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THE APPLICATION OF ECOLOGICAL NICHE MODELING METHODS TO ARCHAEOLOGICAL DATA IN ORDER TO EXAMINE CULTURE-ENVIRONMENT RELATIONSHIPS AND CULTURAL TRAJECTORIES

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ABSTRACT

An objective of archaeology is to describe and understand past human behavior through examinations of cultural variability and cultural trajectories. Since cultures operate within an environmental context, one can argue that it is necessary that we be able to identify and characterize the ecological niches that past populations exploited and take these ecological parameters into consideration when interpreting material culture variability, especially across periods of climate change. Here, the approach termed Eco-Cultural Niche Modeling is briefly reviewed in order to describe how it can be used to explore culture-environment relationships and allow us to better understand the mechanisms that served to shape the cultural trajectories observed in the archaeological record.

Keywords: Eco-Cultural Niche Modeling; Culture-Environment Relationships

RÉSUMÉ

L'APPLICATION DES MÉTHODES DE MODÉLISATION DE NICHES ÉCOLOGIQUES AUX DONNÉES ARCHÉOLOGIQUES AFIN D'EXAMINER LES RELATIONS CULTURE-ENVIRONNEMENT ET LES TRAJECTOIRES CULTURELLES

Un des objectifs de l'archéologie est de décrire et comprendre les comportements humains du passé à travers l'examen de la variabilité culturelle et des trajectoires culturels. En sachant que chaque culture opère dans un contexte environnemental, on peut donc avancer l'argument qu'il est nécessaire de pouvoir identifier et caractériser les niches écologiques exploitées par les populations du passé et prendre ces dernières en considération dans nos interprétations de la variabilité de la culture matérielle, particulièrement au cours des périodes caractérisées par des changements climatiques. Dans ce papier, l'approche nommée « Eco-Cultural Niche Modeling » (la modélisation de niches éco-culturelles) est brièvement passée en revue afin de décrire et démontrer comment elle peut être utilisée pour explorer des relations culture-environnement et nous permettre de mieux comprendre les mécanismes qui ont influencé les trajectoires culturelles que nous observons dans le registre archéologique.

Mots-clés : Modélisation de Niches Eco-Culturelles ; Relations Culture-Environnement

1 – INTRODUCTION

One of the broad goals of archaeology is to describe and understand the behaviors of past populations by documenting archaeological cultural variability and tracing the cultural trajectories that we observe in the archaeological record. Since all cultures operate within an environmental context, it is important that we be able to identify and characterize the ecological niches that past populations exploited and take these ecological parameters into consideration when interpreting past cultural variability, especially across periods of climate change. In so doing, it becomes possible to better understand culture-environment relationships, disentangle the cultural and ecological mechanisms (constellations of factors and their processes of interaction) involved, and understand how they influenced cultural adaptations and documented cultural trajectories (d'Errico and Banks 2013).

This interest in culture-environment relationships is by no mean a recent phenomenon. Over the past several decades, anthropologists and archaeologists have employed a number of heuristic approaches to examine how cultures interact with their respective environments and how such contexts may have been implicated in the records of cultural adaptation and change that we study (Steward 1972; Hardesty 1972; Vayda and McCay 1975; Hardesty 1975; Binford 2001; White 2007). With respect to Paleolithic archaeology, a variety of studies have examined archaeological data in the context of climatic variability in order to infer how changing environmental frameworks may have influenced cultural adaptations and demography (Bocquet-Appel and Tuffreau 2009; Lemmen et al. 2011; Discamps 2014; Birks et al. 2015; Tallavaara et al. 2015; Pétillon et al. 2016). These approaches are of value and greatly aid our ability to identify the factors, be they cultural or environmental, that were potentially implicated in hunter-gather adaptations and cultural change through time. Examinations of culture-environment relationships that take the additional step of specifically considering past ecological niches and ecological niche dynamics are still relatively rare, however. By reconstructing and examining ecological contexts, as well as their variability over time, it becomes possible to explore potential links between cultural traits and ecological parameters thus aiding our ability to identify the long-term trends that played important roles in past processes of culture change (d'Errico and Banks 2013).

2 – ECO-CULTURAL NICHE MODELING

Over the past decade, a number of studies (Banks et al. 2009; Banks et al. 2011; Banks et al. 2013) have detailed an approach, termed Eco-Cultural Niche Modeling (ECNM), that can be used to explore the relationships between archaeological cultures and their paleoenvironments, as well as examine them across periods of climate change. ECNM integrates archaeological, chronological, and paleoclimatic data, via predictive algorithms developed within the ecological and biodiversity sciences, thereby providing a means to estimate the ecological conditions exploited by archaeological populations and evaluate the potential variability of these niches through time. Such an approach offers clear advantages over methods solely based on simple distributional data. For example, the archaeological distribution of past population may not completely or accurately reflect that population's actual range because simply drawing a boundary around known occurrences will, more likely than not, tend to be an underestimation of the real range. Extrapolations of ranges between and beyond known occurrences depend of subjective knowledge and often overestimate a population's distribution. Furthermore, plotting occurrences and comparing them to static backdrops of environmental information cannot accurately characterize the ecological niche exploited by a past human population.

With ECNM methods, one is able to establish quantitatively whether cultural variability and behavioral changes observed in the archaeological record have an ecological basis, or if such shifts and population distributions were more influenced by non-ecological factors. In the case of the latter, detailed analyses of material culture remains and subsequent inferences pertaining to modes of cultural transmission and forms of social organization needed to maintain cultural traditions can allow us to better explore the structure and evolution of past cultural systems.

In order to estimate a past ecological niche with available predictive algorithms or architectures, one must have a variety of detailed data. First, one needs the geographic coordinates of archaeological sites from which material culture assemblages diagnostic of a particular archaeological culture or technocomplex have been recovered. One also must have relatively high-resolution environmental data in the form of raster data layers. We have routinely chosen to use the outputs of high-resolution, regionally-zoomed paleoclimatic simulations produced by forcing either atmospheric or coupled ocean-atmosphere general circulation models with boundary conditions relevant to the time period or climatic event for which paleoclimatic conditions are being reconstructed. The outputs of these simulations can also be input into global vegetation models in order to estimate vegetation cover. Before being used to estimate ecological niches, these paleoenvironmental data must be critically evaluated against terrestrial and marine archives in order to determine whether they accurately reflect past conditions. For example, we found that while simulations of the LGM used in our investigations of the Solutrean archaeological culture were generally in close agreement with pollen data, they did slightly underestimate winter cooling over Western Europe (Banks et al. 2009, p.2859). These cooling underestimations are also evident in reconstructed ranges of past permafrost distributions and associated environmental conditions (Andrieux et al. 2016). Thus, while paleoclimatic simulations may approximate past conditions relatively well, such accuracy cannot simply be assumed and continued efforts are needed to further improve them. Finally, analyses of archaeological chronological data are needed so that archaeological cultures can be accurately placed in time and correlated with specific paleoclimatic events (Banks 2015), thereby allowing one to determine which paleoenvironmental data are the most appropriate for estimating a past niche.

Numerous methods exist for reconstructing ecological niches (for a review, see Peterson et al. 2011). At a general level, they identify the environmental characteristics of known locations of where the population of interest has been observed (i.e., occurrence data: geographic coordinates where the study population has been observed) and employ a variety of methods to define these parameters' relationships. These relationships are used to estimate an ecological niche in environmental space, which can then be projected geographically to determine its distribution. ECNM, thus, reconstructs or estimates a past ecological niche exploited by an archaeological culture, or distinct regional variant of that culture.

While a detailed description of how various methods function is beyond the scope of this paper, it is worth noting that important differences exist, especially with respect to the types of occurrence data needed. Some architectures, such as Bioclim (Nix 1986), work well with presence-only data. One potential limitation of Bioclim, though, is that it cannot extrapolate into combinations of environments not associated with the occurrence data. Other methods require absence data (i.e., locations that have been surveyed and at which the subject of study was not observed) and include Generalized Linear Models, Generalized Additive Models, as well as genetic algorithms (e.g. GARP; Stockwell and Peters 1999). The latter is based on the development of linear string rule sets that are allowed to evolve through an iterative process of training and testing. Because in many instances true absence data may not exist (e.g., in archaeology – issues related to sampling, site preservation and/or visibility), approaches exist with which pseudoabsences for the study area can be generated and used in the modeling process. Such practice expands the range of architectures that can be used to estimate an ecological niche when only presence data are available. Finally, there exist modeling methods, such as Maxent (Phillips et al. 2006), that use presence data in conjunction with background data (i.e., data pertaining to environmental variation across the study area). Maxent is based on the maximum entropy principle such that the generated probability distribution is closest to uniform and avoids assumptions not supported by the data. Its ability to extrapolate into combinations of environments unavailable during model training can be advantageous, but one challenge can be to avoid overfitting (i.e., excessive model complexity) due to its ability to fit extremely complicated response curves.

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 (Araújo and New 2007; Thuiller et al. 2009; Antunes 2015) and that the best single or few should be used in a given situation (Qiao et al. 2015), based on the types of questions being investigated and types of available data (Araújo and Peterson 2012). Once estimations are produced, there exist a variety of methods that serve to reduce excessive model complexity (Peterson et al. 2007), as well as those that allow niche estimations to be better characterized (Warren et al. 2010; Peterson et al. 2011).

Another important capacity of these architectures is that they can be used to examine niches between time periods thereby allowing one to determine whether or not successive populations exploited different niches. By comparing the material cultures of two or more successive archaeological cultures and by taking into account environmental frameworks within which they operated, one can evaluate whether cultural innovations reflect a response to environmental fluctuations. This allows us to significantly improve our ability to understand the complexities of culture-environment relationships through time.

With ecological niche modeling methods, what exactly is it that we are estimating? The concept of an ecological niche was formalized by Grinnel (1917) who defined it as the geographical expression of a species' climatic and habitat requirements. The Grinnellian niche considers the roles that unlinked, non-consumable environmental variables play in the distribution of a species.

Based on the Grinnellian concept, Hutchinson (1957) defined the fundamental niche, which represents the total range of environmental conditions within which a species or population can exist indefinitely. The factors and parameters that are implicated in the composition of an ecological niche, though, are quite diverse. It is for this reason that more recently, Soberón and Peterson (2005) proposed a conceptual framework that attempts to summarize these various factors. This framework, termed *BAM* (Fig. 1), is composed of three broad classes of factors. The first is '*A*', referred to as the 'existing fundamental niche' by Peterson et al. (2011), represents the intersection of Hutchinson's fundamental niche with the set of environments that are actually present on the landscape. Unit '*B*' represents variables that are dynamically linked to a species, which include food resources, as well as the influence of competitors and predators—factors that quantify how a species functions within its niche. Finally, '*M*' stands for the geographic areas that are accessible to a species or population via dispersal and that have been sampled such that occurrences could have been detected. It has been demonstrated that this factor is important to take into consideration when estimating niches (Barve et al. 2011). Since the factors associated with '*B*' are difficult to quantify and integrate into predictive modeling exercises, 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*. The Eltonian Noise Hypothesis (Soberón and Nakamura 2009) suggests that biotic interactions are only influential at finer spatial scales and will rarely be manifested in geographic effects. When this hypothesis holds 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 the niche modeling process, the resulting niche estimations could be considered, at a minimum, as estimating the intersection of the existing niche with regions that would have been accessible to the population under study. Research conducted by Kearney et al. (2010) suggests that correlative predictive methods are capable of effectively estimating the fundamental niche. A multitude of methods exist for characterizing estimated niches and determining under which circumstances and in which dimensions they underrepresent the fundamental niche (for a review, see Peterson et al. 2011).

3 – ECNM EXAMPLE—THE PROTO- AND EARLY AURIGNACIAN IN EUROPE

To provide an example of the application of this approach to the archaeological record, the results of a study conducted for the early part of the Upper Paleolithic are briefly presented here. The Aurignacian technocomplex is comprised of a succession of culturally distinct phases. Between its first two subdivisions, the Proto-Aurignacian and the Early Aurignacian, we see a number of shifts in technology and material culture. For example, we observe a change from single to separate reduction sequences for blade and bladelet production, along with other changes in stone tool typology and technology, the appearance of split-based antler points, as well as changes in symbolic material culture. Bayesian modeling of archaeologically reliable ^{14}C determinations indicates that the cultural changes between the two phases are coincident with abrupt and marked climatic changes between Greenland Interstadials 10/9 and Heinrich Stadial 4. Following this chronological analysis, ECNM was used to quantitatively evaluate whether these material culture shifts are correlated with a significant shift between the niches exploited by these two broad populations (Banks et al., 2013). In other words, did these cultural changes have, at least in part, an ecological basis?

Results indicate that the transition between the Proto-Aurignacian and the Early Aurignacian was associated with an expansion of the ecological niche (Fig. 2). This was determined by first estimating the niches of the Proto-Aurignacian and also the Early Aurignacian phases, with the majority of variability within each of the two niches being primarily explained by temperature variables. Then, the Proto-Aurignacian niche was projected onto conditions associated with the Early Aurignacian (i.e., Heinrich Stadial 4), and the ability of this projected niche to predict Early Aurignacian occurrences was statistically evaluated. Results indicate that the observed failure of the projected Proto-Aurignacian niche to predict a large number of Early Aurignacian sites is significantly greater than one would expect by chance, thus indicating that the ecological niche expanded between these two phases. 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 Heinrich Stadial 4. This exemplifies a situation in which cultural flexibility was used by hunter-gatherer populations to quickly adapt to a rapid-scale and severe climatic fluctuation. Thus, the tendency observed among most animal species to conserve an ecological niche across relatively short time spans characterized by environmental variability (Peterson, 2011) does not appear to hold true for human hunter-gatherer populations in some situations. An issue that warrants further research is if and when the use of cultural solutions to expand the exploited ecological niche occurred with other hunter-gatherer cultures, as well as with other hominins (e.g., Neanderthals).

4 - PERSPECTIVES

In attempts to understand culture-environmental relationships, regional cultural trajectories, and ultimately the mechanisms at work behind the variability that we observe in past material cultural records and their changes through time, ECNM represents an approach that can be extremely informative, especially when combined with other more traditional approaches (e.g., reconstructing technological chaînes opératoires, faunal studies, site function and activity analyses, etc.). With this approach, and resultant comparisons of regional cultural trajectories, we can begin to discern whether adaptive shifts and material culture changes were undertaken so that populations could continue to exploit the same niches in the face of environmental change (niche conservatism), or if such cultural changes were more routinely associated with niche shifts—patterns which are difficult to ascertain when environmental and related data are employed only as static, comparative backdrops. Furthermore, with this approach, one can identify instances in which cultural changes have no ecological basis. In essence, the integration of ECNM into research strategies aimed at better understanding the dynamics of culture change, and the implicated mechanisms, allows one to interrogate, rather than simply document, the archaeological record.

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REFERENCES[WEB1]

ANDRIEUX, E., BERTRAN, P., & SAITO, K., 2016 - Spatial analysis of the French Pleistocene permafrost by a GIS database, *Permafrost and Periglacial Processes*, **27**(1), 17–30.

ANTUNES, N., 2015 - Application d'algorithmes prédictifs à l'identification de niches écoculturelles des populations du passé: approche ethno-archéologique. Ph.D. dissertation, University of Bordeaux, Talence.

ARAÚJO, M. B., & NEW, M., 2007 - Ensemble forecasting of species distributions. *Trends in Ecology & Evolution*, **22** (1), 42–7.

ARAÚJO, M. B., & PETERSON, A. T., 2012 - Uses and misuses of bioclimatic envelope modeling, *Ecology*, **93**(7), 1527–39.

BANKS, W. E., ZILHÃO, 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** (12), 2853–67.

BANKS, W. E., AUBRY, T., D'ERRICO, F., ZILHÃO, 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** (3), 359–74.

BANKS, W. E., D'ERRICO, F., & ZILHÃO, J., 2013 - Human-climate interaction during the Early Upper Paleolithic: testing the hypothesis of an adaptive shift between the Proto-Aurignacian and the Early Aurignacian, *Journal of Human Evolution*. **64** (1), 39–55.

BANKS, W. E., 2015 - Constructing chronologies for the late Middle Paleolithic and Upper Paleolithic: limitations and means to overcome them. *World Archaeology*, **47** (4), 585–600.

BARVE, N., BARVE, V., JIMÉNEZ-VALVERDE, A., LIRA-NORIEGA, A., MAHER, S. P., PETERSON, A. T., SOBERÓN, J., & VILLALOBOS, F., 2011 - The crucial role of the accessible area in ecological niche modeling and species distribution modeling. *Ecological Modelling*, **222** (11), 1810–9.

BINFORD, L. R., 2001 - *Constructing Frames of Reference: An Analytical Method for Archaeological Theory Building Using Ethnographic and Environmental Data Sets*. University of California Press, Berkeley, 563 p.

BIRKS, H. H., GELORINI, V., ROBINSON, E., & HOEK, W. Z., 2015 - Impacts of palaeoclimate change 60 000–8000 years ago on humans and their environments in Europe: Integrating palaeoenvironmental and archaeological data. *Quaternary International*, **378**, 4–13.

BOCQUET-APPEL, J.-P., & TUFFREAU, A., 2009 - Technological Responses of Neanderthals to Macroclimatic Variations (240,000–40,000 BP). *Human Biology*, **81** (2), 287–307.

DISCAMPS, E., 2014 - Ungulate biomass fluctuations endured by Middle and Early Upper Paleolithic societies (SW France, MIS 5-3): The contributions of modern analogs and cave hyena paleodemography. *Quaternary International*, **337**, 64–79.

D'ERRICO, F., & BANKS, W. E., 2013 - Identifying Mechanisms behind Middle Paleolithic and Middle Stone Age Cultural Trajectories. *Current Anthropology*, **54** (S8), S371–S387.

GRINNELL, J., 1917 - The Niche-Relationships of the California Thrasher. *The Auk*, **34** (4), 427–33.

HARDESTY, D. L., 1972 - The Human Ecological Niche. *American Anthropologist*, **74** (3), 458–66.

HARDESTY, D. L., 1975 - The niche concept: Suggestions for its use in human ecology. *Human Ecology*, **3** (2), 71–85.

HUTCHINSON, G. E., 1957 - Concluding Remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, **22**, 415–27.

KEARNEY, M. R., WINTLE, B. A., & PORTER, W. P., 2010 - Correlative and mechanistic models of species distribution provide congruent forecasts under climate change, *Conservation Letters*, **3** (3), 203–13.

LEMMEN, C., GRONENBORN, D., & WIRTZ, K. W., 2011 - A simulation of the Neolithic transition in Western Eurasia, *Journal of Archaeological Science*, **38** (12), 3459–70.

NIX, H. A., 1986 - A biogeographic analysis of Australian elapid snakes, In *Atlas of Elapid Snakes of Australia* (ed. R. Longmore), 4–15, Australian Flora and Fauna Series No. 7, Australian Government Publishing Service, Canberra.

PETERSON, A. T., 2011 – Ecological niche conservatism: a time-structured review of evidence. *Journal of Biogeography*, **38** (5), 817–827.

PETERSON, A. T., PAPEŞ, M., & EATON, M., 2007 - Transferability and model evaluation in ecological niche modeling: a comparison of GARP and Maxent. *Ecography*, **30** (4), 550–60.

PETERSON, A. T., SOBERÓN, J., PEARSON, R. G., ANDERSON, R. P., MARTINEZ-MEYER, E., NAKAMURA, M., & ARAÚJO, M. B., 2011, *Ecological Niches and Geographic Distributions*. Monographs in Populational Biology 49, Princeton University Press, Princeton, New Jersey, 314 p.

PÉTILLON, J.-M., LAROULANDIE, V., COSTAMAGNO, S., & LANGLAIS, M., 2016 - Testing environmental determinants in the cultural evolution of hunter-gatherers: a three-year multidisciplinary project on the occupation of the western Aquitaine basin during the Middle and Upper Magdalenian (19–14 kyr cal BP). *Quaternary International*, **414**, 1–8.

PHILLIPS, S. J., ANDERSON, R. P., & SCHAPIRE, R. E., 2006 - Maximum entropy modeling of species geographic distributions, *Ecological Modelling*, **190** (3–4), 231–59.

QIAO, H., SOBERÓN, J., & PETERSON, A. T., 2015 - No silver bullets in correlative ecological niche modelling: insights from testing among many potential algorithms for niche estimation. *Methods in Ecology and Evolution*, **6** (10), 1126–36.

SOBERÓN, J., & PETERSON, A. T., 2005 - Interpretation of Models of Fundamental Ecological Niches and Species' Distributional Areas. *Biodiversity Informatics*, **2**, 1–10.

SOBERÓN, J., & NAKAMURA, M., 2009 - Niches and distributional areas: concepts, methods, and assumptions. *Proceedings of the National Academy of Sciences*, **106** (Supplement 2), 19644–19650.

STEWARD, J. H., 1972 - *Theory of Culture Change: The Methodology of Multilinear Evolution*. University of Illinois Press, Champaign, 260 p.

STOCKWELL, D., & PETERS, D., 1999 - The GARP modelling system: problems and solutions to automated spatial prediction, *International Journal of Geographic Information Systems*, **13** (2), 143–58.

TALLAVAARA, M., LUOTO, M., KORHONEN, N., JÄRVINEN, H., & SEPPÄ, H., 2015 - Human population dynamics in Europe over the Last Glacial Maximum. *Proceedings of the National Academy of Sciences*, **112** (27), 8232–7.

THUILLER, W., LAFOURCADE, B., ENGLER, R., & ARAÚJO, M. B., 2009 - BIOMOD – a platform for ensemble forecasting of species distributions. *Ecography*, **32** (3), 369–73.

VAYDA, A. P., & MCCAY, B. J., 1975 - New Directions in Ecology and Ecological Anthropology, *Annual Review of Anthropology*, **4** (1), 293–306.

WARREN, D. L., GLOR, R. E., & TURELLI, M., 2010 - ENMTools: a toolbox for comparative studies of environmental niche models. *Ecography*, **33**, 607–611.

WHITE, L. A., 2007, *The Evolution of Culture: The Development of Civilization to the Fall of Rome*, Routledge, Walnut Creek, California, 400 p.

Figure Captions

Fig. 1: *BAM* scheme of the factors that determine a species' distribution.

A – environmental conditions (the existing fundamental ecological niche); *B* – biotic interactions (the interaction niche); *M* – the geographic region(s) accessible to a species. The 'realized ecological niche' represents the environments described by the overlap of these three factors (G_0). Adapted from Soberón and Peterson (2005).

Fig. 1 : Schéma de *BAM* des facteurs qui déterminent la distribution d'une espèce. *A* – conditions environnementales (la niche écologique fondamentale existante) ; *B* – interactions biotiques (la niche d'interaction) ; *M* – les régions géographiques accessibles à une espèce. La niche écologique réalisée représente les environnements décrits par la superposition de ces trois facteurs (G_0). Après Soberón et Peterson (2005).

Fig. 2: Proto-Aurignacian and Early Aurignacian eco-cultural niche estimations made with the predictive architecture Maxent. (A) Proto-Aurignacian niche estimation for the period covering Greenland Interstadials 10 and 9, (B) Early Aurignacian niche estimation for the period of Heinrich Stadial 4, (C) Proto-Aurignacian niche projected onto Heinrich Stadial 4 climatic conditions and compared to sites attributed to the Early Aurignacian. The failure of this projected niche to predict a number of Early Aurignacian sites is statistically significant. For these predictions, colors range from grey to pink to red, or low, medium, and high probability, respectively.

Fig. 2 : Estimations des niches éco-culturelles Protoaurignacienne et Aurignacienne ancien faites avec l'algorithme prédictif Maxent. (A) L'estimation de la niche Protoaurignacienne pour la période des interstadiaires 10 et 9, (B) La niche de l'Aurignacien ancien au cours du stadiaire Heinrich 4, (C) La niche Protoaurignacienne projetée sur les conditions de Heinrich 4 et comparée aux sites de l'Aurignacien ancien. L'échec de cette niche projetée à prédire tous les sites Aurignacien ancien est statistiquement significatif. Concernant ces estimations de niche, les couleurs gris, rose, et rouge représentent des taux de probabilité faible, moyen, et haut, respectivement, de présence de la niche éco-culturelle.