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# **APPROACHING ESTIMATIONS OF THE REALIZED ECO-CULTURAL NICHE: THE POTENTIAL OF ARCHAEOLOGICAL FAUNAL REMAINS FOR TAKING BIOTIC INTERACTIONS INTO CONSIDERATION**

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## **Introduction**

Since cultures operate within an environmental context, it is important to understand the range of environmental conditions they habitually, or could potentially, exploit—i.e., their ecological niche—when examining and interpreting the diversity and complexity of material cultural assemblages, as well as settlement and subsistence systems. In doing so, it becomes possible to better understand culture-environment relationships, begin disentangling the constellations of factors and processes at work behind them, and comprehend how they influenced documented cultural trajectories. When studying prehistoric cultures that lived during periods marked by rapid and dramatic climatic, and thus environmental, change (e.g., Marine Isotope Stages 4–2) and whose behaviors are only attested to by the archaeological record, our ability to reliably estimate the ecological niches that they potentially exploited—termed an ‘eco-cultural niche’—becomes even more critical.

A number of studies have examined archaeological data in the context of climatic variability to infer how shifting environmental frameworks may have influenced Paleolithic cultural adaptations and demography [1–11]. Despite the variety of approaches taken, no real consensus has emerged as to how best to evaluate and interpret adaptive changes documented in the archaeological record, and this is due in large part from a lack of focus on how culture-environment relationships might be intertwined with ecological niche dynamics.

Eco-cultural niche modeling (ECNM), an heuristic approach that integrates archaeological, chronological, and paleoclimatic data, via predictive algorithms developed within the ecological and biodiversity sciences, provides a means to estimate the ecological conditions exploited by culturally cohesive populations and evaluate their potential variability through time—i.e., evaluate potential ecological niche dynamics [12], [13]. By characterizing estimated eco-cultural niches and evaluating them against quantified material culture variability and inferred adaptive shifts, ECNM makes it possible to tease apart the various mechanisms (i.e., suites of factors and their processes of interaction) [14], be they cultural or ecological, implicated in past culture-environment relationships and understand how they influenced cultural trajectories.

Ecological niche modeling methods [15], from which ECNM is derived, are effective for estimating a species' or population's environmental requirements and associated potential geographic distribution, as well as anticipating likely geographic range shifts in the context of climate change. There remain uncertainties, however, concerning how the interplay between abiotic and biotic factors influence a species' ecological niche and potential distribution, and this despite a hierarchical view of these factors' relations. This view, termed the Eltonian Noise Hypothesis (ENH) [16] posits that inter-species interactions and resource distributions (i.e., biotic factors) are important at reduced spatial scales, whereas coarse-scale environmental (i.e., abiotic) factors are more influential on species distributions at broader scales and at these larger scales the influence of biotic factors is difficult to discern statistically [17]. A massive literature supports the general expectations of the ENH (i.e., distributions can be predicted rather well from abiotic conditions only), and some studies whose findings do not [18–20]; the latter are likely a result of biotic interactions that operate across relatively homogenous regions that are abiotically suitable for a species [15]. The degree to which ENH may hold true for human hunter-gatherer populations and estimations of the geographic distributions of their respective eco-cultural niches remains an open research question. This paper argues that archaeologists possess a unique class of data—the presence of faunal remains representing animal species hunted by human groups—that can and should be used to attempt to capture biotic interactions, thereby potentially improving the robustness and accuracy of eco-

cultural niche estimations and allowing the relevance of the ENH to past hunter-gatherer populations to be evaluated.

### **Placing Archaeological Cultures in an Environmental Context**

When the goal is to examine whether cultural shifts documented in the archaeological record may correlate to rapid-scale climate change, the ability to accurately determine with which climatic episode(s) a given archaeological culture was associated is critical. A little more than two decades ago paleoclimatologists discovered that the Late Pleistocene (ca. 120–11k cal BP) in the northern Hemisphere was characterized by abrupt and pronounced climatic fluctuations that occurred on millennial and sub-millennial time scales [21–23]. Temporal resolution of this Dansgaard-Oeschger (D-O) variability has continually increased [24], [25], however completely deciphering the complexity of these events and the mechanisms behind them remains problematic [26–30]. Detailed analyses of marine and terrestrial climatic archives, along with paleoclimatic simulation studies, have allowed detailed reconstructions of climatic and environmental conditions across Europe during the Last Glacial period [31–33]. Tephra signatures suggest that D-O events were largely synchronous across the North Atlantic and Europe [34], [35], although marine and terrestrial archives demonstrate that their regional expressions differed [31], [36–38]. As it concerns the late Middle Paleolithic and Upper Paleolithic, improvements in radiocarbon dating methods [39], [40], calibration curves [41], [42], in conjunction with Bayesian age-modeling methods and readily available software packages (e.g., OxCal, ChronoModel) [43–46] have allowed researchers to better constrain the chronological limits of archaeological cultures and thus more accurately correlate them with specific climatic events and corresponding environmental frameworks [12], [47].

Bayesian age-modeling methods are especially valuable for time periods approaching the chronological limits of  $^{14}\text{C}$  dating (i.e., ca. 40–50k cal BP) since their incorporation of stratigraphic or contextual priors can help reduce the statistical noise due to the relatively large errors of radiocarbon ages associated with late Middle Paleolithic and early Upper Paleolithic archaeological levels. One must be extremely cognizant of contextual and taphonomic issues, however, when compiling and evaluating

radiometric data to be analyzed with such methods [48]. Most Middle and Upper Paleolithic archaeological sites, and their associated cultural levels, have been subjected to some degree of post-depositional modification in addition to the fact that many cultural levels represent palimpsests of cultural activity or occupations. If such factors are not taken into account, then the validity of age model results may be compromised, so it is paramount that all chronological data be adequately evaluated and vetted prior to running and interpreting Bayesian age models.

### **Potential Cultural Responses to Environmental Change**

From an ecological perspective, when faced with rapid-scale climatic change and subsequent reorganization of environments, hunter-gatherers 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. In another scenario, environmental changes could negatively impact demography and social networks, thereby preventing the maintenance of cultural traditions [49]. This effect could lead to loss of certain technological and social adaptations and ultimately niche contraction such that the population would only make use of a subset of the environmental conditions that it used previously. Inversely, periods of climatic amelioration can result in a lowering of ecological risk levels such that a human population may, with the same or similar cultural adaptations, shrink their realized ecological niche by only focusing on certain subsets of the niche exploited previously. Such situations may be characterized by the regionalization of hunter-gatherer populations and cultural drift between macro regions—a situation hypothesized to have occurred between the Middle and Upper Solutrean in Western Europe [13].

It follows, thus, that the fact that culture allows for rapid adjustments and adaptations to changing climatic conditions and new environments must also be considered [50], [51]. This behavioral flexibility among hunter-gatherers may be recognized archaeologically by technological changes (bone and lithic toolkits), shifts in subsistence and settlement systems (mobility structure, geographic ranges, etc.), and shifts in social network structures (inferred from shared material culture styles). As a result, in some

instances, cultural adaptations allow for the potential expansion of the exploited ecological niche as a means of adjusting to abrupt restructuring of environments. An examination of archaeological cultures for early AMH populations in Europe found that the Early Aurignacian cultural technocomplex expanded its niche significantly during a period of marked climatic deterioration [12]. This study demonstrated that the tendency towards niche conservatism generally observed among plant and animal taxa [52–54] does not necessarily apply to human hunter-gatherer populations. Therefore, an important question is, what are the mechanisms (involving ecological or cultural factors, or both) involved in determining whether an archaeological culture conserves, contracts, or expands its exploited niche, with respect to a previous culture, in response to climate change? It is only by reliably and accurately estimating past ecological (eco-cultural) niches, and therefore by attempting to take into consideration all relevant factors that serve to influence an ecological niche (discussed below), that this question can be answered.

## **The Ecological Niche**

The *realized ecological niche*, represents the environments associated with the intersection ( $G_0$ ) of three broad factors: environmental conditions ( $A$ ), biotic interactions ( $B$ ), and geographic regions potentially accessible to the target population ( $M$ ), as depicted by the *BAM* diagram [15], [55] (Figure 1). With respect to human populations, one can substitute the term *eco-cultural niche*. The overlap between  $A$  and  $M$  is termed the *existing fundamental niche*; because biotic interactions [18], [56], [57] are difficult to quantify and incorporate into predictive architectures, many modeling efforts neglect such interactions and allow them either to represent noise in the system or to manifest via correlations with  $A$  or  $M$ . However, the Eltonian Noise Hypothesis [16] suggests that biotic interactions are only influential at finer spatial scales and will rarely be manifested in geographic effects.

When the ENH hold true, the effects of biotic interactions are essentially averaged out over broad geographic scales, thereby making  $A = B$  (Figure 1), and when  $M$  has been incorporated into niche modeling process, then resulting niche predictions could be considered to estimate the realized ecological niche of the population under study. On the other hand, in situations where the ENH does not hold true for

examined hunter-gatherer populations and only climatic variables (abiotic factors: A) are used to produce niche predictions, then those predictions may overestimate hunter-gatherer distributions by estimating the realized fundamental niche rather than the realized niche. This has important implications especially when trying to identify the factors that may have resulted in an archaeological culture having a smaller observed distribution than that predicted with the eco-cultural niche modeling approach—in other words, one must consider the possibility that a lack of agreement between observed and predicted distribution may be a product of the modeling process and the non-inclusion of biotic factors rather than cultural or adaptive factors. Thus, the validity of the ENH with respect to prehistoric hunter-gatherer populations and to estimations of their exploited ecological niches has not been evaluated. The archaeological community, however, is in a unique position to test its validity by incorporating archaeological faunal data into the niche estimation process.

### **Eco-Cultural Niche Modeling**

Before discussing the incorporation of faunal data into the niche estimation process, it is necessary to briefly outline how ECNM works. As pointed out above, this analytical approach, which examines archaeological data, in conjunction with chronological and paleoenvironmental data and via predictive algorithms, allows questions related to the diverse nature of culture-environment relationships to be addressed.

Once an archaeological culture, or a distinct regional variant of a larger technocomplex, has been placed in its correct chronological, and thus, paleoenvironmental framework, appropriate paleoenvironmental rasterized data layers (climatic and vegetation) are selected along with the geographic coordinates of archaeological sites assigned to the targeted with the culture being examined. With the above data as inputs, a number of statistical and mathematical predictive algorithms that work with presence-only data can be used to estimate past ecological niches and population distributions (e.g. envelope models, genetic algorithms, and maximum entropy methods). Because no single predictive algorithm will be the best performer under all circumstances, the ecological community agrees that a

combination of algorithms should be used [58–60] and the best single or few should be used in a given situation [61].

While each predictive algorithm functions differently, at a general level they identify environmental characteristics of known locations (geographic coordinates) of where the population being studied has been observed, create and test rules that define these parameters' relationships, and in effect estimate an ecological niche and its geographic distribution. ECNM thus reconstructs or estimates a past ecological niche exploited by an archaeological culture, or regional expression of that culture, and the geographic expression of this estimated niche.

### **Niche Estimations that Include Faunal Data**

With the approach described above, which relies on paleoclimatic and vegetation variables as environmental data inputs, it is not entirely evident whether the produced niche estimation represents the realized ecological niche ( $G_0$ ) or if the results depict the existing fundamental niche, which is represented by the intersection of  $A$  and  $M$  ( $A \cap M$ ) (Figure 1), thereby overestimating  $G_0$ . As pointed out earlier, if the ENH holds true for the archaeological human population under investigation, then  $G_0$  is in fact equivalent to  $A \cap M$ . If the ENH is not valid in a given situation, then it is important to find a means of capturing biotic interactions ( $B$ ) so that one can attempt to approach  $G_0$  with any produced niche estimations.

I propose that archaeological faunal remains represent an ideal class of data with which to conduct such evaluations of the ENH and to potentially improve our ability to accurately reconstruct the realized ecological niches of past hunter-gatherer populations. Past hunter-gatherer populations' subsistence strategies included the hunting of large herbivores and the evidence of interactions with these mammal species are attested to by the presence of their skeletal remains in archaeological cultural levels. While their subsistence regimes were not entirely dependent on the exploitation of large mammals, in most periods of the Paleolithic, large mammals represented a significant portion of their animal-based diet, and it has been demonstrated that in many instances their mobility and settlement systems were strongly influenced by the presence or seasonal presence of such game. Therefore, by taking large mammal faunal



remains into consideration in the niche estimation process, one can, at least in part, capture biotic interactions. In other words, the presence and distribution of prey species could have played a role in defining a hunter-gatherer population's realized eco-cultural niche. By including these data in the estimations of past eco-cultural niches, one can evaluate whether or not the use of detailed climatic data is indirectly capturing the presence of such species, thereby supporting the ENH, or whether the inclusion of faunal data can add additional details or resolution to estimated niches and should, therefore, be included in all eco-cultural niche estimation studies.

To do this, one can document the presence of particular large mammal species recovered from sites with cultural levels associated with the archaeological culture(s) being investigated. The geographic coordinates of these faunal being sites can be used to create ecological niche estimations for each species (e.g., reindeer, bison, horse, etc.). These faunal niche predictions will be in the form of rasterized geographic distributions where the potential presence and absence of each species is indicated, and these raster data can be included as individual environmental data layers that the predictive algorithms will take into consideration when estimating an eco-cultural niche. Thus, the resulting eco-cultural niche estimation will have a higher likelihood of capturing a hunter-gatherer population's realized ecological niche.

## **Conclusions**

The advantages of the approach outlined above are two-fold. First, it provides archaeologists with the ability to evaluate the validity of the Eltonian Noise Hypothesis with respect to past hunter-gatherer populations in situations where multiple, high-resolution environmental variables are used to estimate eco-cultural niches. Most eco-cultural niche studies to-date have focused on large geographic scales, and based on the substantial literature demonstrating that the ENH hold true for most biological taxa at such scales, it is natural to assume that the same holds true for human populations. Nevertheless, such an assumption must be validated, and if it does not hold true, it is important to understand why and if such situations have a common denominator. Secondly, since one of the principal goals of eco-cultural niche modeling analyses is to identify the mechanisms that operated behind past culture-environment relationships,

including the distributions of large mammal prey species in the eco-cultural niche estimation process should allow us to better capture the factors that potentially shaped the niche exploited by past hunter-gatherers and trace the influence of such factors through time and cultural trajectories.

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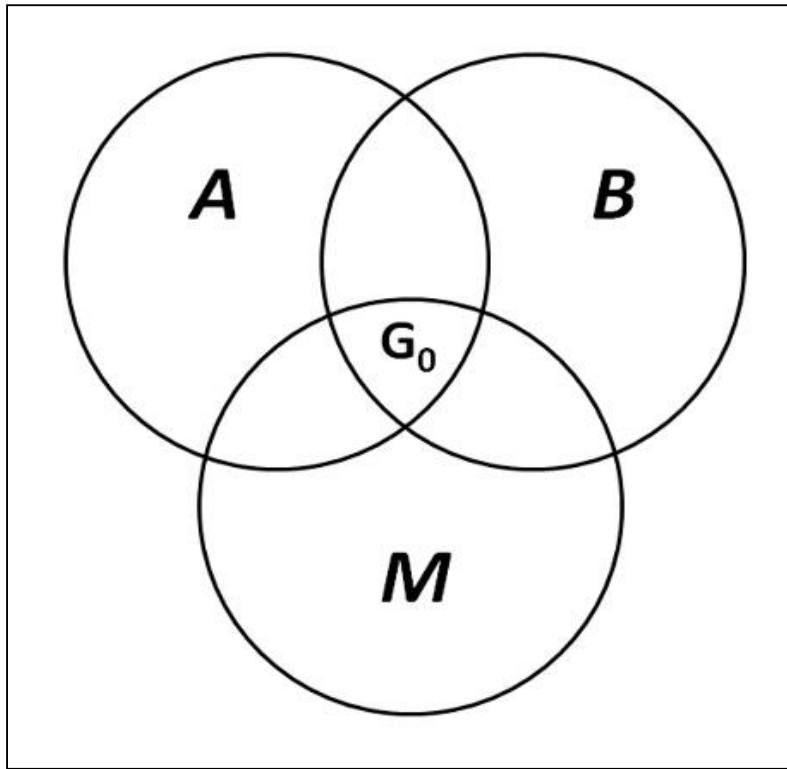


Figure 1: BAM scheme for understanding species' distributions. *A* – environmental conditions (the fundamental ecological niche); *B* – biotic interactions (the interaction niche); *M* – the geographic region(s) accessible to a species. The 'realized niche' is the intersection of environments associated with these three factors, indicated by  $G_0$ . Adapted from [55].