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Paleodistribution modeling in archaeology and paleoanthropology

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ABSTRACT

Species distribution modeling (SDM) is a methodology that has been widely used in the past two decades for developing quantitative, empirical, predictive models of species–environment relationships. SDM methods could be more broadly applied than they currently are to address research questions in archaeology and paleoanthropology. Specifically, SDM can be used to hindcast paleodistributions of species and ecological communities (paleo-SDM) for time periods and locations of prehistoric human occupation. Paleo-SDM may be a powerful tool for understanding human prehistory if used to hindcast the distributions of plants, animals and ecological communities that were key resources for prehistoric humans and to use this information to reconstruct the resource landscapes (paleoscapes) of prehistoric people. Components of the resource paleoscape include species (game animals, food plants), habitats, and geologic features and landforms associated with stone materials for tools, pigments, and so forth. We first review recent advances in SDM as it has been used to hindcast paleodistributions of plants and animals in the field of paleobiology. We then compare the paleo-SDM approach to paleoenvironmental reconstructions modeled from zooarchaeological and archaeobotanical records, widely used in archaeology and paleoanthropology. Next, we describe the less well developed but promising approach of using paleo-SDM methods to reconstruct resource paleoscapes. We argue that paleo-SDM offers an explicitly deductive strategy that generates spatial predictions grounded in strong theoretical understandings of the relation between species, habitat distributions and environment. Because of their limited sampling of space and time, archaeobiological records may be better suited for paleo-SDM validation than directly for paleoenvironmental reconstruction. We conclude by discussing the data requirements, limitations and potential for using predictive modeling to reconstruct resource paleoscapes. There is a need for improved paleoclimate models, improved paleoclimate proxy and species paleodistribution data for model validation, attention to scale issues, and rigorous modeling methods including mechanistic models.

1. Introduction

Understanding how prehistoric human populations used natural resources is a primary goal of archaeology and paleoanthropology. Ethnographic and archaeological observations have shown that hunter–gatherer economies were closely tied to the distributions of animal and plant resources that were themselves subject to dramatic changes in distribution in the past due to environmental changes. In both archaeology and paleoanthropology, information about the link between present-day species distributions and environment has been used in a number of ways. Plant pollen, charcoal, phytoliths, faunal remains, and isotopes that are recovered from archaeological sites and their surroundings, for example, have been widely used to reconstruct the environmental conditions at the time of their deposition based on the modern environmental patterns that are associated with those species (climate, soil, habitat type); here we refer to these kinds of analyses as "paleoenvironmental reconstruction." Other types of models incorporate

Abbreviations: AMH, Anatomically Modern Humans; AOGCM, Atmosphere–Ocean General Circulation Models; CA, Coexistence Approach; ECNM, Eco-Cultural Niche Modeling; GIS, Geographic Information System; LGM, Last Glacial Maximum; PMIP, Paleoclimate Modeling Intercomparison Project; SDM, Species Distribution Modeling.

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fundamental ideas of human behavior that are based on ethnographic observations and archaeological inferences. These models, loosely aggregated into the category of "archaeological predictive modeling," frequently use the present-day distribution of raw materials, resources, and habitat types to predict the locations of archaeological sites, the occurrence of specific raw materials, and also the ranges of human behaviors at sites (e.g., hunting camps, residential sites).

Archaeological predictive models have already been widely discussed and reviewed in the literature (McCoy and Ladefoged, 2009; Kvamme, 2012; Verhagen and Whitley, 2012). In archaeological predictive modeling, as well as in the field of species distribution modeling (Franklin, 2010a), the distribution of phenomena is predicted based on spatial relationships with other variables, and similar statistical frameworks and methods of spatial prediction can be used in both fields. Species distribution modeling (SDM) associates the distribution of taxa, ecosystem types or other biotic response variables with measurements of environmental drivers posited to have causal relationships to species occurrence and abundance (Franklin, 1995; Elith and Leathwick, 2009).

Establishing the distribution-environment link in both paleoenvironmental reconstruction and in distribution modeling requires sufficient species locality and relevant environment data at appropriate spatial and temporal scales, geospatial data analysis tools, and robust statistical modeling frameworks (Franklin, 2010a). There has been rapid innovation in recent decades – in geographic information systems (GIS), geospatial databases, and open source software (Skidmore et al., 2011) – that has supported the expansion of spatial prediction and distribution modeling across a number of fields. Paleoenvironmental reconstruction is widely used in contemporary archaeology and paleoanthropology, while SDM methods are used increasingly to predict future species distributions in response to anthropogenic climate change (Pearson and Dawson, 2003; Hijmans and Graham, 2006). SDM methodology, however, has been underutilized in archaeology and paleoanthropology with the exception of its application to predict site locations (e.g., Ford et al., 2009; Graves, 2011; McEwan, 2012).

Here we propose that SDM could be more widely applied to address research questions in archaeology and paleoanthropology. Specifically, SDM can be used to hindcast paleodistributions of species and ecological communities (e.g., Kozak et al., 2008), but has been used more extensively for forecasting to future climate states. SDM offers rigorous multivariate methods for associating response variables with predictors but its use for hindcasting paleodistributions relies heavily on improved and validated paleoclimate models for spatial prediction and paleodistribution data for evaluation.

We first review species distribution modeling as it has been used to hindcast paleodistributions of plants and animals (paleo-SDM), with an emphasis on studies that are most relevant to archaeology and paleoanthropology (section 2). Then we compare the paleo-SDM approach to paleoenvironmental reconstructions from zooarchaeological and archaeobotanical records (section 3). Paleoenvironmental reconstruction is a broad topic with an extensive literature in archaeology, paleoanthropology, paleobiology and paleoclimatology. Here, we focus on how SDM methods may improve or inform these reconstructions, and especially on how, if the other data requirements for paleo-SDM are satisfied, archaeobiological records may be more useful for paleo-SDM validation than for inductively-driven paleoenvironmental reconstruction. Next, we describe the less well-developed but promising approach of using paleo-SDM methods to reconstruct resource paleoscapes (Section 4). Our discussion emphasizes the data requirements, limitations and potential for using paleo-SDM to reconstruct paleoenvironments in archaeology and paleoanthropology (Section 5). We argue that paleo-SDM may be a powerful tool for understanding human prehistory if used to reconstruct resource-scapes for time periods corresponding to prehistoric human occupation. Key strengths are that it is grounded in ecological theory, generates testable hypotheses, and projects resource-scapes continuously across landscapes, while standard paleoenvironmental reconstruction only provides point-based reconstructions (Section 6) and projection of those point-based reconstructions across landscapes has no formal theoretical justification.

2. Paleodistributions of species: plants, animals, habitats

2.1. Species distribution modeling

Species distribution modeling, also called environmental or climatic niche modeling, is a methodology for developing quantitative, empirical, predictive models of species–environment relationships (Fig. 1). These models are typically estimated using observations of species at locations as the dependent variable, and explanatory variables drawn from maps of the environmental predictors; environmental maps are also required for spatial prediction (Elith and Franklin, 2013). SDM is therefore feasible and informative when species location data are sparse (but comprise an adequate sample for modeling), environmental maps are available, and mapped environmental variables have a strong proximal relationship with species distributions. Ecological niche theory describes how species respond to the multidimensional environmental and resource gradients that define the "niche hypervolume" – the conditions that allow a population to persist (Hutchinson, 1957). Niche theory provides a strong framework for selecting predictors, fitting response curves and choosing appropriate statistical models in species distribution modeling (Austin, 2002; Guisan and Thuiller, 2005; Austin, 2007). Because of the multidimensional nature of the niche (Hutchinson, 1959), a modern multiple regression framework is generally used for statistical modeling (Hastie et al., 2009).

Spatially referenced data on species occurrences available from biological surveys often include measures of species abundance or presence and absence (when species inventories for a taxonomic group are taken for a location), and sometimes are derived from a well-designed probability-based sample of environmental space (e.g., forestry inventories). Presence–absence information is required for discriminative statistical models (e.g., logistic regression) and for estimating species' prevalence on the landscape. For the majority of taxa and regions of the world, however, the only available species data comprise small numbers of records from opportunistic observations or collections (natural history collections) and therefore consist of "presence only" data whose spatial sampling biases are unknown. Because information about species distributions is critical for biodiversity assessment, there has been a concerted effort to develop SDM methods that are robust to small, biased samples and presence-only data (Anderson et al., 2006; Phillips and Dudík, 2008; Phillips et al., 2009), and to understand the effects of sample size, spatial sampling bias, modeling method and model selection on SDM validity (Elith et al., 2006; Hernandez et al., 2006; Wisz et al., 2008; Austin and Van Niel, 2011).

Informative species distribution models that are useful for prediction must be based on the biotic and abiotic factors that limit species distributions (Austin, 2002). Key abiotic factors are the primary environmental regimes of heat, moisture, light and nutrients (Mackey and Lindenmayer, 2001). These can be challenging to map, and often surrogate predictors or proxies are used in SDM. Proxies include attributes of climate, topography, geology and soil – environmental variables that are more easily mapped than, and