we used a high-resolution LGM climatic simulation. The LGM, centered on 21 k cal BP, was the last period of maximum global ice sheet volume, and was characterized by cold and generally arid conditions in northern and western Europe. To capture the climatic impact of LGM conditions, we used an atmospheric general circulation model with a refined grid over Europe (resolution of ~50 km over western Europe), run at the Laboratoire des Sciences du Climat et de l'Environnement, Gif-sur-Yvette, France. This high-resolution LGM atmospheric simulation follows the protocol proposed by the PMIP2 project (Braconnot et al., 2007; <http://pmip2.lscse.ipsl.fr>), with orbital parameters and atmospheric greenhouse gases concentrations set to their 21 k cal BP values (Berger, 1978; Raynaud et al., 1993) and ice-sheet height and extent prescribed according to the Peltier (2004) ICE-5G reconstructions. The PMIP2 protocol is designed for coupled ocean–atmosphere models, whereas an atmosphere-only model was used in the present study, so a prescription of sea-surface characteristics (temperatures and sea-ice extent) was necessary: we used the most recent reconstructions, i.e., the GLAMAP data set (Paul and Schäfer-Neth, 2003; Sarnthein et al., 2003). We compared the results of this simulation, over our area of interest, to pollen-based climatic reconstructions (Wu et al., 2007): they are in close agreement with the pollen data for summer and annual mean temperatures, as well as mean annual precipitation, albeit with some underestimation (of up to 2 °C) of winter cooling over Western Europe and the Mediterranean.

Eco-cultural niche modeling

In GARP, occurrence data (i.e., presence-only data) are resampled randomly by the algorithm to create training 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—Atomic, Range, Negated Range, and Logistic Regression—and applied to the training data 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. 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). For each GARP model, we performed 1000 replicate runs with a convergence limit of 0.01, using 50% of the occurrence points for model training. We used the best subsets protocol described by Anderson et al. (2003) with a hard omission threshold of 10% and a commission threshold of 50%, and summed the resulting 10 grids to create a consensus estimate of the geographic range of the ecological niche associated with the archaeological occurrence data.

The maximum entropy (Maxent) modeling architecture uses the distribution of known occurrences to estimate a species' ecological niche by fitting a probability distribution of maximum entropy (i.e., that which is closest to uniform) to the set of pixels across the study region (Phillips et al., 2004, 2006). This estimated probability distribution is constrained by environmental characteristics associated with the known occurrence localities, while at the same time it aims to avoid making assumptions not supported by the background data. To produce eco-cultural niche reconstructions, we used the following parameters for Maxent version 3.3.1: random test percentage = 50, 500 maximum iterations, 10,000 background points, and convergence limit = 10^{-5} . This configuration approximates that used to produce the GARP predictions, in that half of available occurrence data are set aside for evaluating and refining model rule-sets.

Table 1
Badegoulian sites used to reconstruct eco-cultural niches.

Site	Long.	Lat.	Commune	Department	Level	Reference(s)
Badegoule	1.22	45.13	Lardin-St.-Lazare	Dordogne	Lower/upper	Cheyrier (1949)
Balette	-0.21	44.74	Bellebat	Gironde		Cretin et al. (2007)
Ballancourt	2.38	48.52	Ballancourt-sur-Essonne	Seine-et-Oise		Delarue and Vignard (1964)
Les Battants	3.40	45.17	Blassac	Haute-Loire		Bracco (1992)
Beauregard	-0.26	44.49	Mazerès	Gironde		Lenoir (2000)
Bois des Beauregards	2.69	48.26	Nemours	Seine-et-Marne		Vacher and Vignard (1964)
Bertonne	-0.44	45.04	Peujard	Gironde		Lenoir (2000)
Birac	-0.15	44.67	Castelviel	Gironde		Lenoir (2000)
Bize	2.88	43.32	Bize-Minervois	Aude	petite grotte	Sacchi (1968)
Blot	3.30	45.00	Cerzat	Haute-Loire	13	Delporte (1976)
Bordeneuve	0.59	44.51	Beaugas	Lot-et-Garonne		Ferullo (1995)
Breuil	0.45	45.08	Neuvis	Dordogne		Gausson (1980)
Buisson Pignier	0.93	46.85	Preuilley-sur-Claise	Indre-et-Loire		Aubry et al. (2004)
Cabannes	-0.53	44.04	Brocas	Landes		Gellibert et al. (2001)
Camparnaud	4.52	43.97	Vers-Pont-du-Gard	Gard		Bazile (1977)
Cassegras	0.86	44.43	Trentels	Lot-et-Garonne	9, 10	Le Tensorer (1981)
Casserole	0.38	44.90	Les Eyzies-de-Tayac	Dordogne	4-6	Detrain et al. (1991)
Castelnau-Tursan	-0.41	43.66	Castelnau-Tursan	Landes		Merlet (2005)
Châtenet	0.36	45.05	Saint-Front-de-Pradoux	Dordogne		Gausson and Moissat (1985)
Contree Viallet	3.20	46.10		Allier	3 top	Vernet (1995)
Cottier	4.00	45.40	Retournac	Auvergne	II	Virmont (1976)
La Croix de Bagneux	1.33	47.29	Mareuil-sur-Cher	Loir-et-Cher		Kildea (2008)
Croix de Fer	0.47	45.13	St. Germain-du-Salembre	Dordogne		Gausson (1980)
Cuzoul	1.57	44.48	Vers	Lot	29	Clottes and Giraud (1996)
Fritsch	1.04	46.68	Poulligny-Saint-Pierre	Indre	5b	Allain and Fritsch (1967)
Grand Moulin	-0.16	44.75	Lugasson	Gironde		Lenoir (2000)
Guillassou	0.51	45.10	Neuvis	Dordogne		Gausson (1980)
Houleau	-0.09	44.81	Sainte-Florence	Gironde		Lenoir (2000)
Jean Blancs/Jamblancs	0.77	44.81	Bayac	Dordogne	2	Cleyet-Merle (1992)
Jaubertie	0.49	45.10	Neuvis	Dordogne		Fourloubey (1992)
Lachaud	0.92	45.51	Terrasson	Dordogne	3 and 4	Cheyrier (1965)
Lassac	2.40	43.29	Salleles-Cabardès	Aude		Sacchi (1968)
Laugerie Haute (Est)	1.01	44.93	Les Eyzies-de-Tayac	Dordogne	18, 20	Bordes (1958)
Maitreaux	0.95	46.82	Bossay-sur-Claise	Indre-et-Loire	C2 top	Aubry et al. (2007)
Maubin	1.55	43.65	Beaupuy	Haute-Garonne		Le Tensorer (1981)
La Malignière	1.62	46.39	Crozant	Creuse		Trotignon et al. (1984)
La Millerie	1.05	46.85	Azay-le-Ferron	Indre-et-Loire		Aubry et al. (2007)
Le Mont-Saint-Aubin	3.44	47.47	Oisy	Nievre		Bodu and Senée (2001)
Paignon à Montgaudier	0.50	45.67	Montbron	Charente		Djindjian (2003)
Parrain (Ouest et Nord)	0.38	45.06	Ferrandie	Dordogne		Gausson et al. (1993)
Pégourié	0.90	45.20	Caniac du Causse	Lot	8, 9	Séronie-Vivien (1989)
Petit Cloup Barrat	1.64	44.51	Cabrerets	Lot	8a1	Castel et al. (2006)
Peyrugues	1.67	44.53	Orniac	Midi-Pyrénées	5b	Allard (1992)
Le Piage	1.39	44.80	Fajoles	Lot	CDE	Champagne and Espitalié (1981)
Placard	-0.03	45.80	Vilhonneur	Charente	CRL Brèche1	Roche (1971)
Plateau Parrain	0.37	45.05	St.-Front-de-Pradoux	Dordogne		Gausson et al. (1993)
La Pluche	0.87	46.78	Yzeures-sur-Creuse	Indre-et-Loire		Joannès and Cordier (1957)
Poron des Cueches	4.31	47.37	Vic-sous-Thil	Cote-d'Or		Mouton and Joffroy (1957)
Pourquey	-0.14	44.66	Castelviel	Gironde		Lenoir (2000)
La Pyramide	1.19	47.26	Cere-la-Ronde	Indre-et-Loire		Cleyet-Merle and Lété (1985)
Ragout	0.42	45.68	Vilhonneur	Charente		Balout (1958)
Les Renardières	0.37	45.83	Les Pins	Charente	1013	Dujardin (2001)
La Rivière	2.44	43.25	Malves-en-Minervois	Aude		Sacchi (1986)
La Roche	3.54	45.06	Tavernat	Haute-Loire		Bracco (1994)
Les Roches	0.72	46.94	Abilly	Indre-et-Loire		Bordes and Fitte (1950)
Rond du Barry	3.86	45.07	Polignac	Haute-Loire	F2	Bayle des Hermens (1974)
La Rouquette	4.48	43.95	Collias	Gard		Bazile and Boccaccio (2007)
Le Rozel	1.83	49.47	Goulancourt	Oise		Scuvée and Verague (1984)
Sablons	-0.38	45.07	Marsas	Gironde		Cretin et al. (2007)
Saint-Fiacre	0.96	46.83	Bossay-sur-Claise	Indre-et-Loire		Cordier and Thiennet (1965)
Saint-Mesmin	1.83	47.89	Saint-Mesmin	Loiret		Nouel (1937)
Seyresse	-1.06	43.68	Seyresse	Landes		Lenoir (1989)
Le Silo	0.80	46.92	Grand-Pressigny	Indre-et-Loire		Cordier and Berthouin (1953)
Solvieux	0.39	45.06	Saint-Louis	Dordogne	34	Gausson (1980)
Station de Burin	0.50	45.10	Neuvis	Dordogne		Gausson (1980)
Taillis du Coteau	0.85	46.53	Antigny	Vienne	Vd	Primault et al. (2007)
Tannerie	-0.10	47.00	Lussac-les-Châteaux	Vienne	Terrasse	Pradel (1950)
Les Varennes	0.92	46.84	Preuilley-sur-Claise	Indre-et-Loire		Aubry et al. (2007)

Thresholding

For the ecological niche reconstructions produced by GARP and Maxent, each grid cell is assigned a value that represents model

agreement or probability of occurrence, respectively. Given the frequent problem of overfitting in highly dimensional environmental spaces, continuous outputs are best thresholded to produce binary results (Peterson et al., 2007). As a result, we followed the

procedure detailed by Peterson et al. (2008) for incorporating a user-selected error parameter E that summarizes the likely frequency in the occurrence data set of records that are sufficiently erroneous as to place the species in environments outside its ecological niche. We set this parameter at 5% (i.e., $E = 5$). Such a value is appropriate for occurrence data that are likely to include a small degree of error, as in the case of the Badegoulian data since, as discussed above, the designation as Badegoulian of cultural levels for a small number of sites might be called into question. Hence, the Hawth's Tools extension to ArcGIS 9 was used to identify the GARP and Maxent output levels that included $(100 - E)\%$ of the training occurrence points; this value was used to reclassify the grid cells from the prediction into a binary map. For example, with a hypothetical occurrence data set of 40 points for model training and $E = 5$, we would find the threshold that includes 38 of the points and reclassify all grid cells with values below it as unsuitable and all grid cells with values at or above it as suitable. We applied this thresholding procedure to the raw predictions, and then saved each resulting binary raster grid as an integer data layer.

Eco-cultural niche characterization

Recent years have seen a proliferation of techniques for reconstructing ecological niches and predicting species' distributions, but debate has focused on how best to evaluate resulting models statistically (Araújo and Guisan, 2006; Peterson et al., 2008; Warren et al., 2008). Hence, we use a variety of methods to evaluate and compare the outputs from the two employed modeling algorithms. Warren et al. (2008) described new methods and statistical tests for evaluating overlap between ecological niche models quantitatively, and provided an implementation of these methods with the software package ENMTools version 1.1 (Warren et al., 2010; <http://enmtools.blogspot.com/>). ENMTools allows one to generate ecological niche models (ENMs) with Maxent, calculate similarity measures, and develop randomization-based comparisons of niches.

To examine patterns of niche similarity, we used ENMTools' niche overlap measures I and D and the associated background similarity test. I and D compare two maps (in this case, the ENMs for the two Badegoulian territories) and measure the similarity between them (methods described in Warren et al., 2008). The background similarity test then evaluates whether the observed degree of similarity between the two maps is greater than would be expected by chance. This comparison is accomplished by generating a null distribution for eco-cultural niche model difference expected between one map and another based on occurrence points drawn at random from within a relevant geographic area (Warren et al., 2010). These occurrences are placed randomly within a user-defined region representing an area in which the second population could have been detected. In other words, this user-defined background area, designated M by Barve et al. (2011), corresponds to the geographic region(s) that would have been accessible to the species during the relevant time period and that was sampled such that occurrences could have been detected.

We defined an M for each of the Badegoulian territories based on a generalization of lithic raw material transport within the Badegoulian. For example, Ducasse (2010) observed that the majority of lithic raw materials recovered from Badegoulian levels at the sites of Cuzoul de Vers and Lassic originated from sources located within a 100 km radius of the sites, with only a small percentage (~1%) of materials coming from sources over 200 km away. A similar pattern is observed in the northern territory where transport distances of less than 100 km characterize sites in the Creuse River valley (Aubry, 1991; Aubry et al., 2007), and distances approaching 200 km are observed at sites in the Massif Central. Thus, to generalize the pattern of lithic raw material circulation

and best estimate the region that would have been accessible to Badegoulian populations within each territory, we defined an M for each territory by establishing a buffer with a radius of 175 km and that was centered on clusters of recorded archaeological sites within each territory. When creating these buffers, we also kept intact the boundary between the northern and southern territories, since there are no known instances of lithic raw material circulation between the two. The hypothesized M 's used for each of the territories are illustrated in Fig. 2B. Our initial explorations revealed that very broad definitions of M invariably found that niches were distinct, and that narrow definitions found no differences; hence, we used a definition (described above) that best reflected what is known about the mobility patterns of these human populations.

Because the two modeling techniques used in this study generate predictions with distinct characteristics, and because ENMTools is particularly convenient for work with Maxent, to determine whether GARP and Maxent were reconstructing similar eco-cultural niches for the Badegoulian, we compared their outputs on a per-pixel basis. This comparative approach, described in detail by Papeş and Gaubert (2007), consists of a zonal statistic analysis performed with ArcGIS's Spatial Analyst extension in which the correspondence between the two approaches is assessed to detect areas of disagreement.

Results

Badegoulian

The predicted geographic range of the ecological niche reconstructed for the Badegoulian technocomplex as a whole covers much of present-day France, extending north into southern Belgium and south into the northern third of the Iberian Peninsula (Fig. 4A and B), although the known distribution of the Badegoulian does not extend into either of the two regions. The eco-cultural niche reconstructions made by GARP and Maxent are overall similar to one another, except that Maxent predicted a more limited area of the northern Iberian Peninsula, along with an area of unsuitable conditions along much of the Atlantic coast exposed by lower sea-levels during the LGM. It should also be noted that Maxent's tendency towards micro-prediction (e.g., Peterson et al., 2008) is visible in that areas of higher probability are markedly less extensive, particularly in the northern and eastern portions of the study region. The zonal statistical comparisons demonstrated that, from an ecological standpoint, the GARP and Maxent predictions derived from the same occurrence datasets do not differ from one another. Therefore, the differences between their respective geographic distributions are the result of non-significant ecological differences that can appear more pronounced when they are projected geographically.

The thresholded eco-cultural niche predictions produced with GARP for each of the territories (northern and southern) defined on the basis of lithic raw material circulation are in large part mutually exclusive (Fig. 4C and E), but for the Maxent models this is only the case for the areas with a high probability of predicted presence (Fig. 4D and F). In the GARP models, a minimal area of overlap between the two territories is notable in the southern portion of the present-day region of Poitou–Charentes, the western part of the Limousin region, and southwards along the western margin of the Massif Central. This overlap results from the fact that the northern Badegoulian niche prediction extends slightly beyond its southernmost sites into the region of the northwestern-most sites of the southern territory (see Fig. 5A); the southern territory's niche prediction does not overlap any of the sites in the northern territory (Fig. 5C).

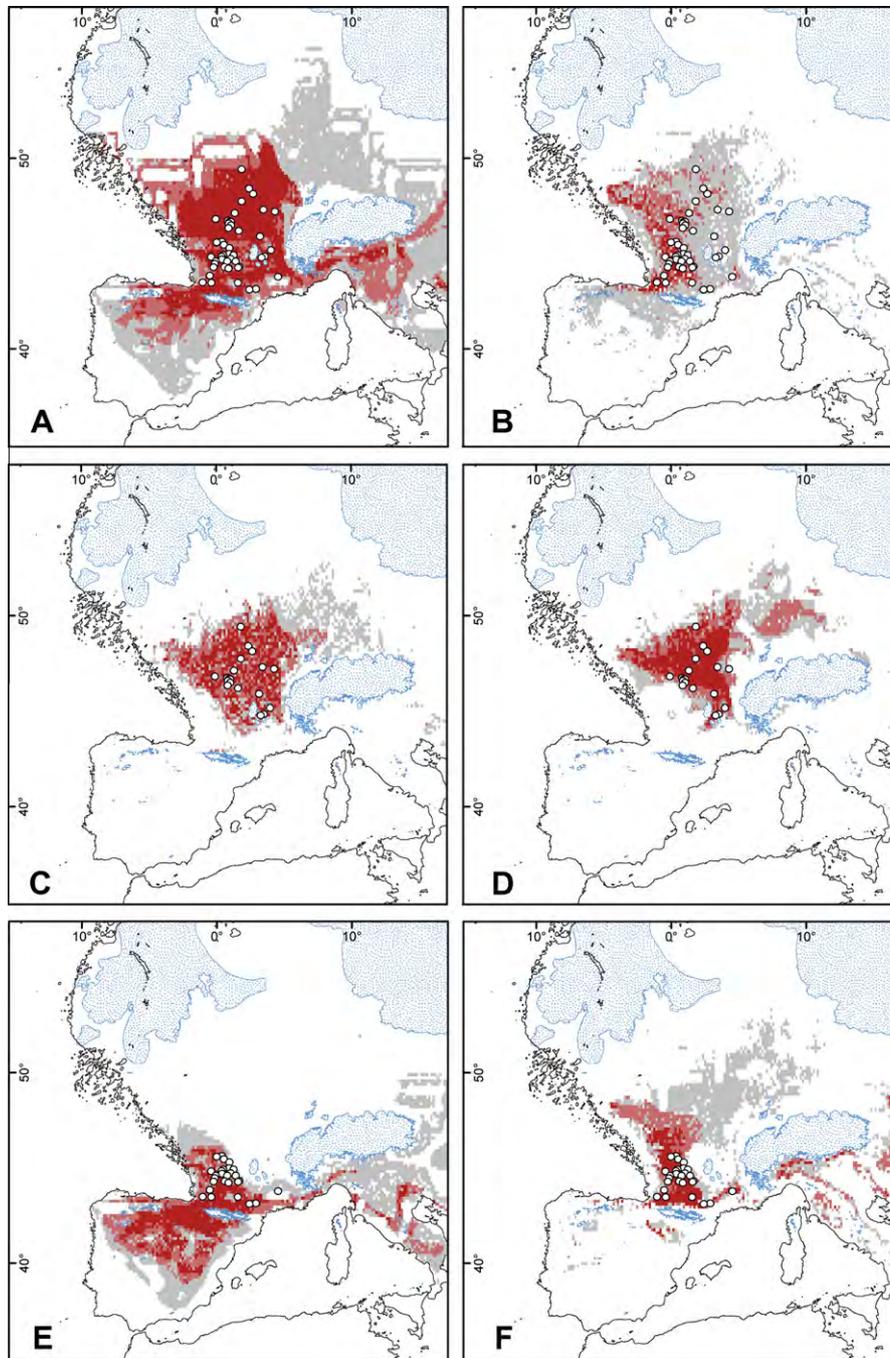


Fig. 4. Badegoulian eco-cultural niche reconstructions: (A) GARP model for the entire technocomplex, (B) Maxent model for the entire technocomplex, (C) GARP model for the northern territory sites, (D) Maxent model for the northern territory sites, (E) GARP model for the southern territory sites, (F) Maxent model for the southern territory sites. For the GARP predictions, grid squares with 1–5 of 10 models predicting the presence of suitable conditions are indicated in gray, grid squares with 6–9 models in agreement are depicted in pink, and squares with all 10 models in agreement are indicated in red. With the Maxent reconstructions, the depicted distribution boundary is determined by the lowest probability level (prediction threshold) that includes all of the known occurrences used to construct the model. These thresholds are as follows: (B) $P = 0.17$, (D) $P = 0.35$, (F) $P = 0.07$. For these Maxent models, colors range from gray, to pink, and to red, or low to high probability, respectively. Ice sheet and glacier limits after Ehlers and Gibbard (2004). LGM coastlines were obtained by lowering sea levels by 120 m (Lambeck and Chappell, 2001; Lambeck et al., 2002). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The Maxent predictions present a different pattern. In these models, the northern territory prediction does not overlap any southern territory sites (Fig. 5B). For lower probability levels, the Maxent prediction of the southern territory overlaps a large portion of the northern territory's eco-cultural niche (comparison between Fig. 5D and B, respectively). The southern territory's Maxent prediction is markedly more constrained than the GARP prediction

(Fig. 4F vs. E): Maxent identified little potential distributional area in the Iberian Peninsula, a region where the Badegoulian is not observed. On the other hand, the GARP reconstruction for the southern territory identified potential distributional area across much of the northern portion of the Iberian Peninsula (Fig. 4E). Considering only the regions in which a Badegoulian presence has been observed, the GARP predictions identified roughly 240,000 km² of

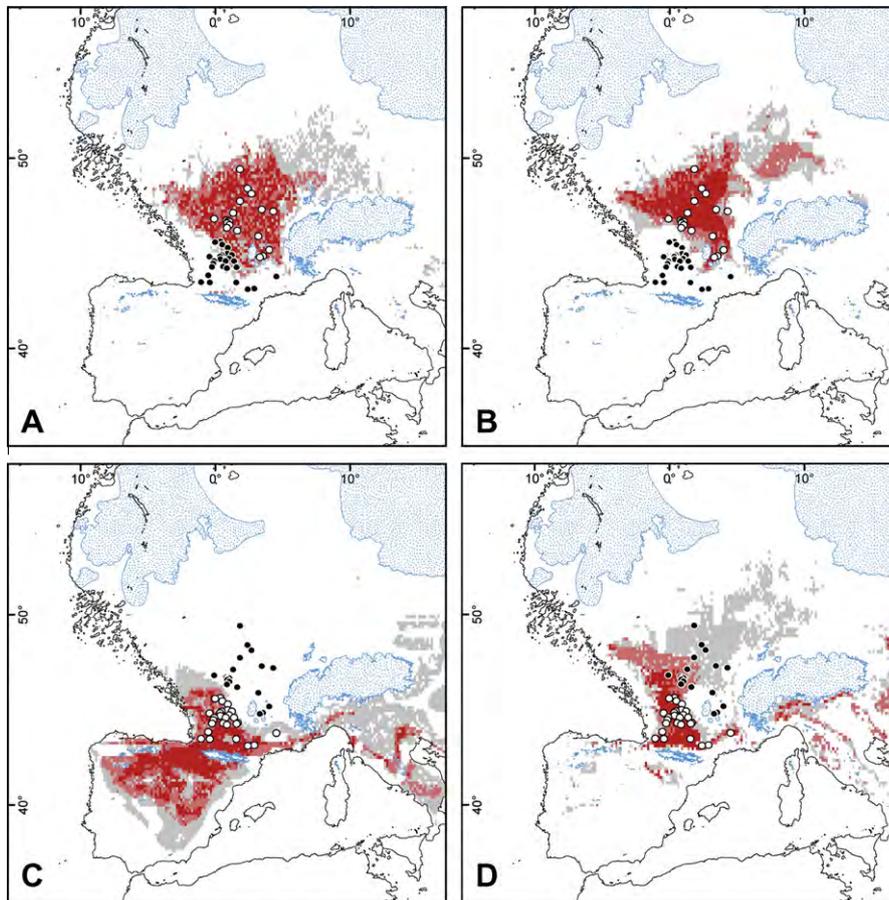


Fig. 5. Northern and southern Badegoulian territory eco-cultural niche predictions depicted with those sites used to produce the reconstruction as well as those sites belonging to the other territory but not used as occurrence data. (A) GARP prediction for northern territory, (B) Maxent prediction for northern territory, (C) GARP prediction for southern territory, (D) Maxent prediction for southern territory. Badegoulian sites outside of the territory and not used as occurrence data are depicted as black circles and those used as occurrence data are depicted as white circles. For the GARP predictions, grid squares with 1–5 of 10 models predicting the presence of suitable conditions are indicated in gray, grid squares with 6–9 models in agreement are depicted in pink, and squares with all 10 models in agreement are indicated in red. With the Maxent reconstructions, the depicted distribution boundary is determined by the lowest probability level (prediction threshold) that includes all of the known occurrences used to construct the model. These thresholds are as follows: (B) $P = 0.17$, (D) $P = 0.35$, (F) $P = 0.07$. For these Maxent models, colors range from gray, to pink, and to red, or low to high probability, respectively. Ice sheet and glacier limits after Ehlers and Gibbard (2004). LGM coastlines were obtained by lowering sea levels by 120 m (Lambeck and Chappell, 2001; Lambeck et al., 2002). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

suitable area for the northern territory, and about 120,000 km² for the southern territory, while Maxent identified 239,000 km² and 164,000 km² for the two areas, respectively.

In ecological dimensions, the northern niche corresponds to slightly cooler and more humid conditions than the southern niche. The zonal statistics demonstrated that GARP and Maxent predictions derived from the same occurrence and environmental datasets do not differ markedly from one another. The slight overlap of the northern territory's potential distribution, as predicted by GARP, onto that of the southern territory corresponds to conditions presenting mean annual temperature isotherms of 3–4 °C and mean annual precipitation values of 1–2 mm/day (36.5–73 cm/year; Fig. 6A).

The background similarity tests indicate that the geographic differences between the eco-cultural niches reconstructed for the two territories are not significant (Figs. 4D, F and 5B, D). The measures of niche overlap are $I = 0.417$ and $D = 0.168$; these statistics can vary between 0 (no overlap) and 1 (complete superposition). When I and D are compared to the pseudo-replicates produced by the background test (North vs. South, South vs. North), neither the northern territory nor the southern territory differs significantly from the other's background region (Fig. 7). These predictions demonstrate these two Badegoulian territories are interpredictive and thus occupy the same ecological niche.

However, despite their ecological similarity, one notes that the territories' geographic expressions are markedly different, especially with respect to the GARP predictions. Fig. 6A and B illustrate that within this climatic envelope, the northern territory is associated with ecological conditions that are slightly cooler and more humid than those of the southern territory. Therefore, we can conclude that the environmental differences between the two territories are a consequence of those portions of their geographic ranges that do not overlap, and do not reflect consistent environmental differences.

Discussion

Diachronic continuity in behavioral trends expressed in the archaeological record sometimes may be missed with traditional analytical approaches that focus solely on technology and typology. Before this study, the archaeological data needed to recognize the existence of distinct Badegoulian lithic raw material circulation networks and their similarity to armature-specific Upper Solutrean territories in present-day France were available. However, these data alone do not provide insight into the culture–environment interactions that operated behind the observed archaeological

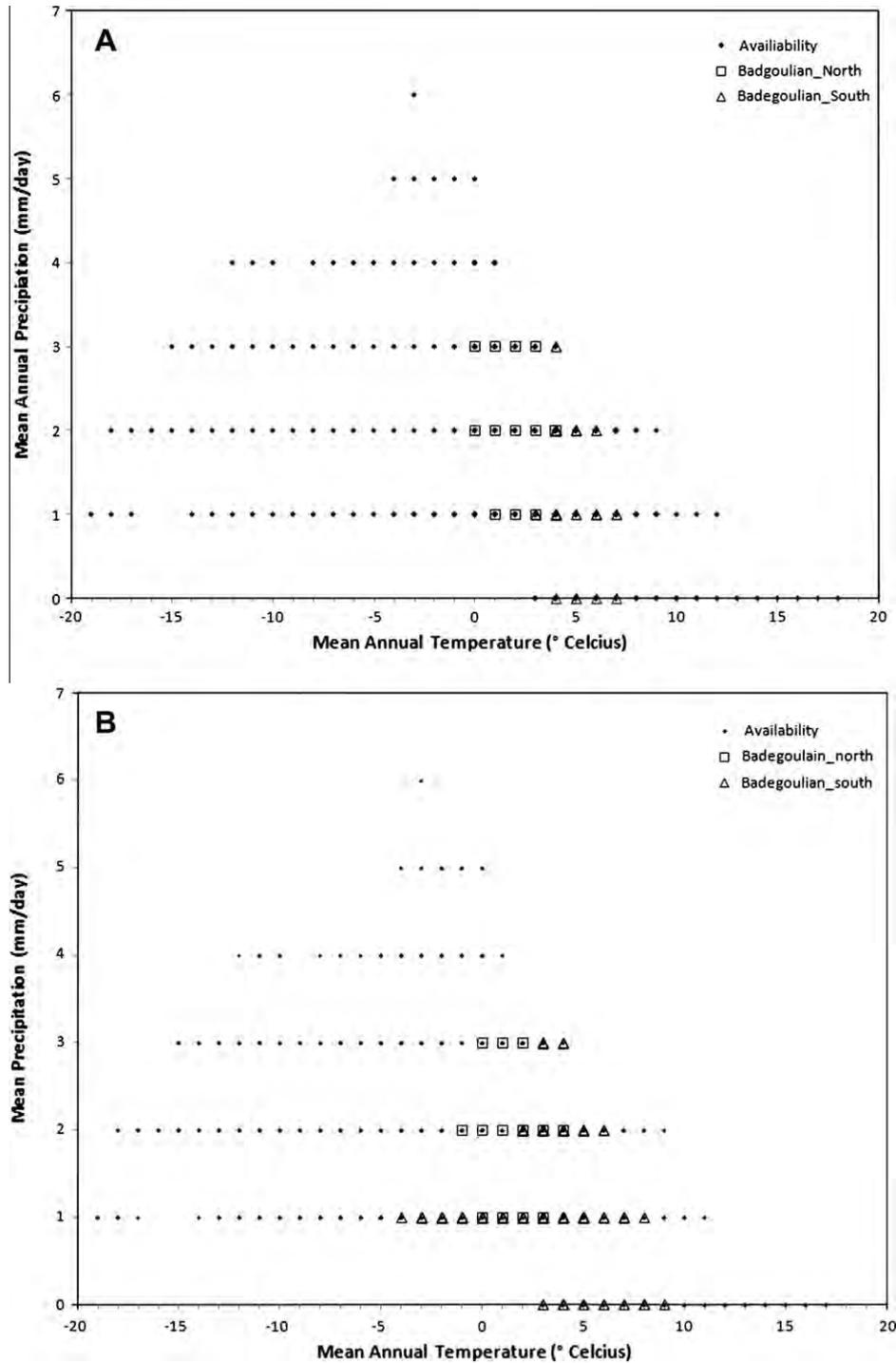


Fig. 6. Plot of the northern and southern Badegoulian ecological niches with respect to mean annual temperature and precipitation: (A) GARP predictions, (B) Maxent predictions.

patterns. Beyond making the link between Upper Solutrean and Badegoulian territories explicit, this study's reconstruction of ecological niches based on archaeological data has allowed us to add a critical dimension to the transition between these two archaeological cultures. This has allowed us to demonstrate that the trend towards territoriality observed in the Upper Solutrean (Banks et al., 2009) carries over into the Badegoulian, during which time territories become more distinct, even if, in the latter, they are not readily apparent in terms of stone tool types. Moreover, although contained within a single ecological niche, Badegoulian lithic raw

material circulation networks are mutually exclusive and associated with slightly different climatic conditions. For the Badegoulian territories, these patterns beg the questions of (a) demographic organization, and (b) implications of the relationship between ecology and territory, and the implications of the latter when applied to archaeological cultures.

At first glance, one might be inclined to interpret the results as reflecting seasonally differential use of this ecological niche by a single migratory human population or cultural group. However, this hypothesis can be rejected because no archaeological evidence

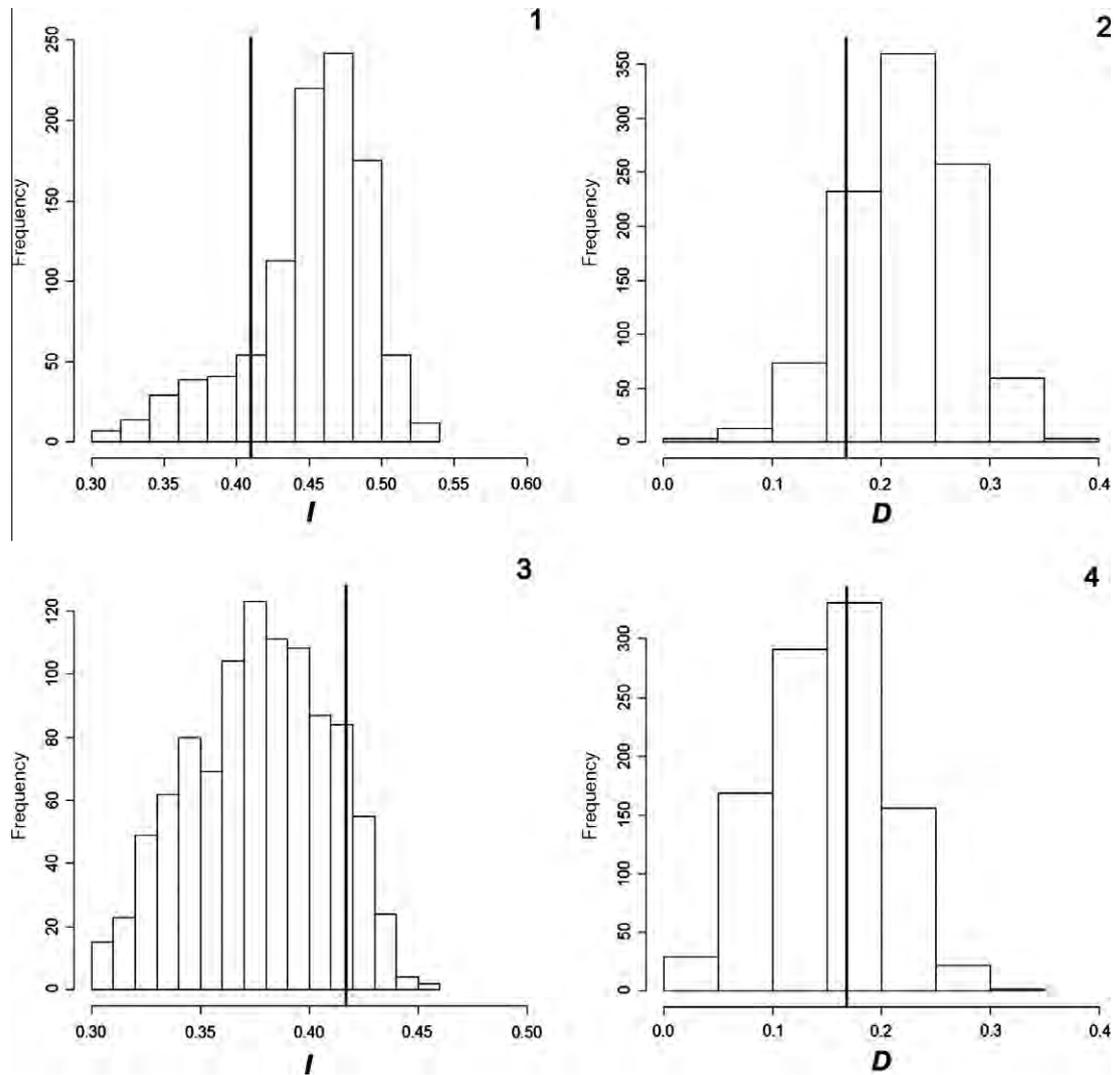


Fig. 7. Histograms of background test replicates: (1) North vs. South Background, I -statistic, (2) North vs. South Background, D -statistic, (3) South vs. North Background, I -statistic, (4) South vs. North Background, D -statistic. Black line indicates calculated overlap value ($I = 0.417$, $D = 0.168$). North vs. South, $P_I = 0.171$; $P_D = 0.160$; South vs. North, $P_I = 0.890$; $P_D = 0.622$.

indicates human circulation between the two regions. If they reflected seasonal territories exploited by a single population, one would expect at least some circulation of lithic raw materials between the two. Furthermore, faunal data (e.g., Castel, 2003; Fontana, 1999) indicate that the two territories were occupied year-round, even if certain sub-regions (Massif Central) had occupations that appear more seasonal. Thus, one can reject the hypothesis of seasonal movements by a single population of hunter-gatherers.

The question that arises is what are the factors that could create a situation in which distinct territories were established within a single ecological niche. One possibility is that the two lithic raw material circulation networks, and their associated eco-cultural niches, reflect distinct social territories, a hypothesis supported by the lack of lithic raw material circulation between the two. If such is the case, the reason for the existence of distinct social territories is of interest. One possibility is that the identified trend towards regionalization during the Upper Solutrean, probably brought about by cultural drift (Banks et al., 2009), continued into the Badegoulian. On the basis of bifacial armature styles, Banks et al. (2009) recognized two ecologically distinct Upper Solutrean territories in present-day France; these

two territories resemble the Badegoulian lithic raw material circulation networks and reconstructed eco-cultural niches. Thus, it is possible that these territories were maintained into the Badegoulian, with regional populations becoming isolated from one another socially, as suggested by the disappearance of regular circulation of lithic raw materials over large distances and between regions, characteristic of the Upper Solutrean. In other words, there was continuity in the human populations, but clearly independent social territories were established within the archaeological culture and within the ecological niche that they exploited.

However, a fact that complicates the idea of continuity between the Upper Solutrean and the Badegoulian is that we see a common lithic technology across the two Badegoulian territories that represents a rupture from the Upper Solutrean. Thus, a second possibility is that this rupture was the result of an influx of new human populations that carried with them different technical systems. The problem with such a scenario is that one has to assume that the new intrusive population adopted and inhabited nearly identical environmentally differentiated territories as the previous populations. One would expect to see at least some degree of restructuring or reorganization of territories, if not a complete

erasure of them, with the influx of a new cultural group. Nevertheless, at present, such a scenario cannot be rejected.

The fact that we see a common lithic technology across the two Badegoulian territories might not be as indicative of a broad cultural homogeneity as it would appear and may not necessarily contradict the apparent pattern of cultural territories. One must keep in mind that the Badegoulian is an archaeological culture defined by the presence of raclettes, often associated with transverse burins, in lithic assemblages. These tools are relatively “domestic” in the sense that they are geared towards processing and manufacturing (i.e., bone tool industry) activities. It is reasonable to assume that the activities in which these tools were employed were the same for the two identified territories and their respective environmental conditions. Such similarity between the two territories may not have existed for other techniques and cultural behaviors (organic industries, symbolic behavior, language, etc.). For example, [Tabarin \(2007\)](#) identifies a lack of homogeneity among Badegoulian personal ornaments, suggesting a degree of social variability within the technocomplex that is not apparent with respect to the lithic industry. Likewise, there does appear to be a difference in the bone tool industry between the northern and southern territories in that the latter features antler sagaies decorated with sinuous, parallel, longitudinal grooves (termed pseudo-excisé; [Séronie-Vivien, 1995, 2005](#)). The presence of shouldered points in sites belonging to the southern territory, but not the northern one, is another indicator of culture–geographic structure. Therefore, some evidence suggests that we may be correct in our identification of distinct social territories within the Badegoulian.

Assuming that we are correct in recognizing two different cultural territories within a single ecological niche, how might they be characterized from a demographic standpoint? [Wobst \(1974\)](#) defined “territorial” as meaning that social groups operated within a geographic area defined by social factors, the proximity of other groups, as well as familiarity with the environment and natural obstacles. With respect to the latter, the divide between the southern and northern Badegoulian territories represents a minor environmental transition (see [Fig. 6](#)) that, geographically, is relatively broad. Similarly, the Massif Central may have served as a geographic barrier that hindered movement between the two territories, while at the same time river drainages may have facilitated movement of people and information within each territory: e.g., within the northern territory, movement between the Paris basin and the northern and eastern flanks of the Massif Central would have been facilitated by the Loire River Valley and its tributary drainages.

[Clark \(1975\)](#) defined a social territory as an area in which a group or number of groups, belonging to a larger social formation, conducted activities that ensured their continued existence. Such social groups could be organized as a dialectic tribe or a macro-band. [Verhart \(1990\)](#) states that within such a social structure, one could expect common kinship and social ties, a common language, a uniform material culture, and exclusive rights of access to a territory. Thus, it would be reasonable to define the Badegoulian social territories as distinct geographic areas with relatively fixed boundaries, recognized by those within and outside them, that were occupied by groups who shared social systems or institutions that served to link them culturally with one another.

Looking further into the concept of social territories and how human populations might be organized within them, we refer to [Steward \(1969\)](#) and his concept of minimum and maximum bands. He defined a minimum band as a group of families or a group of related individuals who share a common settlement and participate in a set range of cultural activities. These minimum bands participate in a larger social network to ensure their biological and cultural survival, and he terms this overarching network of minimum bands that are linked via ritual communication and exchange

the maximum band. [Wobst \(1974\)](#) pointed out that movements of maximum bands could be limited or hindered by environmental conditions, in that moves between different ecological niches would be rare since such displacements would require potentially new and different adaptations. This point, though, seems less relevant to the Badegoulian, since the two social territories were occupied by groups that used the same lithic technology to exploit a single ecological niche. With this point in mind, it seems that a more important barrier to geographic displacements of Badegoulian groups was the existence of a social boundary between the northern and southern territories. In other words, the maximum bands that composed the northern territory shared a common cultural organization or system, which was different from that of the groups that operated within the southern territory, and vice versa. We propose that each of the Badegoulian territories was occupied by a number of socially linked maximum bands and that these two territories were culturally distinct from one another (i.e., language, mating organization, residence patterns, etc.) despite the fact that they shared a common lithic industry, used it to exploit the same ecological niche, and belonged to what we define as a single archaeological culture.

In an effort to model the general demographic implications of band social organization, [Wobst \(1974\)](#) relied on the average of 25 individuals for an area of 1250 km², which is observed in most hunter–gatherer populations. Considering that we are interested in the middle stage of the LGM in Western Europe, which corresponds to relatively harsh environmental conditions with respect to historically documented hunter–gatherer groups, we take a conservative approach and divide this average in half. This reduced figure of 25 individuals per 2500 km² corresponds to the estimate proposed by [Weninger \(1987\)](#) in his study of the Magdalenian of southern Germany. Using this demographic estimate, in tandem with the rough measures of the geographic areas of the reconstructed Badegoulian eco-cultural niches situated in present-day France (see Results above), we arrive at population estimates of ~1600 individuals for the southern territory and ~2400 for the northern territory. However, considering that the northern territory represented colder and more humid climatic conditions and was likely dominated by continuous permafrost conditions (see [van Vliet-Lanoë et al., 2004](#)), along with the fact that fewer archaeological sites are known in the northern territory, population densities there may have been lower than our calculated average. Consequently, we propose that the northern territory likely had a population similar to that of the southern territory, if not smaller; as such, the Badegoulian could have had a total population of roughly 3000 individuals. If we assume that a maximum band would consist of ca. 500 individuals, then one could extrapolate that each Badegoulian territory would have been comprised of three socially linked maximum bands.

We know that Badegoulian populations were reliant on ungulate species common to tundra and steppe-tundra environments, and most Badegoulian assemblages are associated with preserved faunal remains of reindeer. These environments are characterized by low species diversity, but the available species are relatively abundant, seasonally concentrated, and highly predictable in their movements in both time and space. [Dyson-Hudson and Smith \(1978\)](#) proposed that under such conditions human populations will have settlement systems that are territorial. When ungulate populations crash periodically, hunter–gatherers can respond organizationally by switching to settlement systems characterized by passive territoriality. Therefore, it seems reasonable to assume that within each Badegoulian social territory, each maximum band may have operated within its own distinct settlement system, but that during periods of resource scarcity their social links with neighboring culturally related maximum bands would have allowed a degree of territorial flexibility. Such flexibility would be

possible if the maximum bands within each broad Badegoulian territory had some form of networking and informational mobility between them. Such a situation is proposed by Whallon (2006) for Magdalenian groups in Central Europe that occupied steppe-tundra environments. He interprets raw materials to be circulating primarily among local groups within maximal bands, and notes that lithic raw materials rarely were moved over distances greater than 130 km. This pattern is similar to the lithic raw material record associated with the Badegoulian, and fits well with what we propose for the social structure within the Badegoulian territories.

This notion of socially distinct groups with their own specific territories subsumed within a larger territory is also supported by the patterns observed with respect to personal ornaments, assumed to more directly reflect cultural identity since they are not directly involved in subsistence activities. The lack of homogeneity among personal ornaments has been interpreted as reflecting a lack of overarching cultural cohesion within the technocomplex as a whole and the existence of a mosaic of tribes with limited interactions between them (Taborin, 2007). This fits well with our proposition for the existence of three loosely linked maximum bands within each Badegoulian territory.

It is important to reiterate that passive territoriality, if it is indeed the case here, appears not to have overlapped between the two Badegoulian lithic raw material circulation networks. From the standpoint of the latter, we appear to be observing the existence of a strong cultural frontier or boundary that extended from just south of the Creuse River Valley and extending to the southeast along the western margins of the Massif Central. These two lithic raw material circulation networks seem to reflect the movement of groups and interactions between minimum and maximum bands within well-defined social territories that were subsumed within the same ecological niche. Nevertheless, we do see that the two territories reflect specific environmental conditions. It has been argued that such a pattern of sub-niche differentiation allows neighboring populations to minimize competition between them (Holly, 2005). Thus, it appears likely that the regional territories established during the Upper Solutrean were maintained into the Badegoulian, and that their continued existence was facilitated by establishment of territories that focused on specific conditions within the Badegoulian niche.

Conclusions

This study of the culture–environment relationships specific to the Badegoulian has established that this technocomplex's two exclusive lithic raw material circulation networks are associated with slightly differing and geographically differentiated suites of environmental conditions that are contained within a single ecological niche. We propose that these two circulation networks represent well-defined cultural territories with boundaries that were recognized by groups both within and outside of them. What is of anthropological interest is that these two cultural territories shared a common lithic industry and are recognized as belonging to the same archaeological culture. This study describes a situation in which there exists a degree of social variability within an archaeological culture that is not readily apparent when only lithic tool types are considered. Furthermore, the application of ECNM methods has shown that the establishment and maintenance of these social territories did not have an ecological basis, but rather appears to have been more strongly influenced by cultural processes.

As the discussion has pointed out, archaeologists have long realized that ecology can be an important dimension to consider in the concept of territory. We have demonstrated that the application of eco-cultural niche modeling methods can effectively and

quantifiably evaluate ecological aspects of cultural territoriality. What is of interest here is that we have proposed that there was temporal continuity in the occupation of cultural territories that are associated with distinct environmental conditions within a single ecological niche between the Upper Solutrean and the Badegoulian, continuity that persists despite a rupture, or at the very least a dramatic shift, in lithic technology between the two technocomplexes. We have identified two possible scenarios to explain this pattern. First, the two Badegoulian social territories represent a carryover of the establishment of regional territories through cultural drift identified during the Upper Solutrean, but that these socially distinct groups adopted and shared a common lithic industry during the middle part of the LGM. The second scenario proposes that the technological rupture between the Upper Solutrean and the Badegoulian was due to the influx of new human populations that carried with them a different technical system and that these intrusive human groups adopted and exploited the same territories used by the earlier groups. We favor the first scenario but note that, unfortunately, eco-cultural niche modeling methods alone cannot be used to determine which of these is the more likely. Thus, it is critical to continue investigations of and comparisons between the material cultures of these two technocomplexes in an effort to better understand the cultural processes that are behind the archaeological patterns.

Furthermore, we argue that it is necessary to analyze in detail other components of Badegoulian material culture in order to test further our hypothesis that the two lithic raw material circulation networks reflect distinct Badegoulian social territories, as well as to understand better the social dynamics within and between them. Analyses of material cultures associated with traditional societies have shown that differences between groups belonging to the same ethno-linguistic group but that occupy different territories are often expressed through clothing or other stylistic mediums (see for example DeMallie, 2001; Vanhaeren and d'Errico, 2006). Depending on their techniques of manufacture and the materials employed, these traits often have a weak archaeological signature. Thus, it is possible that other differences in the material culture between the two Badegoulian territories will be recognized with the accumulation of additional data or more systematic analyses of existing and future data and that these differences may pertain to symbolic behavior (e.g., personal ornaments, mobiliary art, the style and decoration of bone and antler hunting weaponry). Analyses along these lines may help to clarify the mechanisms involved in the relationship between cultural adaptation and ecology. Such research would serve to add detail to our understanding of hunter–gatherer territories, their internal dynamics, and how they relate to ecological parameters and changing environmental conditions.

Finally, it would be interesting to evaluate whether these Badegoulian cultural territories were maintained into the Initial Magdalenian. This transition occurred during a period of relative climatic amelioration across the boundary between the latter stages of the LGM and Heinrich Event 1, and eco-cultural niche modeling would allow one to evaluate if and how associated cultural transformations were related to ecological parameters, as well as what adaptive and social processes are implicated.

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Human expansion: research tools, evidence, mechanisms

Francesco d'Errico, William E. Banks, and Jean Clobert

35.1 Introduction

Paradoxical as it may appear to some, the processes at work during human expansion parallel, to a large degree, those observed in the expansion of plant and animal species. As with all other species on the planet, the expansion of past human populations (and present-day patterns of dispersal) have been influenced by numerous parameters such as climate and geography (Chapters 25 and 30), vegetation regimes and food availability (Chapters 20 and 30), as well as intra- and inter-species competition (Chapters 1, 20, and 21), to name just a few.

When viewed from a diachronic perspective, expansion by members of our lineage shows a great degree of variability, a pattern that is likely to be correlated with the changes in social behaviour, emergence of innovations, and the inferred complexity of means of communication. For the most part, these changes occurred in our lineage at a higher rate than has been observed in the remainder of the living world (although numerous instances of rapid, human-assisted invasions have been recorded: Chapters in Parts VI and VII). Understanding the numerous human expansions that are known to have occurred in prehistory is therefore a challenge: driving factors may have been different or varied in their influence based on the time period and the hominin species in questions. Thus, when studying human dispersals, each case must be examined in such a way that all possible mechanisms are taken into account, since one cannot assume that a single mechanism consistently played an exclusive role, and it is likely that different mechanisms were interrelated, a situation which

is parallel to many other species (see Part I: the multiple causes of the dispersal process). Our aim here is threefold: 1) we briefly review and critically evaluate the tools that anthropologists and archaeologists have used to tackle these issues; 2) we highlight what we know, and don't know, about the main steps of hominin expansion; and 3) we discuss the possible mechanisms that have stimulated expansion and determined their success or failure, in the light of what we know about plant and animal dispersal.

35.2 Proxies of expansion

Geographic distributions and dated occurrences of hominin remains may be considered the most obvious indicators of the dispersal of members of our lineage. Unfortunately for more ancient periods, human remains are scarce, their recovery often accidental, and too fragmentary for unambiguous taxonomic determinations. There exists, however, sufficient paleontological evidence to establish, on a general timescale, when members of our lineage expanded out of Africa to other regions of the Old World. Also, the last 20 years of paleoanthropological research has significantly enlarged and improved, through the application of new analytical methods, the criteria used to address skeletal variability and make taxonomic attributions (Wood 2010). However, there still exists considerable debate surrounding taxonomic classification and phylogenetic significance of key hominin fossils (Wood and Lonergan 2008; White *et al.* 2010). This is complicated by differential preservation, meaning that sites with well-preserved human remains may

not necessarily be situated in a region that was at the heart of an ancient dispersal corridor. Skeletal morphology has been used to infer the structure and variation in ancient populations (Gunz *et al.* 2009), as well as adaptation to specific environmental conditions or ecological niches and a hominin's ability to migrate to and settle in new regions (Potts and Teague 2010). However, cases are recorded in which there is not a straightforward match between morphology and function (Ungar *et al.* 2008). For more recent periods for which there are large samples of preserved human remains, morphological variability of specific features, such as cranial shape, allow scenarios of demic population diffusions to be proposed (González-José *et al.* 2008; Pinhasi and von Cramon-Taubadel 2009).

As in studies of plant and animal phylogeography, the analysis of genetic data is becoming an increasingly important means to address human expansion. These studies fall into three broad classes. First, present human genetic variability is used to infer the timing, geographic origin, route of dispersal, rate of genetic exchange, and in some cases, the likely size of the migrant population (Cavalli-Sforza *et al.* 1994; Li *et al.* 2008). For example, present-day genetic data demonstrate that anatomically modern humans originated in Africa approximately 200 000 years before present (BP) and has been used to infer the timing and paths of human dispersal through Asia, Europe, Australia, and the Americas (see Henn *et al.* 2011 for a review; Figure 35.1a). Based on the same data, it has been recently proposed that modern humans intermixed with archaic human populations in Africa circa 35 000 BP (Hammer *et al.* 2011). The Neolithic expansion into Europe from the Near East has been repeatedly addressed using the same research philosophy (Chikhi *et al.* 2009). Second, the dramatic improvements in extraction and sequencing technology of ancient DNA seen in recent years, has profoundly impacted our ability to study past human variability and dispersal. The reconstruction of a large portion of the Neanderthal genome (Green *et al.* 2010) and the recent sequencing of the Denisovan genome (Krause *et al.* 2010) has demonstrated that modern humans leaving Africa interbred to varying degrees with two separate archaic

human populations in the Near East and Asia. This has had profound impacts on our understanding of past human dispersals, and the speed at which such methods are improving suggest that this may be one of the most promising approaches with which to study past human expansions. Lastly, human expansions can be traced by examining genetic data from species that accompanied or encountered expanding human populations. Present-day human dispersals are used to trace long-distance animal and plant dispersals (see Chapter 15). Similarly, paleogenetic data of domesticated species have been used to trace the expansion of the first herding societies. A case in point is the use of ancient *Sus* DNA to trace human expansion in South-east Asia and Oceania during the Neolithic (Larson *et al.* 2007). For Europe, genetic data from goats, cattle, and dogs are used to trace Neolithic human expansions (see Deguilloux *et al.* 2009; Larson 2011; Tresset *et al.* 2009). Another interesting example is the use of chicken paleogenetic data to understand prehistoric sources of migration into South America (Storey *et al.* 2007). The genetics of human parasites have proven to be extremely informative in tracing human expansion and contacts between ancient human populations (see Rinaldi 2007 for a review). Lice have been used to indicate direct contacts between modern human colonizers and resident archaic populations in Asia (Reed *et al.* 2004). Other examples (Figure 35.1b) include viruses and bacteria such as leprosy (Dominguez-Bello and Blaser 2011; Monot *et al.* 2005).

Strontium, oxygen, carbon, and nitrogen isotopes, as well as concentrations of major, minor, and trace elements, have also been used to examine paleodiet and infer paleomobility (see Knudson *et al.* 2011 for a review of methods). However, these techniques are more useful at regional scales than they are for tracing geographically expansive human migrations. With respect to other disciplines, such methods have been used to examine bird migrations and dispersals (Sellick *et al.* 2009).

Expansions can also be inferred by examining material remains in the archaeological record. Unlike other animal species, prehistoric humans produced chipped stone-tool industries, one of the most traditional proxies used in archaeology to

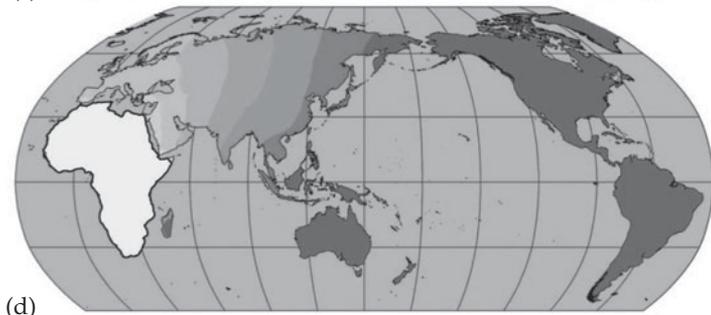
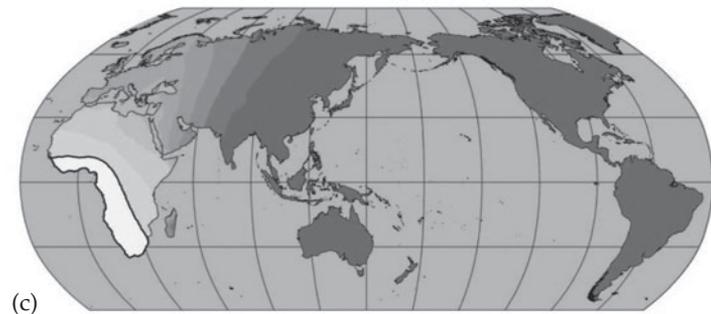
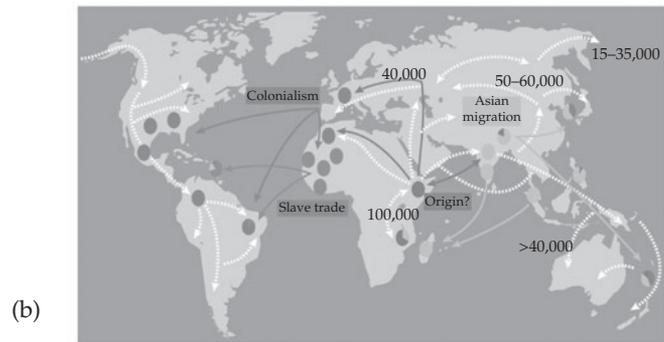
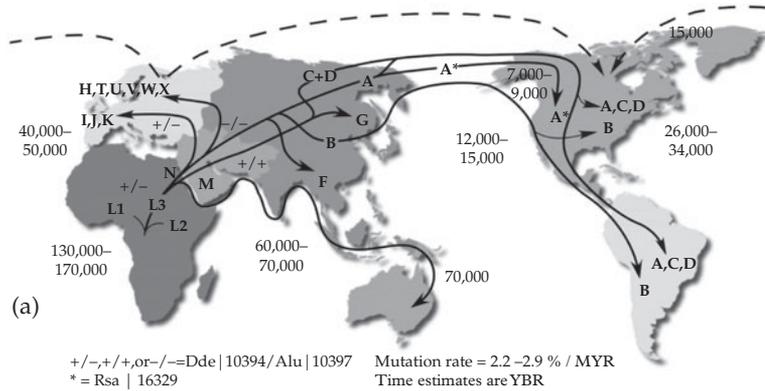


Figure 35.1 (a) *Homo sapiens* migrations based on the modern variability of mitochondrial DNA; (b) dissemination of leprosy in the world, based on the analysis of single-nucleotide polymorphisms. White dotted arrows indicate dispersal of modern humans based on genetic and archaeological evidence. Plain arrows indicate direction of human migration predicted by the polymorphism of the leprosy bacteria; (c)–(d) likely area of language origin under a founder effect model of phonemic diversity inferred from individual languages (a) and mean diversity across language families. (a) modified after <<http://www.mitomap.org/mitomap/WorldMigrations.pdf>>; (b) from Monot *et al.* 2005, used with permission from Science; (c)–(d) from Atkinson 2011, used with permission from Science.

infer past expansions and contractions of geographic ranges. Stone tool morphology and the processes of their manufacture are thought to reflect the maintenance and transmission of cultural traditions (Bar-Yosef and Belfer-Cohen 2012). For most recent prehistoric periods, during which cultural behaviour becomes more complex, lithic technological data are combined with other cultural markers to reconstruct vectors and extents of expansion events. For example, Mellars (2006) uses the presence of ostrich egg shell beads, engraved objects, and crescent-shaped chipped stone tools to identify an expansion of anatomically modern humans from southern Africa into southern and south-eastern Asia (between 60–40 000 BP). For the European Upper Paleolithic (40–12 000 BP), bone tool styles, mobiliary art, and personal ornament types, among others, have been used trace expansion such as the recolonization of Northern Europe after the Last Glacial Maximum (Gamble *et al.* 2005). With the Holocene archaeological record (after 10 000 BP), ceramic morphology and decoration become a major proxy for defining cultural entities and tracing their possible expansions.

One problem with the reliance on material culture and specific artefact styles is that during expansion events, technologies and styles can undergo change or be abandoned as a consequence of adaptation to new environments, cultural drift, or cultural exchanges with encountered populations. This makes it difficult, particularly for early periods, to associate specific technologies with certain hominins (see Bar-Yosef and Belfer-Cohen 2012; Shea 2010). Additionally, with the appearance of complex societies and social stratification we observe an increased frequency of artefacts being moved across the landscape through trade or made locally by travelling specialists.

Tracing and modelling dispersals of human populations via archaeological proxies is strengthened by the incorporation of chronological data. Biochronology (faunal and vegetal associations), paleomagnetic stratigraphy, and radiometric dating are used to trace the expansion of the first member of our lineage to leave Africa (*Homo erectus*). Such methods have improved considerably during recent decades, but in the absence of clearly diagnostic

stone-tool types, archaeologists are unable to determine if an expansion occurred as a single dispersal event or if it represents multiple waves. For early dispersals of anatomically modern humans (AMH), the above methods are supplemented by more precise dating methods such as OSL, TL, and radiocarbon (^{14}C). Examples include dispersals across northern Africa (Barton *et al.* 2009), possible corridors out of Africa (Armitage *et al.* 2011), through southern Asia and into Australia (Balme 2011). For expansions occurring after 40 000 BP, radiocarbon dating and its updated calibration (Reimer *et al.* 2009) are the principal means used to reconstruct the timing of population movements across Eurasia, the arrival of AMH into the European cul-de-sac and the New World, as well as island colonization (e.g. Polynesian chains, Mediterranean islands, Japan, etc.). Radiocarbon chronologies have played a crucial role in modelling the Neolithic expansion into Europe from the Near East (Ammerman and Cavalli-Sforza 1984; Bocquet-Appel and Bar-Yosef 2008; Bocquet-Appel *et al.* 2009). Chronologies at the limit of the method (50 000–30 000 BP) can be tested and verified by the presence of tephra, which serves to fingerprint specific volcanic events of a known age. For example, the Campanian Ignimbrite has been used to trace the arrival of modern humans into Italy and Eastern Europe (Blockley *et al.* 2008; Longo *et al.* 2012).

In and of themselves, radiometric ages have been repeatedly used as proxies by which human dispersals can be measured. The increasing precision and number of more ancient ages, along with recent improvements in radiocarbon calibration, have allowed for the construction of scenarios for the arrival of modern humans into Europe during Marine Isotope Stage 3 (Zilhão and d'Errico 1999; Higham *et al.* 2009), the recolonization of northern latitudes in Europe following the Last Glacial Maximum (Gamble *et al.* 2005), and the colonization of North America (Hamilton and Buchanan 2007).

As in animal and plant species, paleogeographic reconstructions based on tectonics (e.g. Schattner and Lazar 2009) and glacioeustatic and sea level changes (Bailey *et al.* 2011) are also used to constrain the dispersal and development of hominin populations in some regions such as *Homo erectus* in Java or

Homo floresis on Flores Island (Zaim 2010). Information on sea level changes is combined with archaeological information on sea-faring navigation to reconstruct potential dispersal corridors. In examining sea level reconstructions, it becomes clear that parts of south-eastern Asia could only have been populated by *Homo erectus* if they crossed bodies of water (see Balme 2012), but these water barriers would have been less than 20 km due to lowered sea levels. Purposeful and long-distance dispersals by sea crossing are attested to in some regions of the world, such as Sahul, at around 50 000 BP. Much later, the Neolithic expansion along the Mediterranean coast is thought to have been facilitated by an intense use of boats that were of sufficient size to transport both people and domesticated animals (Broodbank 2006). It is important to point out that while human populations used sea-faring technology to settle distant regions and islands, there are several instances in which these technologies were subsequently lost or abandoned by later generations.

As with bird song (Seddon *et al.* 2008), historical linguistic means have been developed to establish language phylogenies which in cases of migration may be used as tracers of the related population expansions. A well-known, but also controversial case is the history of Indo-European languages associated with a number of population movements into Europe from the East (Renfrew 1987). Linguistic variability has been a key element in the study of the Bantu expansion in Africa, which refers to the large population movement throughout sub-Saharan Africa ca. 5000 BP (see Berniell-Lee *et al.* 2009 for a review). In the Pacific, language phylogenies have served to identify periods of expansion and stasis in human settlement (Gray *et al.* 2009). Recently, attempts have been made in using language diversity to predict the African region where modern languages originated (Figure 35.1c–d; Atkinson 2011). For the recent historic period, surnames serve to study mobility and temporal demographic variability (Darlu *et al.* 2011). Finally, we must not forget that humans are the only species to tell and share stories about where they come from, although a social group's history of its origin tends to be influenced by a number of

biases and may not accurately reflect a demographic reality.

The introduction of modelling techniques to dispersal studies, with the aim of creating scenarios and evaluating them against empirical data (e.g. Ackland *et al.* 2007; Banks *et al.* 2008a; Bocquet-Appel *et al.* 2009; Currat and Excoffier 2011; Field *et al.* 2007; Hughes *et al.* 2007), can allow one to determine if deviations from expectations can be accounted for by including additional parameters or different model structures (Steele 2009). For example, with modelling methods, one can include key parameters similar to those used to study plant and animal dispersals such as carrying capacity, population density, and population growth.

35.3 The record of hominin expansions

What have all these different approaches highlighted or revealed about dispersals in general, and more specifically, the successive expansions of members of our lineage since our separation from the common ancestor that we share with chimpanzees?

Between 2 and 3 million years ago (mya) early hominins appear to have exploited ecological situations that were coincident with transitions between wooded and open environments present in both the Rift valley of East Africa and southern Africa. It had been proposed that a shift in climate that occurred in the late Miocene may have favoured evolutionary changes in early hominins, which would have led to bipedalism and their expansion into open savannah environments (Bonnefille *et al.* 2004). This hypothesis has now been largely abandoned after the discovery of earlier hominin remains to the west of the Rift Valley as well as in Chad (Brunet 2009). This does not rule out the idea, however, that climate change led to changes in adaptation and geographic expansion of early hominins (de Menocal 2011), as is currently the case with plants and animals due to global warming (see chapters in Part VI). Selection on the habitat margin (like social adaptations, morphological adaptations, and selection on dispersal capacity which can be viewed as innovation) may have played important roles (Chapters 25 and 26).

The rarity of associated hominin remains makes it difficult to establish the authors of the first unmistakable knapped stone tool industries in East Africa around 2.6 mya (de la Torre 2011). By ca. 1.77 mya the archaeological record indicates a first dispersal of *Homo erectus* bearing a core and flake technology into various regions of Africa (see Bar-Yosef and Belfer-Cohen 2012) as well as into southern Eurasia (site of Dmanisi; Agusti and Lordkipanidze 2011). Almost immediately afterwards, around 1.76 mya, we see in East Africa the earliest instances of a biface-dominated stone tool industry termed the Acheulian (Lepre *et al.* 2011). By 1.5–1.4 mya, the bearers of Acheulian technology had dispersed out of Africa, across western Asia, and into South Asia. It is still unclear whether the Acheulian occupied the whole of Africa before 0.7 mya (Raynal *et al.* 2001). Europe does not seem to have been populated during these expansions and it is not until much later, ca. 1.2 mya, that we find hominin remains and flake/core industries in southern Europe (Carbonell *et al.* 2008). The Acheulian appears in the Iberian Peninsula around 0.9 mya (Scott and Gibert 2009), but does not extend into northern Europe until after 0.5 mya (Monnier 2006). The British Isles do not have a record of occupation before 0.78 mya, and that occupation is not associated with Acheulian technology (Parfitt *et al.* 2010). Recent genetic evidence suggests that the archaic hominins who colonized Europe and Asia became largely isolated by 1.0 mya and gave rise to at least two separate lineages that ultimately led to Neanderthals and Denisovans, respectively (Krause *et al.* 2010; Reich *et al.* 2010). The latter is named after the eponymous site located in the Altai Mountains of southern Siberia from which human remains that preserved ancient DNA were recovered. Paleoanthropological evidence suggests that archaic hominins living in Europe slowly acquired typical Neanderthal features during the late Middle and early Upper Pleistocene, i.e. 400 000–40 000 BP. During this period, pre-Neanderthal and Neanderthal ranges fluctuated such that they intermittently occupied regions such as the British Isles, the Near East, western Asia, and possibly more northern latitudes near the arctic circle (Slimak *et al.* 2011;

Pavlov *et al.* 2001), although the latter still needs further evaluation to be confirmed.

Genetic and paleoanthropological evidence suggests that modern human features appear in West Africa around 200 000 BP (White *et al.* 2003). Due to a lack or fragmentary nature of human remains over large regions of Africa, it is, however, uncertain when expansions of AMH occurred within Africa and whether there was a single expansion or multiple expansions, although the latter is more likely (Gunz *et al.* 2009). Evidence has recently been presented that indicates a genetic contribution of African archaic hominins to the modern African gene pool (Hammer *et al.* 2011). By ca. 130 000 BP modern human populations, with some archaic features and bearing a technology similar to that of coeval Neanderthal populations occupying the Near East, are recognized in the Maghreb and in the Near East. The presence of these populations outside of Africa is limited to the Near East and is not recognized in neighboring regions of Western Asia (Garcea 2012). This suggests that this expansion was not successful and may only represent populations following the natural expansion of their ecological range during this period of climatic amelioration. It is interesting to note that similar differences in colonizing capacity among populations in different refuges are documented in the plant and animal kingdom after the last glacial episode (Hewitt 2008).

It is not until after the cold and rigorous period known as Marine Isotope Stage 4, which terminated around 60 000 BP, that we see a significant expansion of anatomically modern humans out of Africa. The path and timing of this expansion are highly debated, but it was quite rapid towards the East as we recognize a modern human presence in Australia by ca. 50 000 BP (Balme 2012). Genetic evidence indicate encounters between modern humans and resident Neanderthal populations probably occurred just after the former's exit from Africa since Neanderthal genes are present (ca. 2–4%) in all non-African modern human populations (Green *et al.* 2010). During their dispersal through Asia, modern humans also interbred with Denisovan populations as indicated by a relatively large contribution to the modern human genome of popula-

tions in Melanesia (Reich *et al.* 2010). Often considered to be a single event, this major dispersal may have taken a variety of forms with multiple exits from Africa during a period that covered several millennia.

Evidence for the first arrival of modern humans in Europe dates to ca. 42–42 000 BP. The timing of this expansion, Neanderthal disappearance and the mechanisms behind this founder population event are highly debated (Pinhasi *et al.* 2011; Banks *et al.* 2008a). There is evidence suggesting a late survival of Neanderthals in the Iberian Peninsula (ca. 34 000 BP) which supports the idea that modern human dispersal into Europe was not a single, rapid event and may have taken different forms in different regions.

It is debated whether the cultural changes within the Upper Paleolithic are the result of cultural drift (local cultural evolution) or population dispersals. The latter has been proposed for the Gravettian based principally on genetic data (Semino *et al.* 2000) and more convincingly, combining genetic and archaeological data, for the Magdalenian (Gamble *et al.* 2006). It is clear, however, that millennial-scale climatic variability of MIS 3 and 2, as well as the impact in Europe of the Last Glacial Maximum, must have had profound influences on human ranges (Banks *et al.* 2008b). During the Bølling-Allerød climatic amelioration (14 700–12 700 BP) and more intensively at the beginning of the Holocene, ca. 10 000 BP, human populations recolonized northern Europe. Mesolithic hunter-gatherers are recognized in the British Isles and Ireland around 9 000 BP and northern Scandinavia after 8 000 BP. Recent genetic evidence suggests that similar recolonizations may have occurred in Asia well before the spread of the Neolithic (Zheng *et al.* 2011).

Early dates from a number of archaeological sites indicates that the first human colonization of the Americas, favoured by the use of watercraft along the southern coast of the Bering Land Bridge, occurred between 15 000 and 13 500 BP. Pre-Clovis hunter-gatherers were present in the state of Washington by at least 13 700 BP (Waters *et al.* 2011). Radiocarbon ages from South American sites suggest the process was extremely rapid (Figure 35.2a) and may have taken less than a millennium (Rothhammers and Dillehay 2009; Meltzer 2009).

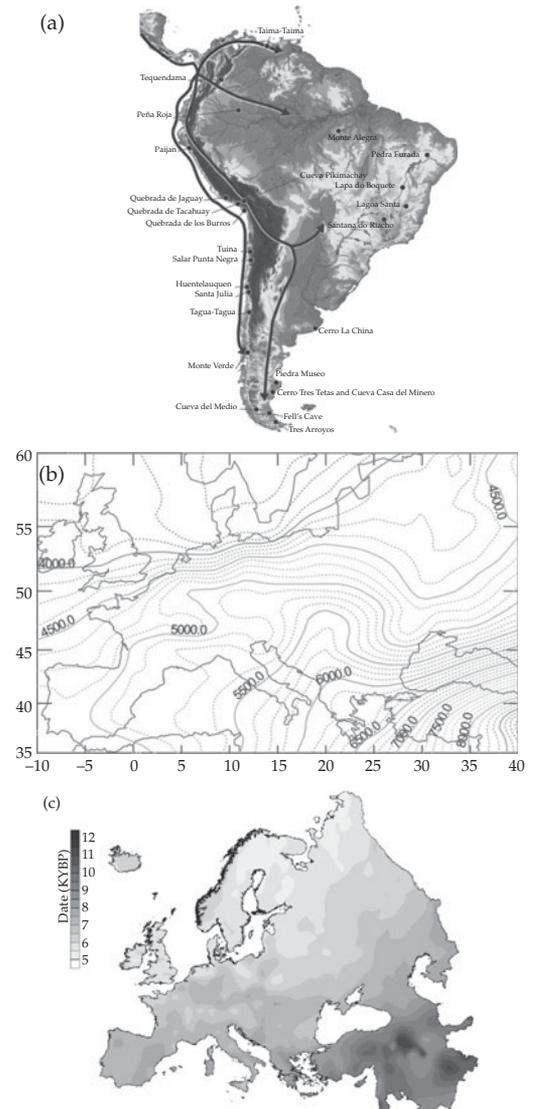


Figure 35.2 (a) Hypothesized migration routes into South America and major archaeological sites dating to the late Pleistocene; (b)–(c) representations of the isochrones of the Neolithic farming expansion into Europe; (a) after Rothhammer and Dillehay 2009, used with permission from John Wiley and Sons; (b) after Bocquet-Appel *et al.* 2012, used with permission from Elsevier; (c) after Balaesque *et al.* 2010.

The transition from hunter-gatherer to farming/herding economies has also led, in many areas of the world, to population dispersals. For many years, it was questioned whether the emergence of

agriculture and animal domestication in Europe was, at least in some regions, the result of independent local invention, the spread and adoption of this adaptation by resident hunter-gather populations, or the actual physical dispersals of populations that used such production-oriented economies. It is now widely accepted that the latter scenario is likely the case for most of Europe and that early Neolithic adaptations spread westward from the Near East (Figure 35.2b, c) at around 10 000 BP across the Mediterranean and reached peripheral zones in northwestern Europe by ca. 4000 BP (Bocquet-Appel *et al.* 2009). The nature of cultural and genetic exchanges between invading Neolithic populations and local hunter-gatherers are still the subject of intense debate fueled by the input of a variety of disciplines (Bocquet-Appel and Bar-Yosef 2008). The process that we observe in Europe was not the rule in all other areas of the world. In North America, the transition to full-scale agriculture was relatively slow and was for the most part characterized by the diffusion of horticultural and agricultural technologies rather than large scale movements or expansion of people. It is possible that differences in dispersal syndrome (Chapter 10), linking colonization ability and agricultural skills, might have differed between regions. Similar instances are recurrently found in animal species, although obviously not involving the same traits (Clobert *et al.* 2009).

More remote regions of the globe were not systematically settled until well after the spread of agricultural economies in mid- and tropical latitudes of continental regions of Eurasia and the Americas. This is the case for the pre-Dorset colonization of Arctic North America by 4500 years ago. This population originated in Siberia and carried with it an adaptation that allowed for the permanent occupation of an arctic landscape. An adaptation to a full arctic landscape is not seen until the Thule expansion from western Alaska around 800 years ago and that reached the southern coast of Greenland 300 years later (Friesen and Arnold 2008).

Human dispersal and colonization has taken various forms, was dependent on the population and species in question, and was influenced by multiple

abiotic and biotic factors. Alone, human dispersal illustrates well the multicausal and multifactorial nature of this complex behaviour (see chapters in Part I).

35.4 Factors behind human expansion

35.4.1 The climate hypothesis

For most species, when expansion is the focus of investigation, climatic and resultant environmental changes are often evoked as the key factors (Chapters 25 and 26). Indeed, models predict that the evolution of dispersal should be more sensitive to environmental stochasticity when all potential causes for its evolution are combined (Gandon *et al.* 2001). For humans, the basic assumption here is that shifts in climate alter the environmental structure, and therefore resource availability, of a given region. Climatic changes can alter the geographic footprint of a given ecological niche, and a population may expand to track this changing footprint (Chapter 25). A good example of this latter scenario is the repopulation of northern Europe by hunter-gatherers during a period of climatic amelioration following the Last Glacial Maximum (Gamble *et al.* 2005). Potential outcomes of environmental change on a population include extinction, migration, isolation, and eventually speciation. The new species may benefit from mutations that allow it to expand its ecological niche (Chapter 26), which can be manifested by a physical expansion. Some have advanced the idea that the key to understanding the successful adaptations leading to the multiple exits from Africa is the process of speciation and the resulting cognitive advantages (McBrearty and Brooks 2000). This would explain the expansion out of Africa by *Homo erectus* as well as by modern humans. Attributing human expansion solely to climate change and speciation, however, can hardly explain why, compared to other species, members of our lineage, spread so quickly across a wide variety of ecosystems.

Clearly other factors were at play during the evolution of our lineage and influenced human expansions to varying degrees depending on the period in question. Many authors have explored the role of culture in its various forms. Such a role can be com-

pared, to some extent, to that of maternal effects and phenotypic plasticity in plants and animals (see chapters in Part III). Richerson and Boyd (2005; Richerson *et al.* 2005) argue that cumulative culture is the means by which our species has escaped the rules of natural selection in order to cope with rapid-scale and high-amplitude climatic changes that increasingly characterized our planet's climate during the last million years. We have created a costly tool that allows us to accumulate and transmit knowledge across generations (Boyd *et al.* 2011). From this perspective, human dispersal is at once the outcome of environmental change and the accumulation of successful cultural adaptations.

Chipped-stone tools, hunting technologies, containers, systematic use of fire, clothing, and sea-faring technology are among the cultural innovations that have certainly played a role in facilitating human expansions by reducing dispersal cost (Bonte *et al.* 2012). In order for expansions to be viable in challenging environments and for complex cultural adaptations to be developed and maintained, the establishment and maintenance of communication systems and social networks is essential. The production of symbolic material culture, including body decoration, art, imposed style in manufactured objects, etc. is the archaeological reflection of the communication systems developed by human groups. Such mechanisms may also serve to distinguish differences between groups and result in the establishment of local or more regional cultural traditions. When seen from an ecological perspective, such processes echo the interplay between dispersal and local adaptation following a colonization event, which we see with the expansion of other animal and plant species.

In turn, the creation of these advantageous cultural adaptations likely favoured organic evolution that allowed and facilitated human expansion. The development of more complex communication systems may have stimulated changes in the brain that led to increased language capacity.

35.4.2 The cultural hypothesis

Recently, the involvement of climatic variability in the process of expansion has been challenged by

researchers who stress the importance of cultural and genetic features associated with different populations to account for success and failure of dispersal events. Each hominin group expanding inside and outside Africa would be characterized, according to them, by an ability to cope with environmental stress that would have conditioned their ability to occupy new territories and have that expansion be viable over the long term (Bar-Yosef and Belfer-Cohen 2012; Chudek and Henrich 2011). A similar situation may have played out in plant and animal expansions, where novelties or selection would have reduced dispersal costs or enhanced settlement success of the dispersers (Bonte *et al.* 2012; Chapters in Part III).

The integration of ecological niche and species distribution modelling methods into archaeological investigations has allowed these issues to be addressed directly via an approach termed eco-cultural niche modelling (Banks *et al.* 2006). The utility of eco-cultural niche modelling is that it allows one to evaluate quantitatively whether links exist between a given adaptive system and ecological constraints, or if the characteristics and geographic distribution of a cohesive cultural system may have been influenced more by non-ecological (i.e. cultural) processes (Banks *et al.* 2009, 2011). Additionally, one can evaluate culture-environment relationships across time and determine if dispersal events were associated with ecological niche shifts or if they represent simple range changes that tracked fluctuating environmental footprints. The interest of this and similar approaches is that: (1) they allow one to disentangle and evaluate the various mechanisms behind specific human dispersal events; and (2) they can be used to create the foundations of a 'unified theory' of human expansion that combines the inputs from modelling techniques, genetic and ecological thinking, and archaeological and paleoanthropological evidence.

35.4.3 The social hypothesis

While climatic factors certainly played a role in past human expansion, in conjunction with the use of culture to reduce dispersal costs, there is a dimension, which can be termed the social dimension,

whose factors might also have played an important role. Evidence of social factors motivating human dispersal is found in most modern human expansions. Social-based factors encompass all factors which arise from interactions either among kin or among congeners (Chapter 1), and as an extension among tribes or groups of humans or tribes (Towner 1999; Kok 2010). Potential examples are numerous. There is a tradition in oceanic island populations of sending selected sons/daughters from different families to colonize new islands, even in the absence of any information about the existence and accessibility of these new islands (Edwards 2003, Finney 1996). This resembles a potential link between kin competition and colonization, a pattern that is found in some animals populations (Sinervo and Clobert 2003; Cote *et al.* 2007). In aristocratic families, often only the oldest male child will inherit the title and domain, the youngest having to develop their own way with a minimum of parental investment (Block 1864; Kok 2010). A similar uneven inheritance principle was applied in farmer families (Furby 1896; Kok 2010). Not surprisingly, the youngest children of aristocratic families have often played an important role in colonizing new territories during the colonization by Europeans of other continents in the last 500 years or so. Competition among congeners for food, territory, or other resources has also play an important role in the same colonization process. The early colonization of North America is a good example of this with numerous people taking the decision of leaving their natal country in the hope of having a better life in those newly available areas. Competition for goods is also playing a major role in the present-day colonization of European countries by people from countries with depressed economies. Sadly enough, the above example also serves to illustrate that colonization comes with some cost: many individuals die during the dispersal process (boat people, ICMC Europe report 2011), or during initial settlement with an increased mortality rate (up to the failing of the colonization) due to small population size, illness, or lack of local adaptation (Greenland colonization by Eric the Red in McGovern 1980; Christopher Columbus' first implantation in Columbus and Fuson 1987).

With respect to animals and plants, the colonization process often involves individuals with a different phenotype than that of the resident individual (chapters in Part III). Although no systematic studies have been conducted on humans (Arango 2000), the actual behavioural profile of human pioneers (Laland and Brown 2011; Massey 1990, Whybrow 2005) suggests such a possibility. To what extent this might explain the current structure and reference values of nations arising from such colonization (such as in North America) is open to debate, especially if the later waves of colonization were achieved by people with different behavioural profiles than those of the first (the colonizer-joiner process, Clobert *et al.* 2009). A comparison between Australia and North America might be of help here since these colonization events were achieved in very different ways.

How social factors may have played an important role in early human expansions is difficult to envision, although it is possible that these forces increased in importance when the adoption of agriculture led to human populations becoming more sedentary (Larsen 1995).

35.5 Conclusions

Our review shows that the mechanisms behind dispersals throughout the history of the human lineage are diverse and serves to illustrate the multiple causes and origins of the dispersal processes and patterns that are observed in other species (see chapters in Parts I and IV). The examples of different dispersal events described above serve to show that there is no common denominator when considering human populations, and that this fact is likely to be true for most other species as well. For example, early dispersals within the African continent and the earliest dispersals of *Homo* out of Africa appear to be related to speciation events and their success tied to biological adaptations (Chapters 25 and 26). Changing environmental conditions seem to have strongly conditioned certain expansions by facilitating movement through geographic corridors during specific climatic events. The movement into regions devoid of human populations, and therefore relatively free from competition, likely favoured early

dispersals out of Africa across the Old World, and also later when populations first entered the Americas. The pioneer syndrome should then have been heavily selected for. Likewise, competition was also a key factor when one sees dispersals into regions that already had resident human populations, as is the case with the earliest, but unsuccessful, expansions of anatomically modern humans out of Africa into the Near East where archaic human populations were present. It is likely that social factors increased in importance when human populations became more sedentary and that the pioneer syndrome was selected against.

In human populations, it is evident that in many instances cultural adaptations played a key role in successful dispersal events, a role which is, to some extent, comparable to phenotypic plasticity and maternal effects in other species. The development of technologies and the appearance of certain social behaviours appear to have conferred slight competitive advantages to expanding populations, as is the case with the second migration of modern humans out of Africa around 50 000 years ago into regions of the Old World that had resident archaic human populations, as well as during the Neolithic some 40 000 years later. However, dispersal comes with a cost, which has probably increased as human populations increased their social structures. Therefore, when one considers human dispersal, each case must be examined individually and all possible factors behind such events must be considered—one cannot assume *a priori* that a single mechanism consistently plays a major role. In other words, causes and consequences of dispersal in humans and other living beings not surprisingly share many common characteristics. Only the relative importance of some mechanisms, such as cultural ones, might have permitted humans to colonize a larger array of habitat types with great success.

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Human–climate interaction during the Early Upper Paleolithic: testing the hypothesis of an adaptive shift between the Proto-Aurignacian and the Early Aurignacian

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Heinrich Stadial 4

ABSTRACT

The Aurignacian technocomplex comprises a succession of culturally distinct phases. Between its first two subdivisions, the Proto-Aurignacian and the Early Aurignacian, we see a shift from single to separate reduction sequences for blade and bladelet production, the appearance of split-based antler points, and a number of other changes in stone tool typology and technology as well as in symbolic material culture. Bayesian modeling of available ¹⁴C determinations, conducted within the framework of this study, indicates that these material culture changes are coincident with abrupt and marked climatic changes. The Proto-Aurignacian occurs during an interval (ca. 41.5–39.9 k cal BP) of relative climatic amelioration, Greenland Interstadials (GI) 10 and 9, punctuated by a short cold stadial. The Early Aurignacian (ca. 39.8–37.9 k cal BP) predominantly falls within the climatic phase known as Heinrich Stadial (HS) 4, and its end overlaps with the beginning of GI 8, the former being predominantly characterized by cold and dry conditions across the European continent.

We use eco-cultural niche modeling to quantitatively evaluate whether these shifts in material culture are correlated with environmental variability and, if so, whether the ecological niches exploited by human populations shifted accordingly. We employ genetic algorithm (GARP) and maximum entropy (Maxent) techniques to estimate the ecological niches exploited by humans (i.e., eco-cultural niches) during these two phases of the Aurignacian. Partial receiver operating characteristic analyses are used to evaluate niche variability between the two phases.

Results indicate that the changes in material culture between the Proto-Aurignacian and the Early Aurignacian are associated with an expansion of the ecological niche. These shifts in both the eco-cultural niche and material culture are interpreted to represent an adaptive response to the relative deterioration of environmental conditions at the onset of HS4.

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Introduction

The Proto-Aurignacian and the Early Aurignacian are chronologically and techno-typologically different phases of the Aurignacian cultural tradition. Between the two, we observe a change in reduction sequences used to produce blades and bladelets, the appearance of split-based antler points in the Early Aurignacian toolkit, and a number of changes in lithic typology as well as in symbolic material culture (e.g., Conard, 2003; Bon, 2006; Liolios,

2006; Vanhaeren and d'Errico, 2006; Teyssandier, 2007; Zilhão, 2007; Teyssandier and Liolios, 2008; Teyssandier et al., 2010).

The Aurignacian traditionally has been viewed as the cultural technocomplex associated with the movement of anatomically modern humans into the European continent and the subsequent replacement of autochthonous Neanderthal populations. Teyssandier (2008) points out that, because of this viewpoint, technological and behavioral variability within the Aurignacian tended to be overlooked, and it was viewed as a homogenous cultural tradition. More recently, the situation has changed and Aurignacian diversity has become a central subject of study (e.g., Bon, 2002; Zilhão and d'Errico, 2003; Bar-Yosef and Zilhão, 2006; Pesse, 2008; Michel, 2010). Such research is aided by the fact that

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our understanding of late Pleistocene millennial-scale climatic variability, and resulting vegetation changes across Europe, has been improved by high resolution studies of Greenland ice core (Svensson et al., 2008; Wolff et al., 2010), Atlantic and Mediterranean marine core (Sánchez Goñi et al., 2008, 2009), and terrestrial (Fletcher et al., 2010) records, as well as by improved climatic modeling methods (Kageyama et al., 2010). Furthermore, improvements in radiocarbon dating methods (Higham et al., 2009; Higham, 2011) and calibration curves (Reimer et al., 2009) make it possible to examine the cultural variability within more precise temporal frameworks, better relate these to specific paleoclimatic events, and evaluate if and how cultural variability is related to changes in human–environment interactions through time. These advances, when paired with recent chrono-stratigraphic studies and reinvestigations of key sites (see below), allow for an examination of whether the cultural differences between the Proto-Aurignacian and the Early Aurignacian may reflect the exploitation of different environmental conditions. In other words, does the behavioral variation between the early phases of the Aurignacian reflect the occupation of different ecological niches through time by these hunter-gatherer populations?

While considerable research exists for which hunter-gatherer adaptations (technology, mobility, social structure, etc.) are viewed against environmental backdrops (e.g., Kelly, 1995; Binford, 2001; Bettinger, 2009), there has been little focus on how culture-environment interactions might be intertwined with ecological niche dynamics. From an ecological perspective, when faced with rapid-scale climatic change and subsequent reorganization of environments, a hunter-gatherer population can respond in a number of ways. First, groups may maintain existing settlement, subsistence, and technological systems, conserve the ecological niche they exploit, and simply track its shifting geographic footprint. Such a situation is inferred by Wobst (1974), who proposed that moves between ecological niches would have been rare since such shifts potentially would require new and different adaptations. There also exists the possibility that during periods of environmental change a hunter-gatherer population could avoid geographically tracking a shifting niche footprint by increasing its exploitation of particular environmental settings within the broader conserved ecological niche. Existing, flexible adaptations would serve as a buffer against environmental change in such a scenario (Riede, 2009). This pattern is described for northwestern Central Europe, where flexible technologies and mobility patterns allowed late Upper Paleolithic populations to adjust to conditions of the Younger Dryas event without substantially shifting their territories (Weber et al., 2011).

In another scenario, environmental changes could negatively impact demography and social networks, thereby preventing the maintenance of cultural traditions (e.g., Henrich, 2004). This could lead to the loss of certain technological and social adaptations and, ultimately, niche contraction. In other words, the population would only make use of a subset of the environmental conditions it did previously, and other portions of the former niche would be completely excluded because groups no longer possessed the means to exploit them.

Lastly, one needs to take into account the fact that culture allows for rapid adjustments and adaptations to changing climatic conditions and new environments (Richerson and Boyd, 2005; Richerson et al., 2009). Such cultural adaptations open the door for the potential expansion of the exploited ecological niche as a means of adjusting to abrupt restructuring of environments brought about by rapid-scale deterioration (or amelioration) of climatic conditions. This adaptive and behavioral flexibility among hunter-gatherers may be recognized archaeologically by technological changes (bone and lithic toolkits), shifts in subsistence and

settlement systems (e.g., mobility structure, geographic ranges, etc.), and shifts in social network structure. Because the success of technological innovations and adaptations is linked to effective population size and density (Shennan, 2001), the maintenance of geographically-broad social networks would become increasingly important if groups rapidly expanded their ecological niche and geographic range, effectively reducing population density. Similarly, social networks would be of increased importance for groups operating at the limits of their expanded ranges (see Whallon, 2006).

Logically, if demography is not adversely affected, the potential for niche expansion would increase during instances in which there was an increase in the level of ecological risk faced by human populations; ecological risk being defined as the amount of variation (seasonally or inter-annually) that a population faces in its food supply over time (see Nettle, 1998; Collard and Foley, 2002). Studies focused on animal taxa have shown, however, that niche conservatism is common (e.g., Peterson et al., 1999; Martínez-Meyer et al., 2004). Does the use of culture as a means of adaptation mean that the general tendency towards niche conservatism may not necessarily apply to human hunter-gatherer populations in certain situations?

The purpose of this study is twofold. First, we use Bayesian modeling methods to examine the corpus of reliable radiocarbon ages associated with the Proto-Aurignacian and the Early Aurignacian to more precisely define the chronological and therefore paleoclimatic contexts of these two phases. Second, we employ eco-cultural niche modeling (ECNM) methods to evaluate whether the material cultural shifts between the Proto- and Early Aurignacian are correlated with an eco-cultural niche shift. An eco-cultural niche represents the range of environmental conditions (i.e., the ecological niche) exploited by a human adaptive system (see Banks et al. [2011] for a discussion of eco-cultural niches). The utility of ECNM is that it provides the ability to evaluate quantitatively whether links exist between a given adaptive system and ecological conditions, or if the characteristics and geographic distribution of an archaeological culture may have been influenced more by non-ecological (i.e., cultural) processes (Banks et al., 2009, 2011). Thus, if significant eco-cultural niche variability exists between the Proto-Aurignacian and the Early Aurignacian, this would suggest that the cultural changes we recognize between these two phases have, in part, an ecological basis.

The Aurignacian technocomplex

Following the expansion of anatomically modern humans out of Africa between 60 and 50 k cal BP (Bar-Yosef and Belfer-Cohen, 2011; Garcea, 2011), the unambiguous presence of these populations in the European cul-de-sac is signaled by diagnostic human fossils (the Oase 1 mandible and the Oase 2 cranium; Zilhão et al., 2007a; Trinkaus et al., 2012) directly dated to the time range of the transition between the Proto- and the Early (or Ancient) Aurignacian, ca. 40 k cal BP. On the basis of this paleontological evidence, it is safe to assume that the Early Aurignacian is modern human-associated, but authorship of the Proto-Aurignacian is a more problematic issue. An argument can be made that it represents, at least in part, the initial expansion of modern human populations into Europe, but it may also stand for the spread of a technological system irrespective of population boundaries between Europe's earliest moderns and its latest archaics.

Immediately prior to the Aurignacian, the initial Upper Paleolithic is characterized by a number of regional transitional industries: the Châtelperronian (France and northern Spain), the Uluzzian (Italy, Greece), the Bachokirian (Bulgaria), the Bohunician (Czech Republic and Poland), the Szeletian/Altühlian (central

Europe), and the Lincombian/Ranisian/Jerzmanowician (northern Europe). It has been intensively debated whether the authors of these industries were modern humans or Neanderthals who, through acculturation, were imitating modern human lithic technologies. It has been demonstrated that the long held view that these industries and the Aurignacian technocomplex were contemporaneous for an extended period of time is untenable (see Zilhão [2007] for a review). The archaeological and chronological data clearly show that the transitional industries are stratigraphically below the Aurignacian, with no interstratification (Zilhão et al., 2006, 2007b; Caron et al., 2011), and that the development of these industries clearly pre-dates the earliest Aurignacian (Zilhão, 2007).

This period is characterized by a paucity of human remains, but all reliable associations between archeological remains and human fossils support the hypothesis that Neanderthals were the makers of these transitional industries. Nevertheless, such a conclusion is still questioned. It has been argued that the association between Neanderthals and the Châtelperronian remains to be satisfactorily demonstrated, that marked differences between many of these transitional industries and the preceding Mousterian indicate that modern humans could have been responsible for their production (Bar-Yosef and Bordes, 2010), and that stratigraphic inconsistencies in radiocarbon dating results for the key site of the Grotte du Renne render suspect the association between Châtelperronian lithic material, symbolic artifacts, and Neanderthal fossils (Higham et al., 2010). Caron et al. (2011), however, have shown that the horizontal and vertical distributions of diagnostic finds and fossils strongly support the stratigraphic integrity of the site and the validity of the association.

Similarly, it has recently been proposed that recovered teeth associated with an Uluzzian industry at Grotta del Cavallo are modern human and not Neanderthal (Benazzi et al., 2011), although stratigraphic, chronological, and definitional issues render such a conclusion tentative at best (Trinkaus and Zilhão, 2012). Aurignacian artifacts are present at the top of the Cavallo Uluzzian complex (Gioia, 1990; Mussi et al., 2006), and six out of the seven radiocarbon dates obtained on shell ornaments from the upper part of the Uluzzian sequence (layer D) fall in a time range between the Epigravettian and the Proto-Aurignacian. Therefore, not only is the taxonomic affiliation of the recovered human teeth problematic, the possibility of post-depositional mixing also needs to be borne in mind. Given this, the hypothesis that the Uluzzian is associated with modern humans cannot be supported at present.

Despite this continued debate, the picture that emerges from the contextually reliable archaeological record is that the transitional technocomplexes clearly pre-date the Aurignacian, they were made by Neanderthals, and their technological complexity and diversity of material remains demonstrate that it is incorrect to attribute “modern behavior” strictly to anatomically modern humans. It is clear that many of the behaviors originally thought to be unique to the Aurignacian and the Upper Paleolithic were also practiced by Neanderthal populations (see Zilhão [2007] and d’Errico and Stringer [2011] for a review, as well as Zilhão et al. [2010] and Peresani et al. [2011] for more recent evidence to that effect).

As pointed out above, sufficient chronological, paleoclimatic, and archaeological data exist such that, with the appropriate methods, it is possible to evaluate if and how human–environment interactions and cultural adaptation shifted in response to rapid-scale climatic shifts characteristic of the Last Glacial period. Attempting to understand the cultural changes observed in the archaeological record from such a perspective is more productive, and more appropriate, than attributing cultural changes to differences in “cognition” or biologically-based “behavioral capacity.” Present-day data from Neanderthal and early anatomically modern

human material culture records show that the latter viewpoint is no longer tenable. That is why, for our purposes here, authorship of the Proto-Aurignacian is a moot point. Whether it is exclusively modern human-related, a technology shared across taxonomic boundaries, or the “hybrid” material culture of a “hybrid,” post-contact, modern-human-with-Neanderthal-traits European population is irrelevant when the focus of study is how human groups responded to environmental variability and since we can assume that the cognitive and behavioral capabilities necessary to adequately adjust to rapid-scale climatic variability were within the reach of any of the implicated human actors.

Technological studies (Bon, 2002; Bordes, 2002; Teyssandier, 2007) indicate that the earliest phases of the Aurignacian, the Proto-Aurignacian, and the Early Aurignacian (Ancient Aurignacian or Aurignacian I), are clearly distinct from one another, authorship issues aside. While both industries are dominated by blades and bladelets, their methods of production differ as do their formalized end products. For the Proto-Aurignacian, blades and bladelets were produced from unidirectional prismatic cores within a single, continuous reduction sequence. It is characterized by Krems points, light and generally unretouched blades, and slender, rectilinear retouched bladelets of the Dufour sub-type. During the Early Aurignacian, blades and bladelets were produced via two distinct core reduction strategies. Blades continued to be produced from prismatic cores, were robust, and were typically heavily retouched on their lateral edges. Carinated “scrapers” served as specialized cores whose reduction yielded short, straight, or curved bladelets that were typically left unretouched. The Early Aurignacian is also characterized by the appearance of split-based bone points. Other aspects of the material record also indicate a shift between the Proto- and Early Aurignacian. For example, while personal ornaments are present in both phases, the range of types is much broader during the latter (Vanhaeren and d’Errico, 2006).

It has been argued that split-based bone points are present at the site of Trou de la Mère Clochette in association with industries of Proto-Aurignacian affinities, based on direct dating results for two such points (Szmids et al., 2010a). However, the palimpsest nature of the cultural level containing this material and the fragmentary nature of the samples make it difficult to demonstrate with certainty that the dated fragments are associated with the Proto-Aurignacian or are indeed wings of split-based points, as diagnosed. One of the ages (OxA-19622: $35,460 \pm 250$ ^{14}C BP; 41,349–40,014 cal BP) falls within our modeled time range for the Proto-Aurignacian (see below), but the authors’ description of the object states that, in contrast to the other possible wing fragment dated to the time range of the Early Aurignacian (OxA-19621: $33,750 \pm 350$ ^{14}C BP; 39,606–37,356 cal BP), “it has scraping marks which are less visible on its exterior surface due to the presence of cancellous material, but much more obvious ones on its lateral edge facets” (Szmids et al., 2010a: 3328); however, no such marks are apparent in the published illustrations.

The lithic component of the assemblage has strong Proto-Aurignacian affinities and lacks Early Aurignacian diagnostics (e.g., carinated scrapers), while the five complete split-based points are unambiguous (but remain undated). Elsewhere, such points occur solely in association with Early Aurignacian lithic tool-kits and, when directly dated, always fall in its time range. Given this, and the length of occupation documented by the dating results, we think that the “red layer” from Trou de la Mère Clochette should be interpreted as a palimpsest combining the remains of a residential Proto-Aurignacian occupation (represented by the on-site production and discard of stone tools) and a logistical Early Aurignacian occupation (represented by the abandonment of used bone points); instances of such Early Aurignacian logistical visits to caves that leave behind no diagnostics other than the characteristic split-

based points are common across the geographic range of the technocomplex (e.g., Istállós-kő, in Hungary). Thus, in this study, we consider the presence of split-based bone points to represent the Early Aurignacian and interpret OxA-19622 as a bone sample (faunal, or industrial but undiagnostic) associated with the Proto-Aurignacian of Trou de la Mère Clochette. Alternatively, one could consider the dated sample as truly representing the broken wing of a split-based point and the result as a statistical outlier, which, for all practical purposes, would be the same.

Originally, the Proto-Aurignacian (Laplace, 1966a; Palma di Cesnola, 1993) was thought to represent a Mediterranean variant of the classical Aurignacian. Excavations at the Grotte du Renne (Bon, 2002), Le Plage (Bordes, 2002, 2006), and Isturitz (Normand and Turq, 2005) demonstrate that the Proto-Aurignacian stratigraphically precedes the Early Aurignacian, and continued dating work supports this pattern from a chronological standpoint. Our Bayesian model, based on all ^{14}C ages from reliable stratigraphic contexts (methods and results detailed below), corroborates the stratigraphic evidence for the Proto-Aurignacian clearly preceding the Early Aurignacian across the entirety of their shared geographic range. The picture that emerges is that the Proto-Aurignacian is solidly situated between 41.5 and 39.9 k cal BP and that the Early Aurignacian occurs between 39.8 and 37.9 k cal BP. Therefore, the Proto-Aurignacian occurred during a period characterized by two phases of relative climatic amelioration, Greenland Interstadials (GI) 10 and 9, punctuated by a short, some 600 year-long cold episode, Greenland Stadial (GS) 9/10 (Fig. 1; Sánchez-Goñi and

Harrison, 2010; Wolff et al., 2010). The Early Aurignacian clearly begins with the onset of HS4 and ends with the onset of GI 8.

Material and methods

To evaluate possible culture–environment links for the Proto-Aurignacian and Early Aurignacian, we used genetic algorithm (GARP; Stockwell and Peters, 1999) and maximum entropy (Maxent; Phillips et al., 2004, 2006) techniques to estimate eco-cultural niches. In biodiversity science, GARP and Maxent have been applied to a diverse set of topics including reconstructing species' distributions, estimating effects of climate change on species' distributions, and forecasting the geographic potential of species' invasions (Peterson, 2003; Martínez-Meyer et al., 2004; Araújo and Rahbek, 2006; Pearson et al., 2007; Barve et al., 2011). For data inputs, GARP and Maxent require the geographic coordinates where the population of interest has been observed and raster GIS data layers summarizing environmental dimensions potentially relevant to shaping its geographic distribution.

Occurrence data

The occurrence data are the geographic coordinates of archaeological sites at which material culture assemblages have been recovered that can be identified as either Proto-Aurignacian or Early Aurignacian (Table 1). Some sites are designated as having Early Aurignacian cultural levels based strictly on the presence of split-based bone points, an artifact class associated only with the Early Aurignacian (see above). This study's occurrence data represent a more exhaustive and accurate sample than those used by Banks et al. (2008). The latter study's dataset represented only sites with Aurignacian levels that had been dated to specific millennial-scale climatic events. Finally, our sample of Proto- and Early Aurignacian sites is restricted to Europe, the region with archaeological components from which these two archaeological cultures have been historically defined. Cultural taxonomic relationships between the European Aurignacian and assemblages from the Ukraine, Western Russia, and the Near East, which have been argued to be Aurignacian, are at present unclear. Whether a true Aurignacian exists in the Near East remains controversial and, despite minor technological similarities, the assemblages from far Eastern Europe appear to represent distinct populations, as otherwise indicated by their symbolic material culture (Otte et al., 2011). If one were to incorporate more eastern sites into the study's sample, one would in fact be reconstructing the ecological niche exploited by a large, culturally diverse human population at a particular point in time. However, the goal of eco-cultural niche modeling is to examine the ecological conditions exploited by a distinct and culturally cohesive human population. It is for this reason that sites situated further to the east were excluded from consideration.

Environmental data

The raster GIS data sets used in this study summarize landscape attributes (assumed to have remained constant) and high-resolution climatic simulations for two periods: one that incorporates GIs 10, and 9 (pre-HS4) and another representing HS4. Landscape variables included slope, aspect, elevation, and topographic index (a measure of tendency to pool water). Elevation was obtained from the ETOPO1 dataset (Amante and Eakins, 2009), and the remaining landscape values were calculated from the ETOPO2 dataset (ETOPO2v2). We approximated coastlines for the European continent during HS4, as well as the period immediately preceding it, by lowering sea levels 90 m. This threshold represents the lower

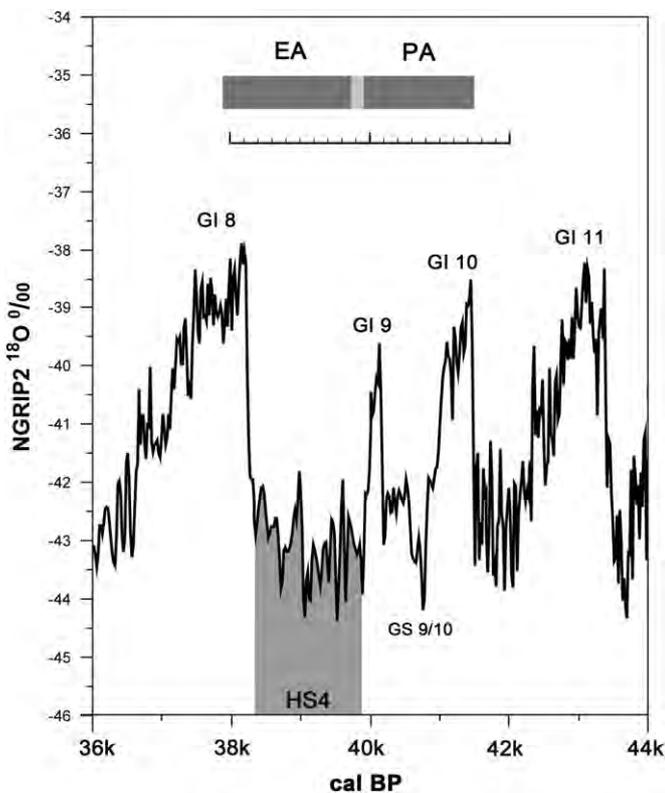


Figure 1. Chronological and paleoclimatic context of the Proto-Aurignacian and the Early Aurignacian. Age distributions summarize the results of a Bayesian model performed with OxCal 4.1 (Bronk Ramsey, 2009) using the IntCal09 calibration curve (Reimer et al., 2009). Principal climatic phases are indicated with reference to the NGRIP2 oxygen isotope curve (Svensson et al., 2006, 2008). Temporal boundaries of Heinrich Stadial 4 (indicated in gray) are derived from Sánchez Goñi and Harrison (2010). Abbreviations are as follows: EA - Early Aurignacian; PA - Proto-Aurignacian; GI - Greenland Interstadial; GS - Greenland Stadial; HS - Heinrich Stadial.

Table 1
Proto-Aurignacian and Early Aurignacian sites used to reconstruct eco-cultural niches^a

Site name	Longitude	Latitude	Country	Level(s)	Proto-Aurig.	Early Aurig.	Reference(s)
Les Abeilles	0.64	43.22	France	2	Yes	Yes	Laplace et al., 2006
l'Arbreda	2.75	42.17	Spain	H	Yes	Yes*	Zilhão, 2006
Aurignac	0.88	43.22	France			Yes	Bon, 2002
Bacho Kiro	25.42	42.93	Bulgaria	6b/7; 7		Yes	Kozłowski, 1982; Tsanova and Bordes, 2003
Balauzière	4.55	43.95	France			Yes	Bazile, 1976, 1977
Barbas *	0.56	44.85	France			Yes	Ortega et al., 2006
Le Basté	−1.45	43.47	France			Yes	Chauchat and Thibault, 1968
Bize (Tournal)	2.88	43.32	France	G, F	Yes	Yes	Tavoso, 1987
Bocksteinhöhle	10.16	48.52	Germany			Yes*	Conard and Bolus, 2006
Brassempouy (Hyènes)	−0.70	43.63	France	2DE		Yes	Bon, 2002
Brillenhöhle *	9.78	48.41	Germany	XIV		Yes*	Conard and Bolus, 2006
Caminade	1.25	44.87	France	F, G		Yes	Bordes, 1998; Zilhão and d'Errico, 1999
Canecaude	2.31	43.33	France			Yes	Bon, 2002
Castaigne	0.21	45.56	France			Yes	Leroy-Prost, 1979; Liolios, 2006
Castanet	1.18	45.03	France	Lower		Yes	Peyrony, 1935; Zilhão and d'Errico, 1999
Castelcivita	15.23	40.48	Italy	6 (??)	Yes		Mussi, 2001
Abri Cellier	1.05	45.00	France	A (II)		Yes	Leroy-Prost, 1979
Chabiague	−1.57	43.46	France			Yes	Bon, 2002; Chauchat and Thibault, 1978
La Chaise *	0.46	45.67	France			Yes	Leroy-Prost, 1979
Abri du Chasseur	0.42	45.68	France	B1, B2		Yes	Balout, 1965; Liolios, 2006
Combe Capelle	0.82	44.77	France			Yes	Leroy-Prost, 1979
Combe Saunière	0.16	45.14	France	VIII		Yes	Geneste, 1994
Corbiac-Vignoble	0.52	44.88	France			Yes	Bordes and Tixier, 2002; Chadelle, 1990
Les Cottés	0.30	46.44	France		Yes	Yes	Soressi et al., 2010; Talamo et al., 2012
La Crouzade	3.05	43.14	France			Yes	Bon, 2002; Henry-Gambier and Sacchi, 2008
Cueva del Otero	−3.54	43.36	Spain	4–8		Yes	Bernaldo de Quirós, 1982
Divje Babe I	14.06	46.00	Slovenia			Yes*	Karavanić, 2000
El Castillo	−3.97	43.29	Spain	18B		Yes	Zilhão, 2006
Esquicho-Grapaou	4.32	43.94	France	SLC 1b	Yes		Bazile, 2005
La Fabbria	11.11	42.76	Italy		Yes		Mussi, 2001
La Ferrassie	0.92	44.98	France	K6		Yes	Delporte, 1984; Leroy-Prost, 1979
Le Flageolet *	0.58	44.82	France	XI		Yes	Lucas, 1997; Rigaud, 1982
Fontêchevade *	0.47	45.68	France	B		Yes	Leroy-Prost, 1979
Fossellone	13.80	41.35	Italy	21		Yes	Palma di Cesnola, 1993
Garet	−0.65	43.66	France			Yes	Klaric, 1998
Gargas	0.52	43.07	France			Yes	Bon, 2002
Gatzarria	−0.92	43.14	France		Yes	Yes	Laplace, 1966b; Bon 2002
Geissenklösterle	9.78	48.40	Germany	III, II		Yes	Hahn, 1988
Gourdan *	0.58	43.08	France			Yes	Bon, 2002
Goyet	5.01	50.45	Belgium			Yes*	Liolios, 2006
Grimaldi sites	7.53	43.79	Italy		Yes	Yes*	Laplace, 1966a; Mussi et al., 2006
Grotta del Cavallo	18.18	40.38	Italy			Yes	Mussi et al., 2006
Grotta di Fumane	10.88	45.55	Italy	A2, D3b	Yes	Yes	Bartolomei et al., 1992; Higham et al., 2009
Grotte du Renne	3.75	47.62	France	VII	Yes	Yes*	Schmider, 2002
Grotta Paina	11.52	45.43	Italy	9	Yes		Leonardi et al., 1962
Grotta Salomone	13.62	42.75	Italy			Yes*	Mussi et al., 2006
Grotte de l'Observatoire	7.41	43.73	Monaco		Yes	Yes	Onorotini et al., 1999; Onorotini, 2006
Grotte des Fours	1.15	44.81	France			Yes	Leroy-Prost, 1979
Istállós-kő	20.43	48.07	Hungary			Yes*	Ringer, 2002
Isturitz	−1.20	43.37	France	C4c4, 4d, C3b	Yes	Yes	Normand, 2002; Normand et al., 2007
Klisoura 1	22.83	37.71	Greece			Yes	Karkanas, 2010
Kozarnika	22.61	43.63	Bulgaria	VII	Yes		Tsanova, 2008
Krems-Hundsteig	15.18	47.03	Austria	Brown	Yes		Hahn, 1977; Teyssandier, 2003
Labeko Koba	−2.51	43.06	Spain	VII, VI–IV	Yes	Yes	Zilhão, 2006
Laouza	4.20	44.00	France		Yes		Bon, 2002
Lommersum	6.96	50.66	Germany			Yes	Hahn, 1989
Mandrin	4.73	44.48	France	1	Yes		Slimak et al., 2006
Le Mas d'Azil	1.36	43.08	France			Yes	Bon, 2002
Mère Clochette	5.56	47.12	France		Yes	Yes*	Szmidt et al., 2010a
Mokriška jama	14.52	46.33	Slovenia			Yes*	Brodar, 1985
Morín	−3.82	43.36	Spain	8, 7–6, 5	Yes	Yes	Maíllo Fernández et al., 2001; Zilhão, 2006
Moulin de Bénesse	−1.03	43.64	France			Yes	Bon, 2002; Merlet, 1993
Paglicci	15.58	41.67	Italy	24	Yes		Palma di Cesnola, 2006
Abri Pataud	1.01	44.93	France	14, 12		Yes	Chiotti, 1999; Movius, 1977
Pêcheurs	4.18	44.40	France			Yes*	Bazile, 2005; Floss, 2003; Lhomme, 1976
Périgaud	7.28	43.79	France			Yes*	Onorotini, 2004, 2006; Floss, 2003
Le Piage	1.39	44.80	France	K, GI	Yes	Yes	Bordes, 2002; Champagne and Espitalié, 1981; Demars 1992
La Quina	0.45	45.82	France			Yes	Henri-Martin, 1936; Leroy-Prost, 1979
Rainaude	6.53	43.53	France		Yes		Onorotini, 1986
Reclau Viver	2.88	41.87	Spain		Yes	Yes	Canal and Carbonell, 1989; Zilhão, 2006
Régismont-le-Haut	3.08	43.31	France			Yes	Bon, 2002
Les Renardières	0.37	45.83	France			Yes	Bouyssonie et al., 1960

(continued on next page)

Table 1 (continued)

Site name	Longitude	Latitude	Country	Level(s)	Proto-Aurig.	Early Aurig.	Reference(s)
Roc de Combe	1.35	44.75	France			Yes	Bordes, 2002; Bordes and Labrot, 1967
Roche à Pierrot	−0.65	45.83	France		Yes	Yes	Morin, 2004
La Rochette	1.10	45.01	France			Yes	Leroy-Prost, 1979
Les Rois*	0.14	45.53	France	B		Yes	Mouton and Joffroy, 1958; Ramirez Rozzi et al., 2009
Abric Romaní	1.67	41.54	Spain	2	Yes		Vallverdú et al., 2005
Rothschild	3.36	43.56	France		Yes		Ambert, 1994
Salpêtrière	4.54	43.94	France			Yes	Escalon de Fonton, 1966
Santimamiñe	−2.63	43.34	Spain	VIII		Yes	Bernaldo de Quirós, 1982; Liolios, 2006
Serino	14.85	40.85	Italy		Yes		Mussi, 2001
Solutré	4.31	46.38	France	M12, lev. 6		Yes	Combier and Montet-White, 2002
La Souquette	1.10	45.00	France			Yes	Leroy-Prost, 1979
Spy	4.70	50.48	Belgium			Yes*	Flas, 2008; Pirson et al., 2012
Tarté	0.99	43.12	France			Yes	Bon, 2002
Tincova	22.13	45.58	Romania		Yes		Mogoşanu 1978; Pă unescu, 2001
Tischoferhöhle	12.22	47.59	Austria			Yes*	Bolus and Conard, 2006
La Tuto de Camalhot	1.62	43.02	France			Yes	Bon, 2002
Les Vachons	0.12	45.51	France	1		Yes	Demars, 1992; Leroy-Prost, 1979
Velika Pećina	16.04	46.29	Croatia	H, I		Yes	Karavanic and Smith, 1998
La Viña	−5.82	43.31	Spain	XIII–XII	Yes	Yes	Fortea Pérez, 1999
Vindija	16.73	46.30	Croatia	F, G		Yes*	Zilhão, 2009
Vogelherd	10.07	47.95	Germany	V		Yes	Conard and Bolus, 2006
Wildscheuer	8.17	50.40	Germany	III		Yes	Terberger and Street, 2003
Willendorf II	15.40	48.32	Austria	3		Yes	Nigst, 2006; Teyssandier, 2003

^a Site names with an asterisk were eliminated from the population of occurrences used to reconstruct the Early Aurignacian eco-cultural niche because they were not spatially unique (see text for explanation). Early Aurignacian presences labeled **Yes*** indicate sites for which the cultural attribution is based solely on the presence of split-based bone points.

end (more negative values) within the confidence interval of reconstructed levels presented by Walbroeck et al. (2002). It also corresponds closely to the reconstructed sea level given by Siddall et al. (2003; Fig. 4) at 40 k cal BP.

The two climatic simulations were created using the LMDZ3.3 Atmospheric General Circulation Model (Jost et al., 2005), in a high-resolution version (144 cells in longitude × 108 in latitude), with further refinement over Europe (final resolution ~ 50 km) obtained by use of a stretched grid. The simulations were performed with boundary conditions representing two climatic situations: pre-HS4 (baseline) and HS4, with mid-size ice-sheets compared to the Last Glacial Maximum. Common to these simulations are the ice-sheets imposed as boundary conditions for which we used the Peltier (1994) ICE-4G reconstructions for 14 kyr cal BP, a time at which sea-level was similar to that of Marine Isotope Stage 3 for which no global ice-sheet reconstructions exist. Orbital parameters and greenhouse gas concentrations were set to their 40 kyr cal BP values (Sepulchre et al., 2007).

The only difference between the two simulations concerned sea surface temperatures (SSTs) and sea-ice extent in the North Atlantic. For the pre-HS4 baseline configuration, we used the GLAMAP reconstruction (Sarnthein et al., 2003). For the HS4 configuration, we subtracted from the reference SSTs an anomaly of 2 °C in the mid-latitude North Atlantic and Mediterranean Sea. Sea-ice cover was imposed if SSTs were lower than −1.8 °C. The model was then run with these boundary conditions for 21 years, the last 20 of which were used to compute atmospheric circulation and surface climate in balance with our defined boundary conditions. European climate proves quite sensitive to these changes in boundary conditions: continental temperatures and precipitation decrease from the baseline to the Heinrich stadial simulation, in a fashion similar to results described elsewhere (Sepulchre et al., 2007). From these climate simulations, temperature (the coldest and the warmest months as well as mean annual temperature) and precipitation values were extracted for use in the predictive algorithm architectures. Since the baseline simulation represents conditions during the period covering GIs 9–10 (pre-HS4), we used it to estimate the Proto-Aurignacian eco-cultural niche. We used

the Heinrich stadial simulation to estimate the Early Aurignacian eco-cultural niche.

Bayesian modeling

Before implementing the genetic algorithm and maximum entropy techniques, we needed to verify that the pre-HS4 (baseline) and HS4 paleoclimatic simulations were appropriate for estimating Proto-Aurignacian and Early Aurignacian eco-cultural niches, respectively. To do so, we used OxCal 4.1 (Bronk Ramsey, 2009) to perform a Bayesian modeling analysis on radiocarbon ages associated with Proto- and Early Aurignacian levels from sites across Europe (Table 2). We did not include the recently published radiocarbon ages from the Early Aurignacian levels of Geißenklösterle (Higham et al., 2012). Some of these ages are substantially older than previously obtained Early Aurignacian ages from the site, but they must be viewed with caution before arguing for a chronological revision of the Early Aurignacian. This site's levels represent palimpsests of cultural occupations and this issue, paired with post-depositional disturbances (Hahn, 1988), poses major problems to chronological studies. It is clear that these issues are especially relevant because Higham et al. (2012) indicate an age on bone (OxA-21661: 32,900 ± 450 ¹⁴C BP) from the Gravettian level (Ic) that falls within the time range of the Evolved Aurignacian (see Higham et al., 2011). They also present an age (OxA-21720: 35,500 ± 650 ¹⁴C BP) from the Middle Paleolithic level IV that falls clearly within the range of the Early Aurignacian. The Early Aurignacian culture represented in Geißenklösterle level III is dated no older than 35,000 ¹⁴C BP across the rest of Europe (Table 2), and a number of the new ages from the site correspond to the broader European radiocarbon record. Palimpsest and post-depositional issues aside, one cannot exclude the possibility that some of the new ultrafiltration ages from Geißenklösterle are in error. For these reasons, we did not include these latest ages in our Bayesian model.

Since we are using ages obtained from numerous sites, and not a stratigraphic succession of ages from a single site, we grouped the ages within two separate phases (i.e., Proto-Aurignacian phase, Early Aurignacian phase) without imposing any relative order on

Table 2

Radiocarbon ages, calibrated dates, and modeled dates associated with the Proto-Aurignacian and Early Aurignacian in Europe. Also included are samples of ages used to constrain the Bayesian model (labeled as Transitional Industries and Aurignacian II).^a

Site name	Level	Lab code	Age	Error	Unmodeled BP (95.4%)		Modeled BP (95.4%)		A _i	C	Reference
					From	To	From	To			
Transitional industries											
Fumane	A3	LTL-1795A	37828	430	43082	41804	43086	41824	100.5	98.9	Higham et al., 2009
Grotte du Renne	VIII	OxA-21683	40000	1200	46064	42336	46057	42348	100	96.5	Higham et al., 2010
Grotte du Renne	VIII	OxA-21573	36800	1000	43600	39945	43515	41022	107.1	98.4	Higham et al., 2010
Grotte du Renne ^a	VIII	OxA-X-2279-14	35450	750	41870	38920	42713	41273	30.2	98.0	Higham et al., 2010
Proto-Aurignacian											
Initial Boundary											
Arbreda	H-BE111	OxA-3730	35480	820	41991	38862	41447	40548	134.9	99.8	Zilhão, 2006
Grotte du Renne	VII	OxA-21569	36500	1300	43821	38948	41230	40298	106.6	99.8	Higham et al., 2010
Grotte du Renne	VII	OxA-21682	35000	650	41419	38751	41135	40234	105.4	99.8	Higham et al., 2010
Grotte du Renne	VII	OxA-21570	34600	800	41469	37738	41142	40211	85.2	99.8	Higham et al., 2010
Grotte du Renne	VII	OxA-21572	34600	750	41415	37885	41125	40204	80.4	99.8	Higham et al., 2010
Grotte du Renne ^b	VII	OxA-21571	34050	750	40931	37090	41249	39816	58.3	99.4	Higham et al., 2010
Esquicho-Grapaou	SLC 1b	MC-2161	34540	2000	44295	35471	41193	40244	125.2	99.8	Delibrias and Evin, 1980
Fumane	A2	OxA-19584	35850	310	41663	40375	41200	40419	88.5	99.8	Higham et al., 2009
Fumane	A2	OxA-17569	35640	220	41392	40315	41131	40419	108.4	99.8	Higham et al., 2009
Fumane	A2	OxA-17570	35180	220	41045	39504	41036	40282	108.1	99.8	Higham et al., 2009
Fumane	A2	OxA-19412	34940	280	40895	39105	41030	40201	65.4	99.8	Higham et al., 2009
Fumane ^b	A2	OxA-19414	34180	270	40084	38563	40775	39765	13.2	99.4	Higham et al., 2009
Isturitz ^b	C 4c4	AA-69184	40200	3600	...	41148	41742	40078	34.9	99.5	Szmidt et al., 2010b
Isturitz ^b	C 4c4	AA-69183	37580	780	43567	41199	41840	40604	28.9	99.4	Szmidt et al., 2010b
Isturitz	C 4c4	AA-69180	37300	1800	45845	38858	41235	40293	81.4	99.8	Szmidt et al., 2010b
Isturitz	C 4c4	AA-69179	37000	1600	44928	38933	41235	40292	89.4	99.8	Szmidt et al., 2010b
Isturitz ^c	C 4c4	AA-69185	36990	720	43040	40840	41519	40481	31.7	99.6	Szmidt et al., 2010b
Isturitz ^c	C 4c4	AA-69181	36800	860	43190	40301	41497	40421	57.5	99.7	Szmidt et al., 2010b
Isturitz ^c	4d	GifA-98232	36510	610	42506	40502	41478	40460	58.5	99.7	Szmidt et al., 2010b
Isturitz ^c	4d	GifA-98233	34630	560	41078	38602	41176	40121	58.4	99.7	Szmidt et al., 2010b
Kozarnika	VII	GifA-99706	36200	540	42199	40310	41245	40384	67.5	99.7	Tsanova, 2008
Kozarnika ^b	VII	GifA-101050	37170	700	43091	41036	41810	40566	49.0	99.5	Tsanova, 2008
Krems-Hundsteig		KN-654	35500	2000	44941	36608	41199	40246	142.5	99.8	Hahn, 1977
La Mère Clochette		OxA-19622	35460	250	41349	40014	41095	40367	123.5	99.8	Szmidt et al., 2010a
Riparo Mochi	E. trench	OxA-3591	35700	850	42191	38954	41200	40286	134.4	99.8	Mussi et al., 2006
Riparo Mochi	E. trench	OxA-3592	34870	800	41799	38410	41150	40230	103	99.8	Mussi et al., 2006
Riparo Mochi	E. trench	OxA-3590	34680	760	41510	38021	41136	40218	86.8	99.8	Mussi et al., 2006
Morin	8	GifA-96263	36590	770	42872	40265	41263	40368	53.1	99.8	Maíllo Fernández et al., 2001
Paglicci ^c	24b1	Utc?	34000	900	41059	36844	41252	40120	53.6	99.7	Palma di Cesnola, 1999
La Viña	XIII-lower	Ly-6390	36500	750	42786	40196	41254	40364	59.6	99.8	Fortea Pérez, 1999
Terminal Boundary											
							40937	39949		98.6	
Early Aurignacian											
Initial Boundary											
Bacho Kiro ^c	7	OxA-3181	32200	780	38751	35111	39241	37931	49.9	99.5	Hedges et al., 1994
Bacho Kiro	6b	OxA-3182	33300	820	40359	36485	39326	38165	105.5	99.7	Hedges et al., 1994
Brassempouy	2DE	GifA SM-11034	33600	240	38999	37486	39018	38203	122.2	99.8	Zilhão et al., 2007b
Brassempouy ^b	2DE	GifA-96105	32410	370	38387	36355	38619	37288	32.3	99.4	Zilhão et al., 2007b
Caminade	F	GifA-97186	35400	1100	42712	38403	39536	38436	62.9	99.7	Rigaud, 2000
Castanet	Lower	GifA-97313	35200	1100	42413	37896	39526	38408	74.8	99.7	Rigaud, 2000
Castanet	Lower	GifA-97312	34800	1100	42056	37361	39502	38340	99.1	99.7	Rigaud, 2000
Combe Saunière	VIII	OxA-6507	34000	850	40995	36900	39427	38250	135.4	99.8	Mellars, 1999
Divje Babe I ^c	2	RIDDL 734	35300	700	41695	38881	39703	38594	50.4	99.5	Lau et al., 1997
Ferrassie	K6	GrN-5751	33220	570	39298	36604	39203	38137	86.2	99.7	Rigaud, 2000
Flageolet I	XI	GifA-95559	34300	1100	41596	36846	39453	38265	124.8	99.8	Rigaud, 2000
Flageolet I	XI	OxA-598	33800	1800	42760	35153	39431	38211	131.6	99.8	Rigaud, 2000
Flageolet I ^c	XI	GifA-95538	32040	850	38777	34965	39273	37943	45.0	99.6	Rigaud, 2000
Geissenklösterle	IIIa	KIA 13075	34330	310	40302	38641	39431	38598	107.7	99.7	Conard and Bolus, 2003
Geissenklösterle	IIIa	KIA 13074	34800	290	40722	38949	39528	38692	45.5	99.6	Conard and Bolus, 2003
Geissenklösterle	IIIb	KIA 8961	33210	300	38731	36967	38925	38139	75.6	99.6	Conard and Bolus, 2003
Geissenklösterle	IIIb	KIA 13076	34080	300	40225	38125	39364	38510	126.1	99.8	Conard and Bolus, 2003
Geissenklösterle	III	OxA-21658	35050	600	41365	38830	39522	38595	52	99.6	Higham 2011
Geissenklösterle	IIa	OxA-5707	33200	800	40239	36431	39316	38168	97.7	99.7	Conard and Bolus, 2003
Geissenklösterle	IIa	OxA-21656	33000	500	38810	36613	39064	38103	65.5	99.7	Higham, 2011
Istállós-kő ^b	7/9	ISGS-A-0187	32701	316	38426	36608	38628	37318	56.9	99.4	Adams and Ringer, 2004
Istállós-kő	7/9	ISGS-A-0184	33101	512	38919	36627	39105	38114	73.8	99.6	Adams and Ringer, 2004
Lommersum		GrN-6191	33420	500	39399	36768	39208	38153	101.9	99.7	Hahn, 1994
Mère Clochette		OxA-19621	33750	350	39606	37356	39256	38248	137	99.8	Szmidt et al., 2010a
Pataud	9	OxA-21673	33400	500	39361	36758	39209	38157	99.7	99.7	Higham et al., 2011
Pataud	10	OxA-21679	33650	500	39939	36971	39299	38197	128.2	99.8	Higham et al., 2011
Pataud ^b	11	GrN-4326	32000	800	38650	35011	39137	37251	54.0	99.3	Higham et al., 2011
Pataud ^c	11	GrN-4309	32600	550	38789	36284	39023	37920	53.1	99.5	Higham et al., 2011
Pataud	11	OxA-21602	33500	500	39556	36803	39233	38164	110.7	99.8	Higham et al., 2011

(continued on next page)

Table 2 (continued)

Site name	Level	Lab code	Age	Error	Unmodeled BP (95.4%)		Modeled BP (95.4%)		A _i	C	Reference
					From	To	From	To			
Pataud	11	OxA-21580	33550	550	39931	36813	39289	38182	117.8	99.8	Higham et al., 2011
Pataud	11	OxA-21581	33550	550	39931	36813	39285	38180	117.8	99.8	Higham et al., 2011
Pataud	11	OxA-21601	34150	550	40694	37586	39450	38375	130.7	99.7	Higham et al., 2011
Pataud ^b	12	GrN-4310	31000	500	36522	34750	38590	37239	0.2	99.1	Higham et al., 2011
Pataud	12	GrN-4327	33000	500	38810	36613	39070	38110	65.5	99.7	Higham et al., 2011
Pataud	12	GrN-4719	33260	425	38906	36806	39068	38122	83.7	99.8	Higham et al., 2011
Pataud	12	OxA-21670	33450	500	39458	36782	39220	38153	105.1	99.7	Higham et al., 2011
Pataud	12	OxA-21672	34050	550	40593	37438	39431	38327	138.8	99.8	Higham et al., 2011
Pataud	12	OxA-21671	34300	600	40951	37759	39482	38412	117.6	99.8	Higham et al., 2011
Pataud	13	OxA-21600	34200	550	40750	37673	39465	38398	126	99.8	Higham et al., 2011
Pataud	13	OxA-21598	34750	600	41202	38642	39510	38536	77	99.7	Higham et al., 2011
Pataud	13	OxA-21599	34850	600	41243	38711	39512	38557	68.6	99.6	Higham et al., 2011
Pataud ^c	13	OxA-15216	35400	750	41835	38890	39710	38588	47.0	99.4	Higham et al., 2011
Pataud	14	GrN-4610	33300	760	40161	36530	39313	38168	102.6	99.8	Higham et al., 2011
Pataud	14	GrN-4507	34250	675	41014	37508	39475	38355	123.9	99.8	Higham et al., 2011
Pataud	14	OxA-21596	34500	600	41178	38103	39494	38469	98.8	99.7	Higham et al., 2011
Pataud	14	OxA-21579	35000	600	41331	38801	39524	38586	56.1	99.6	Higham et al., 2011
Pataud	14	OxA-21597	35000	650	41419	38751	39521	38558	59.9	99.7	Higham et al., 2011
Pataud ^b	14	OxA-21578	35750	700	42072	39237	39959	38779	30.3	99.3	Higham et al., 2011
Quina	3	OxA-6147	32650	850	39547	35249	39255	38139	71.1	99.7	Dujardin, 2001
Roc de Combe	7c	OxA-1263	34800	1200	42184	37142	39491	38316	103.1	99.8	Hedges et al., 1990
Roc de Combe	7b	OxA-1262	33400	1100	41202	35704	39381	38189	119.8	99.8	Hedges et al., 1990
Solutre	M12	SRLA-058	33970	360	40101	37709	39374	38408	138.6	99.8	Montet-White et al., 2002
Tuto de Camalhot	70–80	GifA-99093	34750	570	41135	38679	39505	38549	75.2	99.7	Zilhão et al., 2007b
Tuto de Camalhot ^b	70–80	GifA-99674	32180	570	38505	35322	38781	37282	45.7	99.2	Zilhão et al., 2007b
Velika Pecina	I	GrN-4979	33850	520	40314	37214	39370	38260	144	99.7	Karavanić, 1995
Vogelherd ^b	V	KIA-8969	32500	260	37991	36475	38540	37267	22.7	99.3	Conard and Bolus, 2003
Vogelherd	V	KIA-8970	33080	320	38655	36845	38911	38139	63.7	99.6	Conard and Bolus, 2003
Vogelherd ^b	V	PL-1337A	35810	710	42135	39278	39966	38790	27.2	99.4	Conard and Bolus, 2003
Wildscheuer	III	OxA-7394	34200	900	41236	37009	39456	38282	128.6	99.8	Hedges et al., 1998
Wildscheuer	III	OxA-6920	34100	1200	41645	36627	39436	38236	129.5	99.8	Hedges et al., 1998
Wildscheuer	III	OxA-7393	33350	750	40171	36561	39317	38175	106	99.7	Hedges et al., 1998
Wildscheuer	III	OxA-7390	32650	700	39140	35501	39181	38117	58.7	99.7	Hedges et al., 1998
Terminal Boundary							38792	37920		99.2	
Aurignacian II											
Pataud	7	OxA-21680	32850	500	38724	36554	38256	36537	107.2	98.9	Higham et al., 2011
Pataud	7	OxA-21583	32400	450	38551	35705	38172	35656	107.7	98.9	Higham et al., 2011
Pataud	7	OxA-21584	32200	450	38430	35505	37992	35434	105	98.7	Higham et al., 2011
Pataud	7	OxA-2276-20	32150	450	38386	35402	37911	35370	104.4	98.5	Higham et al., 2011

^a The column labeled 'C' contains the convergence value. The results of the final Bayesian model are illustrated in Figure 2.
^b indicates ages that had a poor agreement index (A_i) in the first Bayesian model and were eliminated from the second Bayesian model.
^c indicates ages that had a poor agreement index (A_i) in the second Bayesian model and were eliminated from the third and final Bayesian model. The final model had an agreement index of 99.9 and an overall agreement index of 69.7.

the measurements within each phase. We also included starting and ending boundaries for each phase but did not constrain them chronologically, leaving them undefined so that the Bayesian analysis could determine where they fell based on the radiocarbon measurements included within each phase.

The use of such boundaries to establish sequential phases, rather than overlapping ones, is appropriate for a number of reasons. Firstly, the archaeological record indicates that the Proto-Aurignacian precedes the Early Aurignacian, and there are no documented instances of these two archaeological cultures being interstratified. At sites where both are present, the former always underlies the latter. Secondly, when radiocarbon ages are considered, it can be expected to observe some degree of overlap between the two technocomplexes considering that for the time period in question one is approaching the chronological limits of the radiocarbon method and many ages have standard errors that exceed 700 years. Lastly, a Welch's *t*-test demonstrates that the Proto-Aurignacian and Early Aurignacian radiocarbon age samples do not come from the same statistical population. To conduct this test, we first normalized the standard error associated with each radiocarbon measure. Each age was multiplied by its normalized error to obtain a weighted age. A Shapiro–Wilk normality test shows that the ages associated with each archaeological culture are

normally distributed (Proto-Aurignacian: $W = 0.941, P = 0.25$; Early Aurignacian: $W = 0.976, P = 0.39$). Since these two samples have unequal sample sizes and unequal variances, we used R (v. 2.11.1; R Development Core Team [2011]) to perform a Welch's *t*-test. The result ($t = -2.523, df = 24.539, P = 0.018$) allows one to reject the null hypothesis that the Proto-Aurignacian and Early Aurignacian age samples issue from the same population. Therefore, considering the above reasons, our Bayesian model structure allows one to overcome the inherent noise in these radiocarbon age data, better constrain this observed archaeological succession, and obtain reliable estimates of the age and duration of these two archaeological cultures.

To better constrain the boundaries between phases, as well as the Proto- and Early Aurignacian phases themselves, we included a sample of Châtelperronian and Uluzzian radiocarbon measurements in a 'Transitional Industry' phase that preceded the Proto-Aurignacian. Following the Early Aurignacian, we included an 'Aurignacian II' phase with a sample of ages from the recently re-dated Abri Pataud sequence (Higham et al., 2011). Thus, the Bayesian model had four phases (Transitional Industries, Proto-Aurignacian, Early Aurignacian, Aurignacian II) and between each phase we placed two boundaries, identified as 'end' and 'start.' In an effort to identify measurement data (i.e., radiocarbon ages) that did

not agree with the model, we relied on OxCal's agreement index, which is a measure of the overlap between the likelihood and marginal posterior distributions (Bronk Ramsey, 2009). We ran an initial Bayesian model using all of the radiocarbon ages listed in Table 2, which produced a model with an overall agreement index below 60%. We removed all the ages having a poor agreement index ($A_i < 60\%$; after Bronk Ramsey, 2009) and ran a second model with the remaining measurements. The agreement index evaluation and elimination process was performed again, and a third Bayesian model was run resulting in an overall agreement above the standard accepted threshold of 60% (Bronk Ramsey, 2009). The boundaries returned by this third run were retained and are depicted in Figure 1. The final boundaries do not differ significantly from those of the earlier runs, thus strengthening our confidence that these chronological limits are appropriate and unlikely to be affected significantly by the addition or deletion of measurements not considered here or obtained in the future.

Eco-cultural niche modeling

In GARP, occurrence data (i.e., presence-only data) are resampled randomly by the algorithm to create training 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 – Atomic, Range, Negated Range, and Logistic Regression – and applied to the training data to develop specific rules (Stockwell and Peters, 1999). These rules evolve to maximize predictivity by several means (e.g., crossing-over among rules). 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. 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). For each GARP model, we performed 1,000 replicate runs with a convergence limit of 0.01, using 50% of the occurrence points for model training. We used the best subsets protocol described by Anderson et al. (2003) with a hard omission threshold of 10% and a commission threshold of 50%, and summed the resulting 10 grids to create a consensus estimate of the geographic range of the ecological niche associated with the archaeological occurrence data.

The maximum entropy (Maxent) modeling architecture uses the distribution of known occurrences to estimate a species' ecological niche by fitting a probability distribution of maximum entropy (i.e., that which is closest to uniform) to the set of pixels across the study region (Phillips et al., 2004, 2006). This estimated probability distribution is constrained by environmental characteristics associated with the known occurrence localities, while at the same time it aims to avoid making assumptions not supported by the background data. To produce eco-cultural niche reconstructions, we used the following parameters for Maxent version 3.3.3a: random test percentage = 50, maximum iterations = 500, background points = 10,000, and convergence limit = 10^{-5} . This configuration approximates that used to produce the GARP predictions, in that half of the available occurrence data are set aside for evaluating and refining model rule-sets.

Since these predictive architectures use subsamples of occurrence data for training and testing during model development, it is important that each occurrence point be spatially unique in order to produce robust niche predictions. This means that an individual archaeological site cannot share a grid cell in the environmental coverage with another site. With respect to the Early Aurignacian data, a number of grid cells are associated with more than one archaeological site. These spatially redundant sites were eliminated

from the occurrence data used to reconstruct the eco-cultural niches (Table 1).

When estimating ecological niches, it is important to consider the geographic areas that would have been accessible to the species or population in question via dispersal, and which have been sampled archaeologically, so that such occurrences could have been detected (Barve et al., 2011); this area is termed "M" in the BAM framework of Soberón and Peterson (2005). One should incorporate M into model training because it represents the geographic area in which presences may exist and within which absences are meaningful in ecological and environmental terms. Barve et al. (2011) point out that using overly broad designations of M can significantly influence predicted geographic distributions. As a result, in this study we did not use the entire geographic coverage of our environmental variables in calibrating eco-cultural niche models. Instead, we estimated M for the Proto- and Early Aurignacian as the area comprising the European continent below 54° N latitude. We eliminated regions above 54° North latitude because before and during Heinrich Event 4, they were characterized by periglacial conditions that are devoid of an Aurignacian archaeological record, strongly suggesting that they were not exploited. Northern Africa was eliminated as well since the Mediterranean Sea served as a physical barrier to settlement of this region by Aurignacian populations resident in Europe. Finally, we removed areas farther to the east in the Near East and central Asia from consideration because these eastern industries are geographically separated from the European Aurignacian, are contemporaneous only with the Early Aurignacian, and appear to represent distinct populations from those on the European continent (see above).

Thresholding

For the ecological niche reconstructions produced by GARP and Maxent, each grid cell is assigned a value that represents model agreement or probability of occurrence, respectively. Given the frequent problem of overfitting (i.e., excessive model complexity) in highly dimensional environmental spaces, continuous outputs are best thresholded to produce binary results (Peterson et al., 2007). Therefore, we followed the procedure detailed by Peterson et al. (2008) for incorporating a user-selected error parameter E that summarizes the likely frequency in the occurrence data set of records that are sufficiently erroneous as to place the species in environments outside its ecological niche. We set this parameter at 5% (i.e., $E = 5$). Such a value is appropriate for occurrence data that are likely to include a small degree of error, and is appropriate considering the ambiguity of material cultural assemblages at a handful of Aurignacian sites. Hence, the Hawth's Tools extension to ArcGIS 9 was used to identify the GARP and Maxent output levels that included $(100 - E)\%$ of the training occurrence points; this value was used to reclassify the grid cells from the prediction into a binary map. For example, with a hypothetical occurrence data set of 40 points for model training and $E = 5$, one would find the threshold that includes 38 of the points and reclassify all grid cells with values below it as unsuitable and all grid cells with values at or above it as suitable. We applied this thresholding procedure to the raw predictions and then saved each resulting binary raster grid as an integer data layer.

Eco-cultural niche characterization

To evaluate the possibility of changes in niche dimensions through time, we used partial ROC (Receiver Operating Characteristic) tests (Peterson et al., 2008) to evaluate model predictivity among time periods. The partial ROC method calculates the Area Under the Curve (AUC) of the ROC as per normal ROC AUC testing

but truncates the curves to reflect a sensitivity threshold for the niche predictions being compared. In other words, the user-chosen error parameter E is used to target and evaluate different critical area thresholds for the two ROC curves (see Peterson et al. [2008] for a detailed discussion). This AUC value and the AUC null expectation (i.e., the straight line connecting 0,0 and 1,1 in ROC plots) are used to calculate an AUC ratio. Bootstrapping manipulations, via 50% resampling with replacement, use the predicted suitability value associated with each occurrence point along with the proportion of the area predicted present (with respect to the total coverage area of the environmental layers) for each suitability value to calculate a set of AUC ratios for each niche prediction (Barve, 2008). One-tailed significance of differences between each niche prediction's AUC ratios is assessed by direct count, summing the number of partial ROC ratios that are ≥ 1 and calculating a p -value as the proportion out of 1,000. If the probability is low (i.e., below 0.05), one can conclude that the niches are significantly differentiated, thus indicating a niche shift through time.

Since the Proto-Aurignacian and Early Aurignacian are associated with different climatic periods, we used GARP and Maxent's capability to project a niche prediction onto the environmental conditions of a subsequent time period in order to evaluate possible eco-cultural niche variability. The resulting projection can be compared to the locations of known occurrences of the later period to see whether the projected prediction successfully predicts their archaeologically observed spatial distribution. It is this level of prediction success that is evaluated with the partial ROC test. Thus, with respect to the Early Aurignacian occurrence data, we compared the level of prediction success between the Early Aurignacian niche estimation and the niche prediction resulting from projecting the Proto-Aurignacian eco-cultural niche onto HS4 paleoclimatic conditions.

Results

Bayesian age model

The final Bayesian model indicates that the Proto-Aurignacian is situated between 41.5 and 39.9 k cal BP and that the Early Aurignacian occurs between 39.8 and 37.9 k cal BP (initial and terminal boundaries in Table 2; Fig. 2). Therefore, the Proto-Aurignacian occurred during GI 10 and 9, and was punctuated by GS 9/10. The Early Aurignacian clearly begins with the onset of HS4 and comes to an end with the onset of GI 8. The final age model has an overall agreement index of 69.7%, and a model agreement index of 99.9%. As described above, a number of ages were indicated to be outliers. This is not unexpected since we included in the analysis ages derived from a number of different materials, some of which had relatively large errors, and a variety of pre-treatment methods and measurements performed at a number of different radiocarbon laboratories. This age model serves to accurately place these two Aurignacian phases into a well-constrained chronological framework.

Eco-cultural niche estimations

The reconstructed eco-cultural niche of the Proto-Aurignacian produced with GARP is present across the majority of present-day France, the Italian Peninsula, southeastern Europe, the Balkan Peninsula, and the northern two-thirds of the Iberian Peninsula (Fig. 3A). If one considers only the regions in which all ten models predict a presence, we see that much of the Iberian Peninsula is not included except for Cantabria, the Ebro River valley, and small isolated regions along the western and southern margins of the Central Meseta. The same is true for northern France, the French Massif Central, and the Balkans. The Proto-Aurignacian Maxent

prediction (Fig. 3B) has much the same geographic footprint as the highest prediction levels of the GARP reconstruction.

The GARP prediction for the Early Aurignacian (Fig. 3C) has a broader geographic footprint than that of the Proto-Aurignacian and at moderate and high prediction levels includes regions above 50° N latitude. The presence of this predicted eco-cultural niche in more northerly latitudes serves to link regions of Western and Central Europe, a pattern absent prior to Heinrich Stadial 4. Much of this northern presence is at medium prediction levels. One also observes that there is an absence of prediction in southern Iberia, many areas within the Spanish Central Meseta, the Pyrenees, the French Massif Central, the exposed Adriatic Plain, the mountainous regions of the Balkans, and the Carpathian mountains. The Early Aurignacian Maxent prediction (Fig. 3D) is more constrained than the GARP prediction and the regions with the highest level of predicted presence are restricted to present-day France and northern Iberia. One observes that regions in Western Europe above 48° N latitude are predicted at medium and low probability levels. The same holds true for northern regions of the Italian Peninsula and southeastern Europe.

As described above, the partial ROC tests examined predictive success, with respect to Early Aurignacian occurrences, between the Early Aurignacian eco-cultural niche prediction and that of the Proto-Aurignacian prediction projected onto the environmental conditions of Heinrich Stadial 4. Results indicate that the eco-cultural niches of the Proto-Aurignacian and Early Aurignacian are significantly differentiated (Table 3). By referring to the maps of the Proto-Aurignacian eco-cultural niche prediction projected onto HS4 environmental conditions (Fig. 3E and F), we see that these significant partial ROC results reflect an expansion of the eco-cultural niche during the Early Aurignacian. In other words, for both the GARP and Maxent projections, the projected Proto-Aurignacian niche fails to predict the presence of Early Aurignacian sites in Belgium (Spy and Goyet), southern Germany (Bocksteinhöhle, Geissenklösterle, Lommersum, Vogelherd, and Wildscheuer), and Austria (Tischoferhöhle). Furthermore, the sites of La Mère Clochette (France), Willendorf (Austria), and Istállós-kő (Hungary) are only predicted at lower probability levels.

Discussion

The Bayesian portion of this study is fully consistent with the evidence for the temporal precedence of the Proto-Aurignacian over the Early Aurignacian observed in a number of stratigraphic sequences. It also serves to delimit these cultural phases chronologically and, more importantly, demonstrates that the appearance of the Early Aurignacian broadly coincides with the onset of a rigorous climatic phase—Heinrich Stadial 4.

Our results are comparable to those of a recent, regional (south-western France) chrono-stratigraphic synthesis (Discamps, 2011). The modeled age ranges for the Proto-Aurignacian and Early Aurignacian presented by Discamps et al. (2011: Table 5) are extremely broad, likely because they worked with a much smaller population of radiocarbon ages from a geographically restricted region of Western Europe. Nonetheless, their Bayesian sum calculations (Discamps et al., 2011: Fig. 9) indicate that the Proto-Aurignacian precedes the Early Aurignacian and place the latter within Heinrich Stadial 4.

Faunal associations recovered from Proto-Aurignacian and Early Aurignacian archaeological contexts across Europe are also consistent with our results. In Proto-Aurignacian assemblages, it is common to find a relatively broad spectrum of fauna indicating environmental conditions less severe than those typical of a Heinrich stadial (e.g., Altuna, 1971; Altuna and Mariezkurrena, 2000; Goutas et al., 2012). In contrast, Early Aurignacian assemblages are dominated by fauna typical of stadial conditions, such as reindeer,

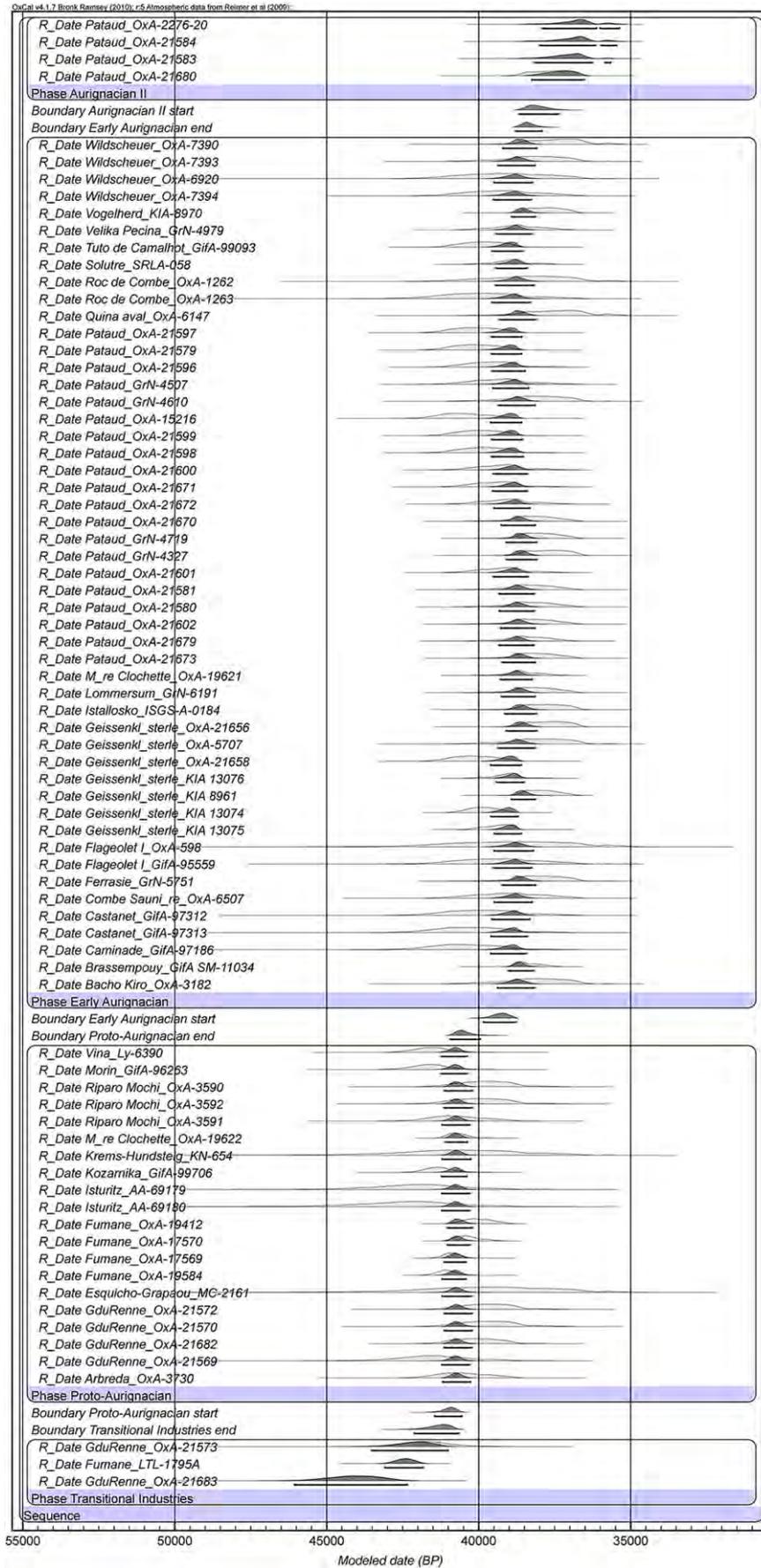


Figure 2. Final Bayesian model for the Proto-Aurignacian and Early Aurignacian phases using the radiocarbon measurements listed in Table 2.

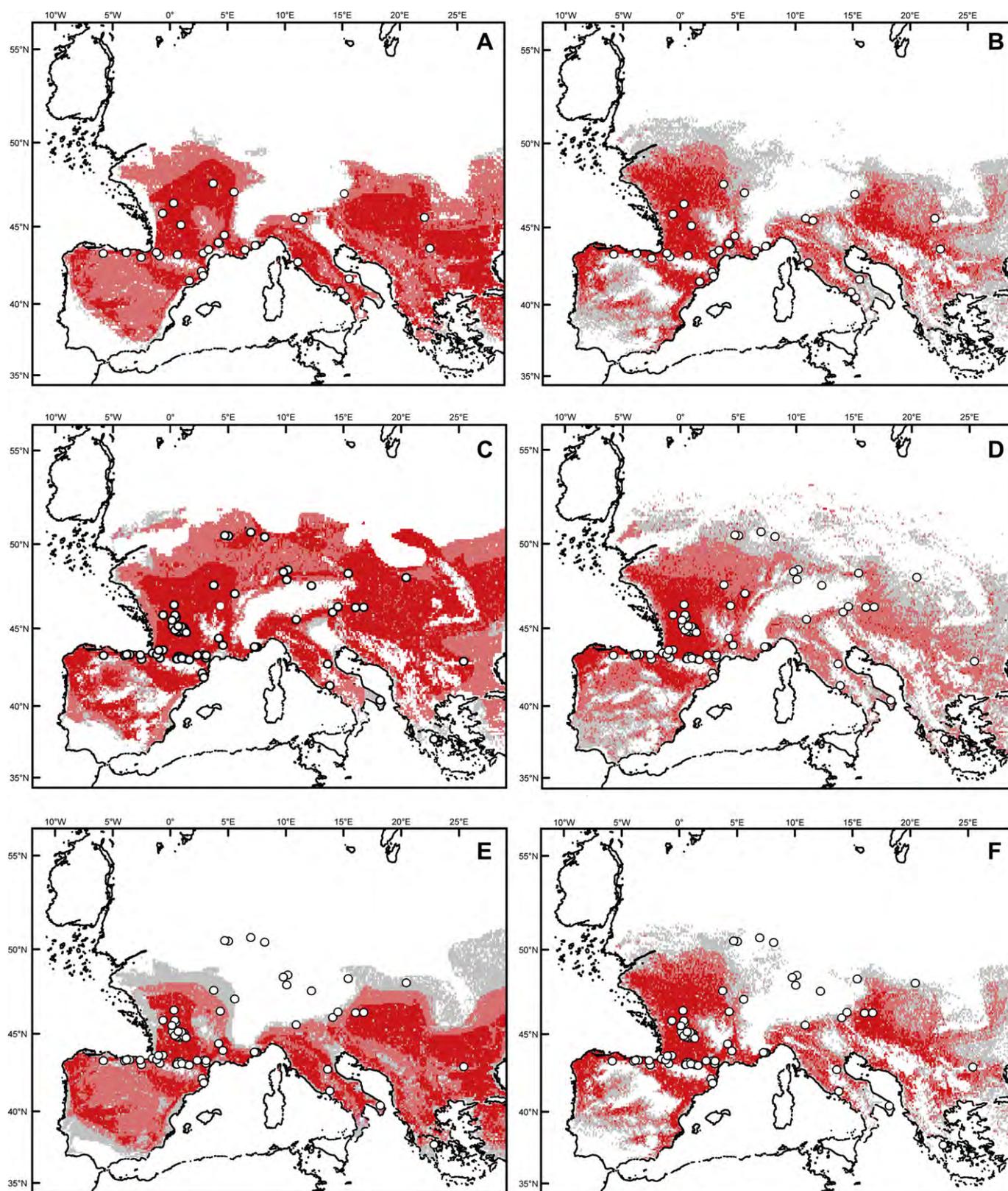


Figure 3. Proto-Aurignacian and Early Aurignacian eco-cultural niche reconstructions: (A) GARP prediction for the Proto-Aurignacian, (B) Maxent prediction for the Proto-Aurignacian, (C) GARP prediction for the Early Aurignacian, (D) Maxent prediction for the Early Aurignacian, (E) GARP projection of the Proto-Aurignacian prediction onto HS4 climatic conditions and compared to Early Aurignacian occurrence data, (F) Maxent projection of the Proto-Aurignacian prediction onto HS4 climatic conditions and compared to Early Aurignacian occurrence data. For the GARP predictions, grid squares with 1–5 of 10 models predicting the presence of suitable conditions are indicated in gray, grid squares with 6–9 models in agreement are depicted in pink, and squares with all 10 models in agreement are indicated in red. For these Maxent models, colors range from gray to pink to red, or low, medium, and high probability, respectively. Coastlines were obtained by lowering sea levels 90 m. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3
Partial ROC comparison results^a

	GARP predictions		Maxent predictions	
	Projected PA ratio	EA ratio	Projected PA ratio	EA ratio
Mean	1.1479	1.5058	1.2325	1.4208
Variance	0.0122	0.0009	0.0214	0.0172
Observations	1001	1001	1001	1001
Z-score	98.96		−30.33	
One-tailed prob.	0.00		0.00	
Critical Z-value	1.64		1.64	

^a Partial ROC ratios represent the ratio of predicted AUC (area under the curve) at the 1-E omission threshold to the AUC at 50% (random). PA = Proto-Aurignacian; EA = Early Aurignacian. Tests compared the level of prediction success between the Early Aurignacian niche estimation and the niche prediction resulting from projecting the Proto-Aurignacian eco-cultural niche onto HS4 paleoclimatic conditions.

and are less diverse than the preceding period (e.g., Grayson and Delpéch, 2003; Niven, 2007; Discamps, 2011).

Between the Proto- and the Early Aurignacian, one observes a number of technological changes, and in conjunction with them there was an expansion of the geographic range occupied by Early Upper Paleolithic human populations. This study demonstrates that these changes are associated with an ecological niche expansion—the situation outlined above in which cultural adaptation and flexibility is used to quickly adjust to rapid-scale climatic variability.

Heinrich Stadial 4 was characterized by extremely cold and dry conditions and semi-desert vegetation in southwestern Europe, as well as cold but slightly less arid conditions at higher latitudes, for which we see an expansion of open grassland environments (Sánchez Goñi et al., 2008; Fletcher et al., 2010). It is during these rigorous climatic conditions and open-environment vegetation regimes of HS4 that the human ecological niche in Europe was expanded. We propose that technological changes observed between the Proto- and the Early Aurignacian had, in part, an ecological basis and served to facilitate ecological niche expansion. It is likely that these technical changes were associated with other behavioral changes that are archaeologically invisible or unrecognizable. It appears that cultural solutions enabled Early Aurignacian populations to adapt to and, in fact, use these climatic changes advantageously. D'Errico et al. (2006) argue that, in Europe, open environments during stadial events led to an increase in ungulate biomass. Thus, the Early Aurignacian population's eco-cultural niche expansion and associated technical changes reflect behaviors that allowed these hunter–gatherer populations to take advantage of this environmental restructuring. In addition to a diversification of technical traditions during the Early Aurignacian, we also see an increase in the frequency and diversity of forms of symbolic material culture. We hypothesize that this trend is associated with an expansion of social networks within and among regional Early Aurignacian populations. Such a pattern would have been critical for a successful expansion of their realized ecological niche with the onset of HS4, an event that would have confronted those hunter-gatherer populations with an increased level of ecological risk.

While certainly not universal, niche conservatism is common. Parmesan and Yohe (2003) analyzed the distributions of over 1,700 plant and animal species against a backdrop of climate change and found that most species exhibit niche conservatism when faced with climatic changes. Similarly, Wiens and Graham (2005) point out that many of the earth's past mass extinctions linked to rapid-scale climatic change may be explained by the tendency of many species to conserve their ecological niche. We observe a different pattern with the Aurignacian populations of Europe. These results run counter to Banks et al. (2008), who described niche conservatism across the same time interval examined for this study. The reason for this discrepancy is that the former study considered only Aurignacian sites with radiometric age determinations in the

construction of occurrence datasets. Thus, those occurrence data did not capture the full range of environmental conditions occupied by Aurignacian populations. This serves to highlight the importance of including non-radiometrically dated sites into an ECNM analysis when studying an archaeological culture (or cultures) characterized by diagnostics (index fossils) that can serve as precise chronological markers. Such inclusions increase occurrence data samples, thereby allowing one to capture a more representative range of environmental conditions exploited by a past population and estimate ecological niches more accurately.

Conclusions

The eco-cultural niche expansion between the Proto-Aurignacian and the Early Aurignacian associated with the onset of the rigorous climatic conditions of Heinrich Stadial 4 exemplifies a situation in which cultural flexibility allowed hunter-gatherer populations to quickly adapt to rapid-scale climatic fluctuation. This is the first time that niche expansion has been formally demonstrated for an archaeological cultural transition.

An examination of niche stability during a more recent period (the Last Glacial Maximum: LGM) indicated niche conservatism across the transition from HS2 into the LGM (Banks et al., 2009). It should be pointed out, however, that the methods used to evaluate possible niche variability in that study were relatively coarse, and it is possible that finer-scale shifts might have gone unrecognized. Nevertheless, the present study raises the question of whether other such expansions occurred with earlier human populations: is the use of culture to expand the exploited ecological niche unique to modern humans, or do we see similar patterns in the archaeological record associated with anatomically archaic humans?

While the initial Out-of-Africa expansion of humans in the Lower Pleistocene may be construed as an adaptive radiation that filled a single, homogenous, savannah-like niche (Dennel and Roebroeks, 2005), the Middle Pleistocene colonization of present-day Germany and other European regions at similar latitudes may represent niche expansion among earlier humans, in this case either *Homo heidelbergensis* or Neanderthals. The later Neanderthal record attests to complex cultural behaviors even back in the Middle Paleolithic Mousterian (i.e., the production of symbolic material culture; cf. Zilhão et al., 2010), so similar analyses that focus on the Neanderthal archaeological record at a more restricted geographic scale are warranted.

These research questions are the focus of the current ERC-funded TRACYSMBOLS project, which aims to evaluate human–environment interactions for modern human and Neanderthal populations during MIS 6–3 in southern Africa and Europe, respectively. One principal goal of the project is to determine if, and how, material cultural innovations and eco-cultural niche variability were related during a broader span of human prehistory.

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Ecological constraints on the first prehistoric farmers in Europe

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ABSTRACT

The Neolithic Revolution, which witnessed the transformation of hunter–gatherer groups into farming communities, is traditionally viewed as the event that allowed human groups to create systems of production that, in the long run, led to present-day societies. Despite the large corpus of research focused on the mechanisms and outcomes of the Neolithic transition, relatively little effort has been devoted to evaluating whether particular production-oriented adaptations could be integrated into a broad range of ecological conditions, and if specific cultural traditions differed ecologically. In order to investigate whether the differences between the adaptations and geographic distributions of three major Early Neolithic archaeological cultures are related to the exploitation of different suites of environmental conditions, we apply genetic algorithm and maximum entropy ecological niche modeling techniques to reconstruct and compare the ecological niches within which three principal Neolithic cultures (Impressed Ware, Cardial Ware, and Linearbandkeramik) spread across Europe between ca. 8000 and 7000 cal yr BP. Results show that these cultures occupied mutually exclusive suites of environmental conditions and, thus, were adapted to distinct and essentially non-overlapping ecological niches. We argue that the historical processes behind the Neolithization of Europe were influenced by environmental factors predisposing occupation of regions most suited to specific cultural adaptations.

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1. Introduction

The Neolithic Revolution represents the process by which human groups switched from hunting and gathering wild resources to a reliance on systems of food production based on domesticated plants and animals (Barker, 2006). The reasons for this transformation, which occurred independently and at different times in various regions of the world, have been debated for decades and are not fully understood (Bellwood, 2005; Barker, 2006). Proposed causes include climate change (Richerson et al., 2001; Weninger et al., 2006; Gronenborn, 2009; Rowley-Conwy and Layton, 2011), human–plant co-evolution (Rindos, 1984), demography (Bocquet-Appel, 2002; Bowles, 2011), social competition and inequality (Mithen, 2007), or a combination of these (see Ammerman and Biagi, 2003 as well as Bocquet-Appel and Bar-Yosef, 2008 for detailed reviews of the topic). Despite considerable debate concerning proposed causes and mechanisms, consensus exists that

this revolution helped create the economic and social foundations on which present-day societies are based, such as diversified food production and storage techniques, surpluses, sedentism, labor specialization, social complexity, and ultimately state institutions. Along with these changes, it is generally recognized that the switch to agriculture resulted in, at least during initial phases, more intense labor, a less diversified diet, increased morbidity, decreased life expectancy, precarious household-based production systems, and increased intra- and inter-group conflict (Cohen, 2008; Hershkovitz and Gopher, 2008; Wittwer-Backofen and Tomo, 2008), although a number of recent studies present evidence to the contrary (Auerbach, 2011; Marchi et al., 2011; Temple, 2011). Despite these potential disadvantages, the Neolithic Revolution is traditionally perceived as the adaptive transformation that allowed human groups to move away from a reliance on predation and gathering to fulfill their subsistence needs. Little effort, though, has been made to quantitatively evaluate to what extent early production economies were sensitive to environmental constraints, if particular adaptations could be integrated into a broad range of environmental conditions, and whether specific cultural traditions differed ecologically. Here, we investigate whether the differences between the adaptations and geographic distributions of three major Early Neolithic archaeological cultures associated with the

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expansion of farming economies across the majority of the European continent are related to the exploitation of different ecological niches. First, we aim to quantify the environmental variables that define each reconstructed eco-cultural niche and identify those that were most influential for each. Second, if differences are identified between eco-cultural niche predictions, we intend to determine if they are significant. Such a focus should allow us to establish if distinct Early Neolithic cultural trajectories occurred within specific environmental settings, or if they were largely divorced from ecological factors.

We address these issues by reconstructing and comparing the eco-cultural niches (ECNs) occupied by Early Neolithic cultures in Europe: the Impressed Ware, Cardial, and Linearbandkeramik archaeological cultures. ECN modeling methods combine archaeological, chronological, geographic, and paleoclimatic datasets via biocomputational architectures, derived from biodiversity studies (see Peterson et al., 2011 for a detailed discussion of these architectures and methods), to reconstruct ecological niches occupied by prehistoric human populations. An ECN represents the array of environmental conditions within which an archaeologically recognizable human adaptive system can persist without needing to substantially shift its geographic range (Banks et al., 2008a). This methodological approach employs the Grinnellian concept of ecological niche, for which niche is defined as the subset of unlinked, non-consumable, abiotic factors that define the environmental space occupied by a given species (or population) and serve as the basis for understanding its geographic distribution (Peterson et al., 2011). In such a framework, the combination of paleoclimatic and geographic variables that we employ can be used to effectively approximate a past ecological niche.

The human populations being examined are represented by archaeologically-defined cultures. While archaeological cultures are modern constructs and debate exists as to what degree they reflect actual past cultural entities, our assumption is that an archaeological culture represents a population whose cohesion was based on a body of shared and transmitted knowledge that is reflected by an archaeologically recognizable suite of material culture traits (e.g., specific methods of pottery production and broad classes of decoration styles, subsistence methods, house forms, etc.). It is also important to keep in mind that a cohesive population's system of behaviors operated within an environmental context. Our focus is on relatively broadly defined archaeological cultures rather than minor and more regional subdivisions that might be defined on the basis of interrelated material culture diversity within them.

This study examines the ecological contexts of Neolithic archaeological cultures at a particular moment in which these different production economy adaptations had spread across much of the European continent and were in relative equilibrium with the environments they occupied. Therefore, our focus is not on eco-cultural niche dynamics through time (e.g., Banks et al., 2013), nor on the processes potentially involved in the colonization of new territories by an invasive population (e.g., Gallien et al., 2010, 2012). Rather, once they had expanded and were in relative equilibrium, we aim to understand whether these farming adaptations were ecologically distinct from one another or if they exhibited some degree of overlap with respect to the environmental conditions they occupied. Such patterns have important implications for understanding the processes of cultural change that took place during the Early Neolithic.

Following an initial settlement in southeastern Europe, the transition to production economies across Central and Western Europe as well as northern Mediterranean regions is recognized by the spread of three cultural packages defined by different ceramic traditions and distinct suites of subsistence and settlement systems

(Dolukhanov et al., 2005; Burger and Thomas, 2011). The Linearbandkeramik (LBK), thought to have originated out of the Starčevo–Kőrös cultural complex, dispersed through Central Europe and into northwestern Europe along the Danube corridor from ca. 7700 to 7000 cal BP (Price et al., 2001; Davison et al., 2006). This cultural tradition is characterized by pottery forms decorated with series of parallel, incised lines organized in bands that either meandered or took the form of spirals or chevrons. The Impressed Ware culture and, later, the Cardial Ware culture that emerged out of it, diffused west along the Mediterranean coast with the help of seafaring technology between ca. 8000 and 7200 cal BP (Zilhão, 2001). The Impressed Ware tradition is recognized by vessel forms decorated with casually made impressions often produced with spatulas or shells. One also finds grooved impressions associated with incisions organized in geometric motifs. The Cardial Ware tradition is also characterized by ceramics decorated with impressed designs, but the impressions were typically created by imprinting the clay surface with a *Cardium edulis* marine shell, although fingernail and finger impressions are occasionally present. These decorative motifs are contained in delimited bands arranged in chevron or triangular motifs, and undecorated surfaces are polished. When radiocarbon ages obtained from diagnostic materials (as opposed to bulk charcoal samples) from Impressed Ware and Cardial archaeological contexts are examined (e.g., Coppa Navigata, Arene Candide; see Zilhão, 2001), one notes that more easterly Mediterranean occurrences of these cultures are contemporaneous with early LBK occupations in Central Europe (Stäuble, 1995). Genetic evidence, as well as modeling work, indicate that the expansions of these roughly contemporaneous cultural traditions are associated with a demic diffusion (Chikhi et al., 2002; Fort, 2012; Pinhasi and von Cramon-Taubadel, 2009; Skoglund et al., 2012), although autochthonous hunter-gatherers likely played significant roles in either facilitating or delaying the dispersal of these farming economies (Galeta et al., 2011; Isern et al., 2012). Populations associated with the LBK and Impressed Ware/Cardial archaeological cultures appear to have come into contact only in limited areas of Western Europe (Constantin and Vachard, 2004; Bocquet-Appel et al., 2009).

Behind the issues outlined earlier lies the question of whether the cultural processes that occurred during the evolution of these different Neolithic cultures took place within broad, but distinct, environments or if they were driven primarily by historical contingencies in which ecology played little or no role. With respect to the former, one would expect little to no interpredictivity between the ecological niches associated with different cultural entities. For example, for the scenario in which different, neighboring archaeological cultures are characterized by distinct farming adaptations associated with well-constrained suites of ecological conditions, one would expect the particular culture–environment relationships that exist to be such that these different adaptive packages have few or no ecological similarities between them. Furthermore, given this strong correspondence between type of adaptation and ecology, one would expect each archaeological culture's predicted ecological niche to correspond closely to its actual geographic distribution. Alternatively, if reconstructed ecological niches for two cultures overlap broadly, then no relationship, or at least a very weak one, likely exists between a specific cultural adaptation and ecological parameters. In such a situation, these cultures' differing geographic distributions are likely more constrained by cultural factors and historical contingencies. Previous eco-cultural niche modeling work has shown that both scenarios can be recognized among Paleolithic hunter-gatherer populations (Banks et al., 2009), and although hunter-gatherers differ from farmers with respect to how their settlement systems and social networks are structured, it is our assumption that the expected relationships

outlined above between adaptation, ecology, and geographic distribution are equally applicable to low-level production farming economies. Hence, we apply eco-cultural niche modeling methods to the European Early Neolithic in order to quantitatively assess the degree to which these farming economies were constrained by environmental constraints.

2. Materials and methods

To estimate eco-cultural niches for the Impressed Ware, Cardial, and Linearbandkeramik Neolithic cultures, we used genetic algorithm (Genetic Algorithm for Rule-Set Prediction: GARP; Stockwell and Peters, 1999) and maximum entropy (Maxent; Phillips et al., 2006) techniques. GARP and Maxent have been applied to a diverse set of topics including reconstructing species' distributions (Pearson et al., 2007; Barve et al., 2011), estimating effects of climate change on species' distributions (Araújo and Rahbek, 2006; Banks et al., 2008b), and forecasting the geographic potential of species invasions (Peterson, 2003; Medley, 2010). For data inputs, GARP and Maxent require the geographic coordinates where the target population has been observed, and raster GIS data layers summarizing environmental dimensions potentially relevant to shaping the geographic distribution of that population.

2.1. Occurrence data

Occurrence data were obtained from the published literature and consist of the geographic coordinates of archaeological sites containing material culture remains associated with the Impressed Ware, Cardial, or Linearbandkeramik cultures (Table S1). We included in this dataset only those archaeological sites with material remains that had been recovered from intact stratigraphic contexts and for which clear chrono-cultural identification is possible. Sites for which cultural materials only occur as surface scatters were excluded. We restricted our occurrence data for the Impressed Ware culture to sites documented in Italy since this pottery style represents a type that emerged in the region and that is substantially different from ceramic technologies recognized in the Balkans (Mazurié de Keroualin, 2003: 100). Impressed Ware pottery on the eastern coast of the Adriatic, as well as on the Mediterranean coast west of Italy, represents regional variants that post-date the initial Impressed Ware of the Italian Peninsula (Mazurié de Keroualin, 2003: 102, 112). Restricting our Impressed Ware occurrence data to sites in the Italian Peninsula provides a sample sufficient to produce robust niche predictions.

2.2. Environmental data

The raster GIS datasets used in this study summarize landscape attributes (assumed to have remained constant) and a high-resolution paleoclimatic simulation for the mid-Holocene (6000 cal BP). Landscape variables included slope, aspect, elevation, and topographic index (a measure of tendency to pool water). Elevation was obtained from the ETOPO1 dataset (Amante and Eakins, 2009), whereas the remaining landscape values were calculated from the ETOPO2 dataset (ETOPO2v2). It would be ideal to include data layers pertaining to soil type or soil characteristics. Such data would be extremely pertinent for studies at restricted geographic scales (i.e., regional or micro-regional). Compiling regional records of soil type data into raster data layers for the entire European continent, however, represents a daunting and time-consuming task, and it would be difficult to ensure that data would be geographically consistent at such a large scale. It is for these reasons that soil type data were not included as a landscape variable.

Furthermore, these heterogeneous data would be less likely to influence niche predictions significantly at our scale of analysis.

The high-resolution paleoclimatic simulation for the mid-Holocene (6K; Sepulchre et al., 2008) was derived from the LMDZ4 three-dimensional Atmospheric General Circulation Model (Li and Conil, 2003). The LMDZ4 model was forced by 6K values for sea surface temperatures, vegetation albedo, and surface roughness length in order to create the 6K paleoclimatic simulation and derive values for mean annual temperature, warmest month temperature, coldest month temperature, and mean annual precipitation. The simulation has a horizontal resolution between 70 and 90 km over Europe, which is sufficient for examining ECN variability at a continental scale.

2.3. Eco-cultural niche modeling

In GARP, occurrence data (i.e., presence-only data) are resampled randomly by the algorithm to create training and test datasets. An iterative process of rule generation and improvement then follows, in which a method is chosen randomly from a set of inferential tools—Atomic, Range, Negated Range, and Logistic Regression—and applied to the training data to develop specific rules (Stockwell and Peters, 1999). These rules evolve to maximize predictivity by several means (e.g., crossover, mutation) via a process that evaluates predictive accuracy based on an independent subsample of presence data and a set of points sampled randomly from regions where the species has not been detected. The final rule-set defines the distribution of the target population in environmental dimensions (i.e., the ecological niche: Peterson et al., 2011), which is projected onto the landscape to estimate a potential geographic distribution. For each GARP model, we performed 1000 replicate runs with a convergence limit of 0.01, using 50% of the occurrence points for model training. We used the best subsets protocol (Anderson et al., 2003), with a hard omission threshold of 10% and a commission threshold of 50%, and summed the resulting 10 grids to create a consensus estimate of the geographic range of the ecological niche associated with the archaeological occurrence data.

The maximum entropy (Maxent) modeling architecture uses the distribution of known occurrences to estimate a species' ecological niche by fitting a probability distribution of maximum entropy (i.e., that which is closest to uniform) to the set of pixels across the study region (Phillips et al., 2006). This estimated probability distribution is constrained by environmental characteristics associated with the known occurrence localities, while at the same time it aims to avoid making assumptions not supported by the background data. To produce eco-cultural niche reconstructions, we used the following parameters for Maxent version 3.3.1: random test percentage = 50, maximum iterations = 500, background points = 10^4 , and convergence limit = 10^{-5} . This configuration approximates that used to produce the GARP predictions, in that half of available occurrence data are set aside for evaluating and refining model rule-sets.

When reconstructing ecological niches, it is important to consider the geographic areas that would have been accessible to the species or population in question via dispersal, and that have been sampled such that occurrences could have been detected (Barve et al., 2011; Peterson, 2011); this area is termed “*M*” in the BAM framework (Soberón and Peterson, 2005). It is important to incorporate *M* into model training because it represents the geographic area in which presences may exist and within which absences are meaningful in ecological terms. Using overly broad designations of *M* can significantly influence predicted geographic distributions (Barve et al., 2011). As a result, we did not use the entire geographic coverage of our environmental variables in

calibrating eco-cultural niche models. Instead, our *M* definitions incorporated into model training relatively broad regions (Fig. S1), beyond the known archaeological distributions, that potentially could have been occupied. In this way we avoided the possibility of erroneously restricting the potential limits of an archaeological culture's predicted niche.

2.4. Eco-cultural niche characterization

Recent years have seen a proliferation of techniques for reconstructing ecological niches and predicting species' distributions, and debate has focused on how best to evaluate resulting models statistically (Araújo and Guisan, 2006; Peterson et al., 2008; Warren et al., 2008). We use a variety of methods to evaluate and compare the outputs from the two employed modeling algorithms. New methods and statistical tests (Warren et al., 2008) for quantitatively evaluating overlap between ecological niche models are available in ENMTools (enmtools.blogspot.com; Warren et al., 2010). ENMTools allows one to generate ecological niche models (ENMs) with Maxent, calculate similarity measures, and develop randomization-based comparisons of niche predictions.

To characterize each ECN, we used *R* to perform Principal Component Analyses (Figs. S2, S3), as well as descriptive statistics of environmental variables (Figs. S4–S7). To examine patterns of niche similarity, we employed ENMTools' niche breadth measure (inverse concentration; Table S2), overlap measures *I* and *D*, and background similarity tests. Niche breadth is a measure of the range of abiotic conditions within which a species can maintain populations (Carnes and Slade, 1982; Levins, 1968; Soberón, 2007). Overlap measures *I* and *D* compare two ECNs and measure the similarity between them (Warren et al., 2008). The background similarity test evaluates whether the observed degree of similarity between two ECNs is greater than would be expected by chance. This comparison is accomplished by generating a null distribution

for ECN model difference expected between one region and another based on occurrence points drawn at random from within a relevant geographic area (Warren et al., 2010), which corresponds to the *M*s defined for this study (described above). If the calculated overlap value is significantly greater than the distribution of overlaps from the pseudo-replicates, the null-hypothesis of niche identity cannot be rejected and the two niches can be considered inter-predictive. If niche overlap is significantly less than the pseudo-replicate overlaps distribution, the null hypothesis of no difference can be rejected, meaning that the two niches are more different from one another than would be expected by chance.

3. Results

Niche predictions produced with GARP and Maxent are presented in Fig. 1. Both architectures provide comparable outputs. The predicted geographic ranges for the Impressed Ware and Cardial ECNs are virtually identical and cover portions of the Near East, the majority of the Anatolian, Balkan, Italian, and Iberian Peninsulas, as well as the Atlas Mountains and limited areas of Tripolitania and Cyrenaica in Northern Africa (Fig. 1A, B, D, E). Measures of niche overlap (Table 1) confirm this visual similarity. A background similarity test shows the Impressed Ware and Cardial ECNs to be inter-predictive (Fig. 2A, B). These archaeological cultures can be considered as ensuant cultural phases with similar settlement and subsistence strategies, despite varying degrees of internal variability. What one is witnessing here is the dispersal of a specific adaptation within a distinct ecological niche through time rather than two cultures whose distributions differed due to environmental factors. For this reason, these cultures' respective archaeological sites were combined into a single occurrence dataset to produce an ECN prediction for this Mediterranean adaptation (Fig. 1C, F). This combined Impressed Ware/Cardial ECN (ICECN) closely resembles those of each individual phase. It occupies a

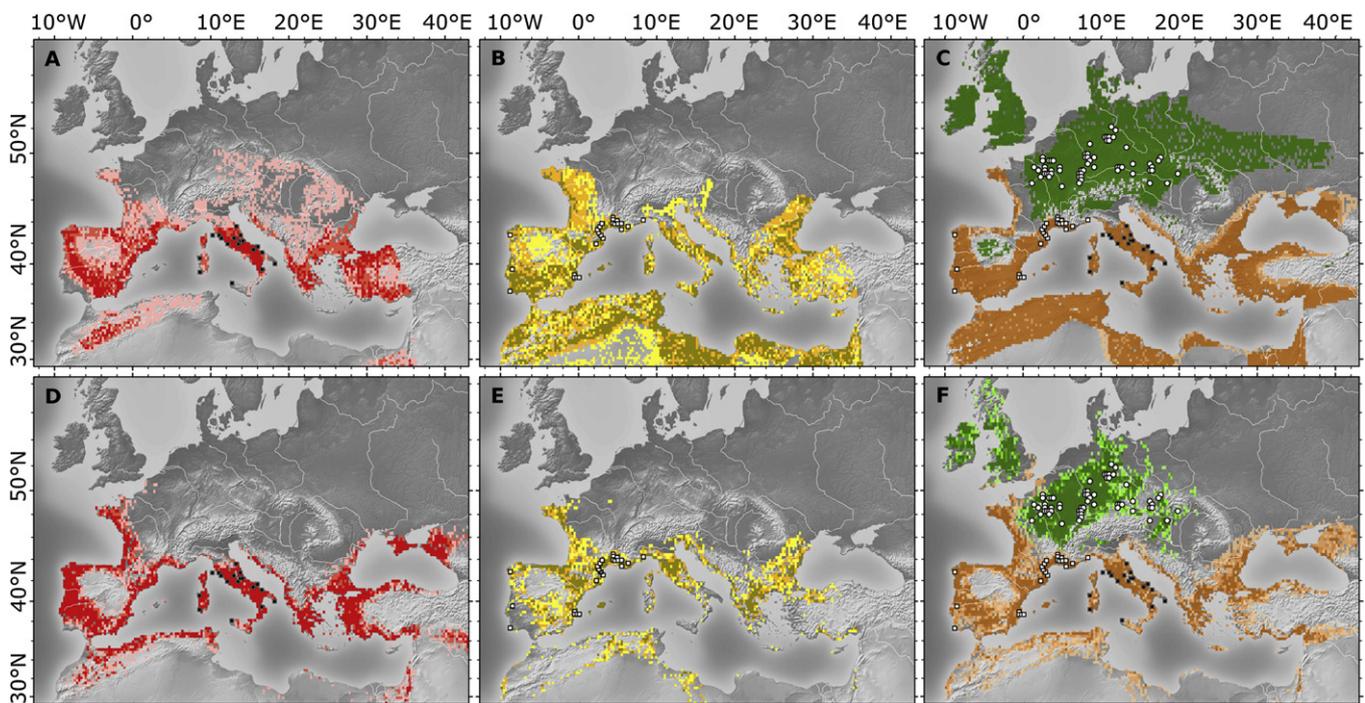


Fig. 1. Eco-cultural niche (ECN) predictions. GARP-produced: **A**) Impressed Ware culture, **B**) Cardial culture, **C**) Impressed Ware/Cardial combination (depicted in orange) and Linearbandkeramik (depicted in green); Maxent-produced: **D**) Impressed Ware, **E**) Cardial, **F**) Impressed Ware/Cardial combination (depicted in orange) and Linearbandkeramik (depicted in green). Colors range from light to dark, or low to high probability of presence, respectively.

Table 1
Measures of overlap between eco-cultural niche (ECN) predictions.

	<i>I</i> -statistic	<i>D</i> -statistic
GARP ECNs		
Cardial vs. Impressed Ware	0.546	0.373
Mediterranean vs. LBK	0.000	0.000
Maxent ECNs		
Cardial vs. Impressed Ware	0.969	0.787
Mediterranean vs. LBK	0.003	0.002

latitudinal band with mean annual temperatures between 8 and 16.5 °C and mean annual precipitation ranging between 360 and 1100 mm/year (Figs. 3, S5, S7).

The ECN for the Linearbandkeramik (LECN) covers much of the Danube River Valley, the Po Valley, the northern European Plain, and most of the British Isles (Fig. 1C, F). It occupies a range of mean annual temperatures between 3.0 and 8.5 °C and mean annual precipitation ranging between ca. 700 and 1800 mm/year (Figs. 3, S5, S7).

Evaluation of the degree of overlap (Table 1) between the predictions indicates that the ICECN and LECN represent two different and essentially exclusive ecological niches. Background similarity evaluations demonstrate that these ECN predictions are significantly different (Fig. 2C, D). Principal Component Analyses show that temperature and precipitation are the principal parameters defining these environmental envelopes (Figs. S2, S3). With respect to the ICECN prediction, mean annual precipitation is negatively correlated with temperature variables. The inverse is true for the LECN. Topographic variables (elevation, slope, and drainage index) play an important, albeit secondary, role in the definition of the two niches (ICECN and LECN). LBK sites are generally located in unbroken landscapes below 500 m, whereas sites belonging to the

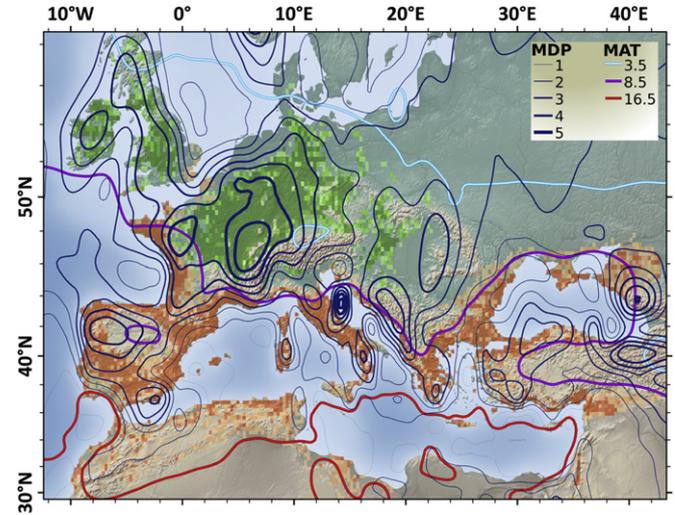


Fig. 3. Maxent-produced eco-cultural niche predictions for the Impressed Ware/Cardial combination (orange) and the Linearbandkeramik (green) in relation to mean annual temperature (MAT, °C) and mean daily precipitation (MDP, mm) isotherms.

combined Impressed Ware/Cardial group reveal a distribution that includes a broader range of elevations (Figs. S5, S7).

4. Discussion and conclusions

As stated above, instances in which the geographic footprint of a cultural entity reflects adaptation to specific environmental conditions would be indicated by a close correspondence between an

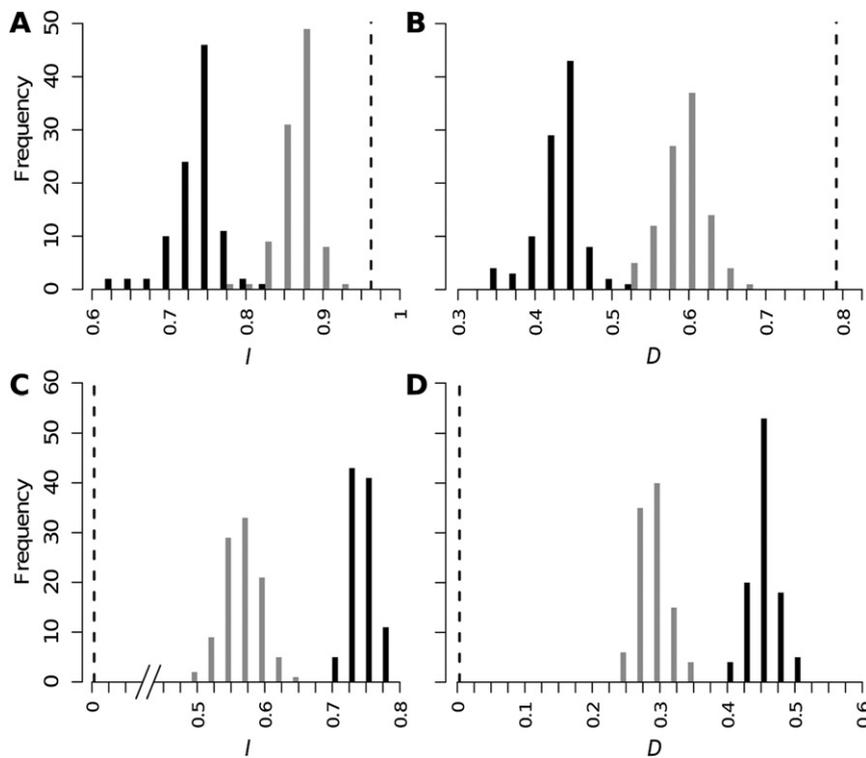


Fig. 2. Histograms of background similarity replicate overlap measures issued from comparisons between Maxent-produced niche estimations. **A)** Impressed Ware vs. Cardial, *I*-statistic, **B)** Impressed Ware vs. Cardial, *D*-statistic. For **A** and **B**, gray bars represent Cardial vs. Impressed Ware and black bars reflect Impressed Ware vs. Cardial; **C)** Impressed Ware/Cardial combination vs. Linearbandkeramik, *I*-statistic, **D)** Impressed Ware/Cardial combination vs. Linearbandkeramik, *D*-statistic. For **C** and **D**, gray bars represent Impressed Ware/Cardial vs. LBK and black bars reflect LBK vs. Impressed Ware/Cardial. Dashed vertical line indicates calculated overlap values between Maxent-produced ECNs (see Table 1).

ECN prediction and the distribution of the archaeological sites used to reconstruct it. One also should observe little or no overlap between the ECNs of neighboring cultural traditions in instances where each culture was adapted to a specific suite of environmental conditions and is characterized by a strong culture–environment relationship. Inversely, if the distribution of an archaeological culture reflected more the outcome of historical processes and had little or no relation to environmental factors, one would expect the distribution of known sites to occupy a minor proportion of the predicted potential niche. In such a situation, one would also expect ECNs for different, neighboring cultures to overlap broadly.

Our results indicate that the ICECN and LECN predictions match, to a relatively large degree, the distribution of their respective sites. Therefore, early European Neolithic settlement represented a dynamic process of range expansion up to the near complete occupation of each archaeological culture's potential niche. Furthermore, the two niche predictions overlap minimally (Fig. 1C, F). As detailed above, these results can be interpreted to indicate that environmental factors had an influential role in the distribution of these Neolithic cultures and their relationship to one another. Thus, for the Early Neolithic, we see cultural processes and the appearance of regional variants, both in terms of ceramic traditions and agricultural adaptations, occurring within relatively broad but distinct ecological niches. The reconstructed ECNs demonstrate that the technological innovations and social practices of the LBK and Impressed Ware/Cardial cultures were tailored to specific and mutually exclusive ecological niches. One might argue that such a finding is not entirely unexpected if one assumes that these archaeological cultures were associated with different environments from the onset. What is important and informative, however, is the absence of overlap between their respective ecological niche predictions. It is this lack of overlap that signals the presence of a strong culture–environment relationship and thus can be used to infer the important role of environmental factors on the cultural processes associated with the expansion of these particular Neolithic adaptations. The next logical question is whether this close correspondence between cultural adaptation and environment, along with marked ecological differentiation between neighboring archaeological cultures, are common among food producing adaptations in other regions and time periods.

One must keep in mind that with the Neolithic Transition in Europe, one is witnessing the replacement of hunter–gatherer adaptations with those of food-production, and this transition is characterized by the introduction of both domesticated plants and animals. It is reasonable to expect that these new practices would be conditioned by the different ecological settings into which the LBK and Impressed Ware/Cardial cultures expanded. Our results indicate that these early agricultural technologies were conditioned by environmental parameters, thus one should expect to see the use of different suites of cultigens between these two archaeological cultures. The dominant use of einkorn (both 1-grained and 2-grained varieties), a relatively low-yield cereal, by LBK groups exemplifies this expectation. Einkorn was well-suited to the relatively high precipitation characteristic of northern Europe during the Atlantic period because it remains standing after periods of high rainfall (Kreuz, 2007). LBK populations also cultivated free-threshing hexaploid wheat, as well as emmer and striate emmeroid wheats. The selection of cereals in the Mediterranean settings of the Impressed Ware/Cardial cultures differs from what is observed in northern Europe. For example, emmer and 1-grained einkorn wheat, along with free-threshing tetraploids are common in western Mediterranean regions. Additionally, pulse crops were more diverse in Mediterranean regions since many (e.g., lentils, chickpeas) were not well-suited to northern latitudes and were abandoned during settlement of those regions (Bakels, 2012). This

Mediterranean diversity fits with the more varied landscapes and environments of the region (Zapata et al., 2004) and is reflected by the ICECN's broader niche breadth (Table S2).

This is not to say, however, that historical contingencies played no role in the European Neolithic transition. Firstly, one notes that the reconstructed potential niches for the Impressed Ware and Cardial cultures, as well as the Impressed Ware/Cardial grouping, covers regions of Anatolia, the Near East, and northern Africa that were not occupied by these populations. Thus, these groups did not occupy their entire potential niche, indicating that cultural processes did influence their geographic distributions to some degree. The relatively rapid and coastal-oriented spread, and settlement of island regions, of the Impressed Ware/Cardial tradition across the Mediterranean was made possible by the use of seafaring technology (Zilhão, 2001). The creation of a maritime-based communication network was a key binding element of this cultural adaptation and likely explains the absence of settlements in inland regions of the Iberian Peninsula and northwestern Africa contrary to its predicted ECN. One also notes that the LBK culture is absent in some regions where its ECN is predicted present. This culture spread across Central and Northern Europe via major river valleys and did not possess maritime technologies, thereby preventing the diffusion of this cultural package into the British Isles, a process that would only take place during later phases of the Neolithic (Zvelebil and Rowley-Conwy, 1986; Bonsall et al., 2002; Davison et al., 2006). Cultural resistance of autochthonous hunter–gatherer populations to the adoption of agriculture (Raemaekers, 1997; Klassen, 2004), or a demographic shift in populations that practiced agriculture along the frontier zone of the Neolithic wave of advance (Hinz et al., 2012) could also have significantly stalled the spread of this adaptation into regions of Northern and Northwestern Europe. Both scenarios may have worked in concert to prevent the Linearbandkeramik adaptation from spreading into these northern areas.

Secondly, still with respect to cultural processes, both the LBK and the Impressed Ware/Cardial cultures used a reduced set of cultigens compared to the crop suite observed in earlier Neolithic contexts in Anatolia (Conolly et al., 2008), and it has been argued that these regional changes in plant assemblages cannot be explained solely with respect to ecological or climatic conditions (Colledge et al., 2005; Coward et al., 2008). An example along such lines is that while einkorn performed well in high rainfall conditions characteristic of the reconstructed LECN, it originated in hot and dry conditions of the Near East, yet it is absent in the analogous environmental conditions of the Mediterranean. This apparent absence, along with its presence in contrasting conditions of the LECN, does not lend itself to a purely adaptive explanation (Kreuz and Boenke, 2002; Kohler-Schneider, 2003; Fuller et al., 2012). Lastly, for the Linearbandkeramik, there is a decrease in cultigen diversity (Kreuz et al., 2005; Kreuz and Schäfer, 2011) as one moves from east to west within the LECN. Because this occurs within a single ecological niche, it suggests that cultural choices, and not simply environmental constraints, played a role in this reduction of crop diversity.

This study's results lead us to conclude that environmental factors influenced the cultural processes that characterize the Neolithization of Europe. This finding does not imply, however, that these adaptations were inflexible. It also does not suggest that these cultures were unable to adapt their subsistence systems to the new territories into which they moved, nor incorporate input from autochthonous hunter–gatherer populations. Our results show, though, that any adaptive changes that occurred along the way did not result in the creation of distinct local variants that significantly fragmented the homogenous nature of these adaptive systems, each operating within one of the two main ecological zones that existed in Europe during the early and middle Holocene.

Instead of representing a moment during which populations freed themselves from environmental constraints, our results indicate that early Neolithic adaptations in Europe reflect marked correspondence to ecological parameters. During the Neolithic Transition, cultures became reliant on specific suites of environmental conditions and many of the cultural processes at work in the evolution of these archaeological cultures appear to have operated within distinct and mutually exclusive ecological niches. Future research should focus on whether this pattern holds true for the other instances of Neolithization across the globe.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jas.2013.02.013>.

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