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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 (paleoscaping) 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 paleoscaping. 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 paleoscaping. 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.

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## 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 paleo-environmental 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. Paleo-environmental 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 paleo-climate 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 paleo-environmental reconstructions from zooarchaeological and archaeobotanical records (section 3). Paleo-environmental 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 paleo-environmental 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 paleo-environmental reconstruction only provides point-based reconstructions (Section 6) and projection of those point-based reconstructions across landscapes has no formal theoretical justification.

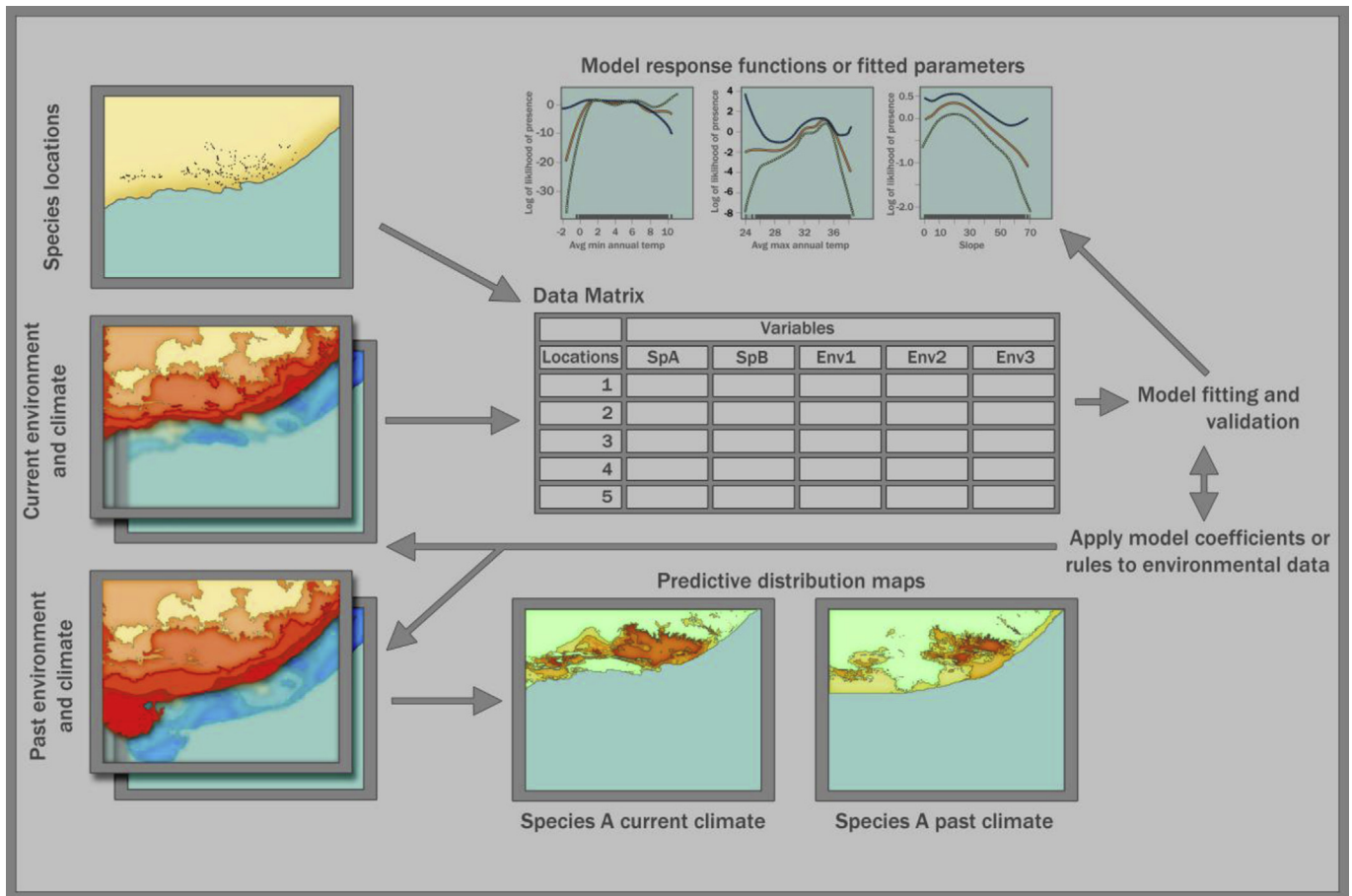
## 2. Paleodistributions of species: plants, animals, habitats

### 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



**Fig. 1.** Diagram outlining data and procedures used in species distribution modeling, calibrated from contemporary species locations and environmental (including climate) data and applied to other climate states (Past environment and climate), to predict the current and paleodistributions (Predictive distribution maps) for a hypothetical species (A) and geographical area.

that give rise to the distributions of, the primary environmental regimes (Franklin, 2010a). Care must be taken, however, when using proxies such as elevation whose relationship to the primary environmental regimes may vary over space and time – Austin (2002) calls these “indirect gradients.”

Species distributions are also shaped by exogenous (competition, facilitation) and endogenous (dispersal) biotic interactions and processes (Clark, 1998; Wisz et al., 2013). Biotic factors such as the location of a competitor, prey species, or vegetation community can be included (Franklin, 2010a) and dispersal can be accounted for (Franklin, 2010b) within the SDM framework; it is an acknowledged limitation, however, that correlative SDMs alone cannot fully represent spatially explicit processes or biotic interactions with feedbacks that affect species distributions (Guisan and Thuiller, 2005).

Extensive methodological research has resulted in a good understanding of the strengths and limitations of SDM when used for spatial prediction or “interpolation” – filling in the gaps in maps of present-day species distributions. However, in the face of rapid environmental change, SDMs are increasingly being used to extrapolate into the future to predict the effect of 21st century climate change on species distributions (Franklin, 2010b). Using SDMs in this way has been criticized because it requires applying a statistical model to conditions beyond the range used for calibration – to non-analog conditions – and also because it ignores dynamic ecological processes (population dynamics, dispersal, biotic interactions) that affect species range changes (Pearson and

Dawson, 2003; Hampe, 2004; Araújo and Luoto, 2007; Wiens et al., 2009). Further, SDMs driven by climate models are subject to a number of sources of uncertainty (Thuiller, 2004; Buisson et al., 2010; Synes and Osborne, 2011). These same issues affect SDM when it is used for hindcasting distributions based on modeled paleoclimatic conditions, but the advantage when hindcasting is the model can be validated with empirical observations.

Often, when SDM is used to forecast the effects of 21st century anthropogenic climate change on species distributions, only climate variables are used as predictors although it is well known that other environmental factors constrain species distributions. If predictors such as geology, landform, topography or soils are included, they are assumed to be static (Fig. 1); this may be a reasonable assumption for 21st century forecasting but not in all cases when hindcasting to the distant past. Elevation in particular should not be used for hindcasting species paleodistributions; while elevation is strongly correlated with precipitation and temperature regimes and therefore species distributions within a particular region and time period, the relationship between elevation and the primary environmental regimes is not stable over time as the climate state changes (Franklin, 1995).

## 2.2. Paleo-species distribution modeling

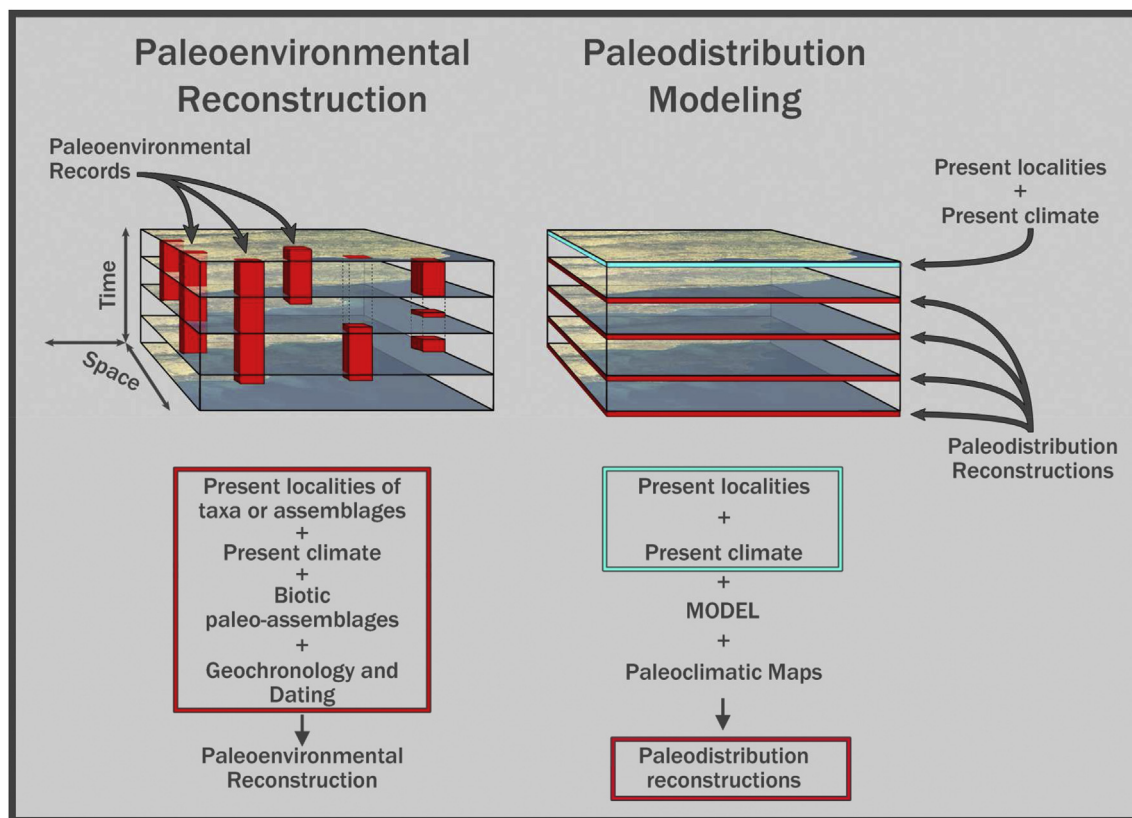
Species distribution models can be developed based on the relationship between contemporary species distributions and climate (and other environmental predictors) and then applied to

modeled or interpolated paleoclimate data in order to hindcast species distributions to previous time periods, e.g., paleo-SDM (Figs. 1 and 2). In a rapidly growing literature, paleo-SDM has been used to answer questions in paleobiology that require information about the distribution of organisms in the past, e.g., historical biogeography and phylogeography (Nogués-Bravo, 2009; Svenning et al., 2011; Varela et al., 2011; Gavin et al., 2014). These predictions have, in some cases, been validated against paleodistribution data from fossils, pollen, etc. (Martinez-Meyer et al., 2004; Waltari and Guralnick, 2009; McGuire and Davis, 2013).

Fossil pollen records from sediment cores are particularly rich datasets for reconstructing plant species distributions when they are aggregated into large regional databases, as they have been for northern hemisphere temperate regions ([www.neotomadb.org](http://www.neotomadb.org); <http://www.europeanpollendatabase.net>). For example, Pearman et al. (2008) hindcast European tree species distributions over the last 6000 years and validated them using pollen records. Pearman et al. also developed SDMs using pollen records and modeled paleoclimate and forecast to the present. Discrepancies between these two sets of models highlighted species for which dispersal limitations best explains contemporary absence from climatically suitable habitat. A similar effort for North American trees showed SDMs calibrated from contemporary distributions and climate to be effective at overcoming the challenge of non-analog climates and reconstructing Late Pleistocene tree distributions (validated against pollen records) – a space-for-time substitution (Blois et al., 2013b). These studies found that summer temperature (and climate variables in general) was an important predictor of the turnover (dissimilarity) in tree species assemblages over time and space since the Last Glacial Maximum (Blois et al., 2013a).

The studies by Blois et al. (2013a,b) used community distribution modeling – both the response (all species in the community) and predictors (environment, climate) were multivariate – an approach known as “assemble and predict together” (Ferrier and Guisan, 2006). Community distribution modeling methods (Clark et al., 2014; Ferrier et al., 2007; Ohmann et al., 2011; Ovaskainen et al., 2010; Ovaskainen and Soininen, 2011) have rarely been used in paleodistribution modeling to date. Another method of community distribution modeling is to treat a vegetation type (plant community, biome) as the unit of interest (Franklin, 1995). This approach to community distribution modeling is described as “assemble first, predict later” (Ferrier and Guisan, 2006). For example, the distributions of vegetation types including Australian wet tropical forests (Hilbert and Ostendorf, 2001; VanDerWal et al., 2009), Brazilian Atlantic Forest (Carnaval and Moritz, 2008) and Albany subtropical thicket (Potts et al., 2013b) have been hindcast using paleoclimate data. The third approach to community modeling, stacking individual species distribution models, has been used to estimate species richness (Guisan and Rahbek, 2011) and forecast species turnover (Thuiller, 2004), but does not seem to be widely used in hindcasting paleodistributions of communities.

While the literature on species distribution modeling in paleobiology has recently been reviewed (Svenning et al., 2011; Varela et al., 2011), only a few studies clearly illustrate the link between paleo-SDM, paleoclimate modeling, and archaeology or paleoanthropology. Banks et al. (2008a) modeled the Last Glacial Maximum (LGM) distribution of caribou and red deer in Europe using paleoclimate predicted from regional climate models and paleodistribution data obtained from archaeological sites. They wished to determine whether the climatic niche of these species had changed



**Fig. 2.** In paleoenvironmental reconstruction, present-day localities of taxa or species assemblages are associated with parameters of the current climate (temperature, precipitation) or other environmental factors such as habitat, and compared with a dated paleoassemblage of taxa to establish a paleoclimate estimate for the site. In paleodistribution modeling, present-day species localities or other geolocated biotic variables are associated with mapped environmental predictors (including interpolated or modeled climate) to develop a statistical model that can be applied to paleoclimate maps (see Fig. 1) in order to hindcast paleodistributions as different time periods.

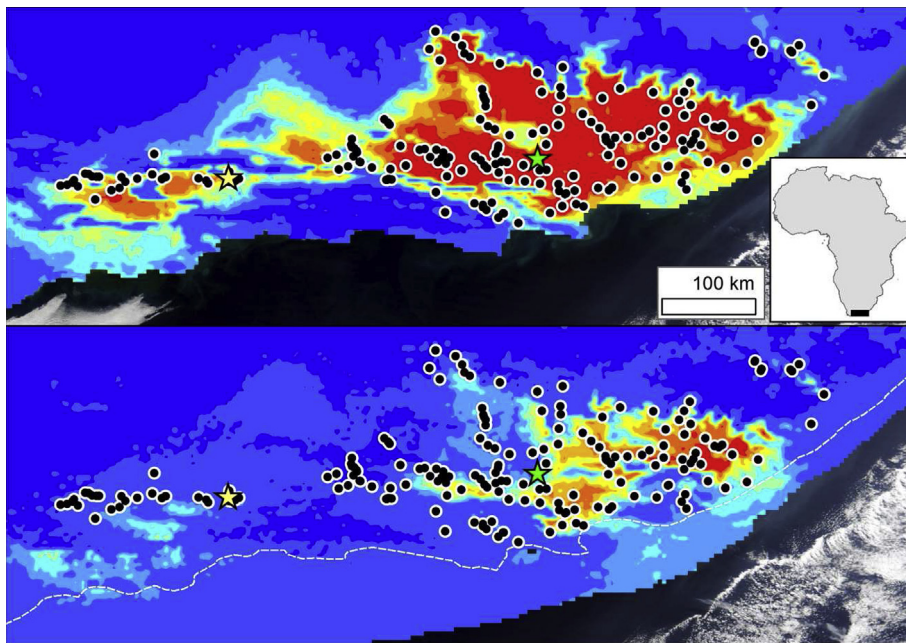
over time. They mentioned that their modeled paleodistributions might be useful from an archaeological perspective because these were prey species for prehistoric hunter–gatherers.

Hufford et al. (2012) used the modern distributions of the closest wild relatives of domesticated maize to develop a climate-driven distribution model (using the MaxEnt modeling software), and applied that model to paleoclimate reconstructions for Last Interglacial and LGM conditions. Predictions were compared to archaeological evidence of ancient maize. Their results supported previous findings that domesticated maize spread rapidly in the New World; they found little change in the distributions of wild subspecies since the LGM, and little overlap between domesticated maize in archaeological sites and modeled distributions of progenitors. In another example that used archaeological data for validation, Moriondo et al. (2013) modeled the modern distribution of olive cultivation in the Mediterranean Basin as a function of climate; they then hindcast olive distributions to two late-Holocene time periods and validated them against distribution data from archaeobotanical and pollen evidence. Their reconstructions gave them confidence that the distribution model could be reliably used to project future climate change impacts on olive production.

Distribution models that are used to hindcast should always be checked against independent evidence, such as the remains found in the archaeological record or other paleoarchives. Yet, these datasets are often geographically sparse, they may not intersect with the time period of interest, or the data may be available at timescales too broad for reliable comparison. In these cases, the SDM can be evaluated with other lines of evidence, such as phylogenetic data (Gavin et al., 2014). For example, at Boomplaas and Melkhoutboom Caves in South Africa, large storage pits containing seeds of *Pappea capensis* (a member of the litchi family) were observed in layers associated with Holocene archaeological deposits (Deacon, 1995), most likely harvested for their oil. Such caches of these easily harvested fruits were not noted prior to the Holocene. SDMs of *P. capensis* hindcast onto LGM conditions support one of the hypotheses proposed by Deacon that the resource

was not readily available prior to the Holocene; dramatic range contractions into isolated populations were predicted for this species (Fig. 3) and other elements of the thicket vegetation with which this species is strongly associated (Potts et al., 2013b). In this region there are few archaeological or other paleoarchives available to test paleo-SDM predictions; however, the phylogeographic patterns of *P. capensis* offer substantial support for the predicted LGM distribution as the patterns of genetic diversity match the predictions of fragmented and restricted distributions (Potts et al., 2013a). Other lines of evidence can also be used to support paleo-SDM predictions. For example, sub-zero temperatures (i.e. frost events) were identified as important predictors in the SDM. Ecophysiological experiments demonstrated that thicket species, including *P. capensis*, are frost-intolerant, thereby supporting the hindcasted decline during regionally cooler periods (Duker et al., 2015). Thus, paleo-SDM, backed up by such interdisciplinary research, can spatially contextualize a single archaeological site and provide glimpses into what was occurring at a wider spatial scale.

Banks and colleagues have described a specific form of archaeological predictive modeling that they call eco-cultural niche modeling (ECNM), aimed at understanding the impact of climate on ancient human populations. They construct paleodistribution models based on archaeological site locations using SDM methods. ECNM, like paleo-SDM, relies on the availability of high-resolution paleoclimate data from climate simulation models. For example, Banks et al. concluded that climatic temperature most influenced the distribution of the Solutrean technocomplex of western Europe, an archaeological culture dating to the early part of the LGM (Banks et al., 2006). In a subsequent analysis, two different Badegoulian (an archaeological culture in Europe dating to mid-LGM) social territories were found to have strongly overlapping ‘climate niches,’ therefore it was concluded that the different territories did not have an ecological basis and must have been caused by cultural processes (Banks et al., 2011). Similarly, Neanderthals and anatomically modern humans (AMH) were found to occupy the same climatic niche in Europe; therefore it was argued that contraction of



**Fig. 3.** The ensemble species distribution models of *Pappea capensis* (Sapindaceae) under present (top) and LGM (bottom) climate conditions on the south coast of South Africa (adapted from Potts et al., 2013b). Warm and cool colors represent high certainty of occurrence and absence, respectively. Intermediate colors indicate model uncertainty in the SDM ensemble. Presence localities (modern-day occurrences used to develop the model) are shown (black dots) as well as the positions of Boomplaas and Melkhoutboom Caves (yellow and green stars, respectively). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Neanderthal range after arrival of AMH was due to competition, not climate change (Banks et al., 2008b).

Motivated by the need to forecast the impacts of rapid 21st century anthropogenic global change (climate, land use, invasive species) on ecosystems, the SDM literature has recently called for more ecophysiology-informed SDMs (Kearney and Porter, 2009), and greater development of process-based models of ecological population and community dynamics (Franklin, 2010b; Dormann et al., 2012). There are a few examples of mechanistic process models of community dynamics being applied to previous time periods in order to understand, for example, vegetation responses to climate change and prehistoric human impacts (Henne et al., 2013).

One of the most comprehensive examples demonstrating the potential of paleo-distribution modeling in archaeology and paleoanthropology using a mechanistic vegetation model has been the Stage Three Project (van Andel, 2002). In this project climate data from global climate models, downscaled using regional climate modeling (see section 5.1), were used to drive the BIOME3.5 vegetation model in order to investigate climatic and environmental conditions during parts of Marine Isotope Stage 3 (MIS3), ca 45–30 ka, that may have influenced early modern human and Neanderthal populations (Barron and Pollard, 2002; van Huissteden et al., 2003). The BIOME3.5 vegetation model is a dynamic global vegetation model based on ecophysiological processes that link climate to vegetation. As such, it does not predict specific species occurrence, but rather broad patterns of vegetation (forest, shrubland, grassland) or plant functional types. These models have been widely used with paleoclimate models to predict past vegetation (e.g., Pound et al., 2011). This simulated distribution of biomes during MIS3 cold and warm events was compared with the pollen-based biome records, showing reasonably good fit especially for southern Europe (Alfano et al., 2003). Their modeled paleotemperatures during glacial cold stages overestimated the expected temperatures that would lead to the formation of ice wedges dated to the time period. An important distinction made by the authors, however, is that ice wedge formation could occur at the decadal scale, which is too fine for their regional climate model.

An interesting example of a mechanistic distribution model directly relevant to paleoanthropology is one based on modern baboon socioecology and used to predict the distribution of extinct baboon species of different body sizes (Bettridge and Dunbar, 2012). This model addressed the effects of temperature and other aspects of climate on species ecophysiology, as have mechanistic SDMs (Buckley et al., 2010a), and then linked this to time budgets. This model allowed prediction of group size as a function of body size under a range of climate conditions. Bettridge and Dunbar predicted that large-bodied species would have smaller ranges, a pattern corroborated by fossil evidence.

These examples suggest an unrealized potential to use paleo-distribution modeling to address questions in archaeology and paleoanthropology, and to use archaeological data to validate those models. Such recursive studies would be most powerful when carried out within the same narrow regional contexts.

### 3. Reconstructing paleoenvironments from zooarchaeological and archaeobotanical records using modeling methods

Paleoenvironmental reconstructions from plant and animal materials are commonplace in the paleosciences and these reconstructions rely on direct evidence like pollen and phytoliths or faunal remains, and indirect evidence like stable isotopes, dental wear, and use-wear on stone tools. In a widely used approach, the relationship between contemporary distributions of plant and

animal species and modern climate or other environmental parameters (for example closed versus open habitat or mesic versus xeric climate) is established and used to characterize the climate/environment at sites through time, contemporaneous with those materials (Fig. 2). We limit our review to a few examples from this large literature in order to highlight the use of modeling methods to answer questions in archaeology and paleoanthropology, draw parallels with SDM, and show how methods developed for SDM may be used to improve paleoenvironmental reconstructions if the data requirements are met.

Modeling methods used to reconstruct paleoclimate for the Cenozoic (Neogene) from fossil floras and faunas are based on using contemporary relationships between climate and distributions of species, nearest living relatives of extinct taxa (frequently required when modeling distant time periods), or functional types in order to establish the overlap of climate variable values for taxa found together. These methods include BIOCLIM (Nix and Busby, 1986), widely used in species distribution modeling and advocated for paleo-SDM (Varela et al., 2011), and the “Coexistence Approach” (CA) (Mosbrugger and Utescher, 1997), developed for reconstructing paleoclimate from plant fossils. In CA the interval of coexistence is defined as the overlapping range (the intersection) of temperatures shared by all species in the fossil assemblage. For example, Porch (2010) used a coexistence method to reconstruct paleoclimates in Australia from fossil beetle assemblages. Marra et al. (2004) proposed an alternative method using maximum likelihood estimates of the range of climate variables associated with each species in fossil beetle assemblages in New Zealand to reconstruct paleotemperature based on overlapping climate envelopes. Their method accommodates non-normal response functions (relationships between species distribution and temperature). Multivariate alternatives have been developed in this field (Teodoridis et al., 2011) and seem to be gaining traction. In the archaeological context, Bruch et al. (2012) have used the coexistence approach to investigate paleoclimate through the Middle Stone Age from the plant fossil material from Sibudu Cave, South Africa.

Those familiar with species distribution modeling methods will recognize a limitation of climate reconstruction based on overlapping ranges of tolerance for multiple taxa; only one climatic variable is examined at a time, and therefore these methods do not examine the niche hypervolume (Hutchinson, 1959). Nor can these methods determine the importance of climatic variables to species distributions. Important limiting climatic factors must be identified *a priori*, and so this approach works best when the biogeography of a particular taxonomic group is known to be sensitive to a single aspect of climate (e.g., beetles and climatic temperature). At Sibudu Cave the CA method was applied to plants, which have many species-specific limiting factors; in order to deal with this Bruch et al. analyzed 19 bioclimatic variables (Booth et al., 2014) separately without accounting for multicollinearity. In addition, simple maximum and minimum values of climate data from species localities were used, making the method susceptible to outliers or misclassification in terms of climate layers or localities.

Recently, some studies have applied SDM methods that are able to incorporate multiple predictors and address their multicollinearity (Dormann et al., 2013) to reconstruct paleoclimatic conditions associated with archaeological sites. Politis et al. (2011) modeled the distribution of three South American ungulate species important to prehistoric pampean hunter–gatherers based on correlation with modern climate using the MaxEnt modeling software (Phillips et al., 2006). These distributions were compared to faunal remains in archaeological sites and used to infer Late Holocene climatic conditions at those sites. Conolly et al. (2012) used MaxEnt as well as linear models to model the distribution and

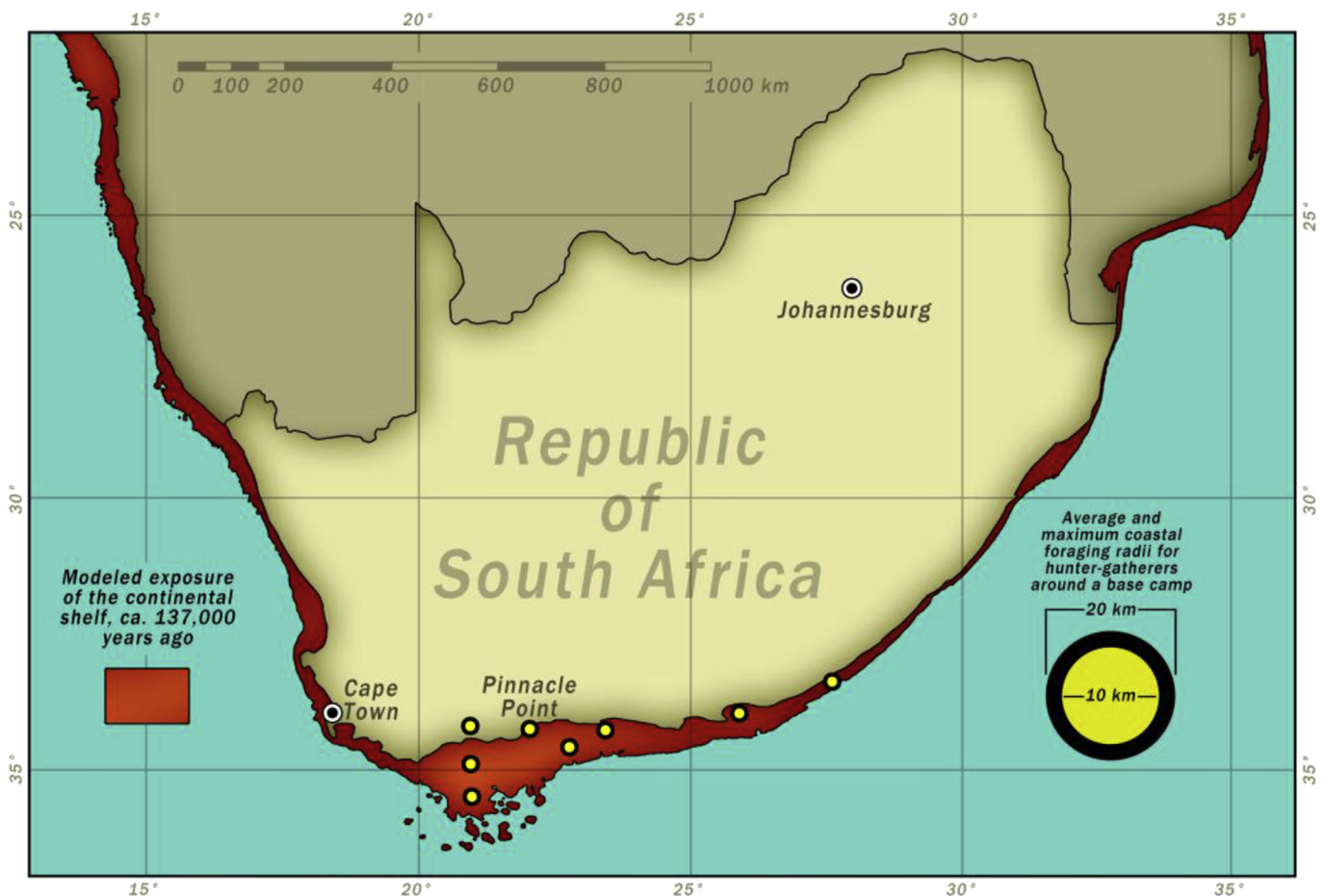
abundance of ancient wild and early domestic cattle based on faunal remains in archaeological sites in Eurasia in order to shed light on the biogeography of cattle domestication. Oddly, they used modern climate variables as predictors of these mid-Holocene distributions because of the availability of modern climate data, assuming that the relative difference in climate variables between the two time periods is constant.

Paleoenvironmental reconstruction based on faunal and floral assemblages is often done precisely because there are no other data available on i.e. paleoclimate of a site; inferences are stronger, however, when results can be compared to independent paleoclimate reconstructions from climate models or other proxy datasets. For example, in a volume addressing the ancient human occupation of Britain, bioclimatic envelope models were constructed from correlations between modern climate and modern distributions of mammal species that were found in Britain in the Pleistocene (Polly and Eronen, 2011). Maximum likelihood methods were used to estimate the most likely climate based on paleofaunas from different sites and time periods while considering the differences in range and climatic overlap from the past to the present (non-analog or disharmonious faunas). They compared their estimates of paleoclimate to those from regional paleoclimate models (Polly and Eronen, 2011).

Key aspects of paleoenvironments other than species distributions have also been modeled. Fisher et al. (2010) modeled the changing distance to the coast at 1.5 kyr time steps over the last

420,000 years on the south coast of South Africa. They were interested in understanding changing hunter–gatherer behavior in relation to coastline distance, for example when the coastline was close enough to several cave sites to have facilitated coastal intertidal foraging during the Middle and Late Pleistocene (Fig. 4). Their model was validated by multiple independent datasets, including ethnographic and archaeological observations of hunter–gatherers, direct dating of terrestrial high sea stand indicators, and by changes in strontium stable isotopes measured in dated speleothems (strontium isotopes change as a function of input from seawater, seaspray, and coastal fog).

A way forward in reconstructing environments associated with archaeological sites is greater integration of reconstruction from biological proxies from the sites themselves, as described in this section, with SDM based on modern distribution and climate data and with independent paleoclimate reconstructions. SDM requires reliable modern distribution and climate data of sufficient quality and quantity for quantitative modeling, and paleoclimate projections at a suitable spatio-temporal scale for hindcasting, whereas paleoenvironmental reconstruction methods typically look at community overlap. Community SDM (see Section 2) could be more fully exploited for paleoenvironmental reconstruction (reviewed in Gavin et al., 2014). Perhaps a recursive approach of hindcasting and validation with paleoarchives will provide a clearer picture of past environments associated with human occupation.



**Fig. 4.** Modeled exposure of the South African continental shelf during the Penultimate Glacial Maximum, ca. 137 ka, from Fisher et al. (2010). This exposed plain is believed to have supported a now-extinct migration ecosystem (Marean, 2010) that bands of hunter–gatherers (foraging radii represented as yellow dots) would have intersected for food resources. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

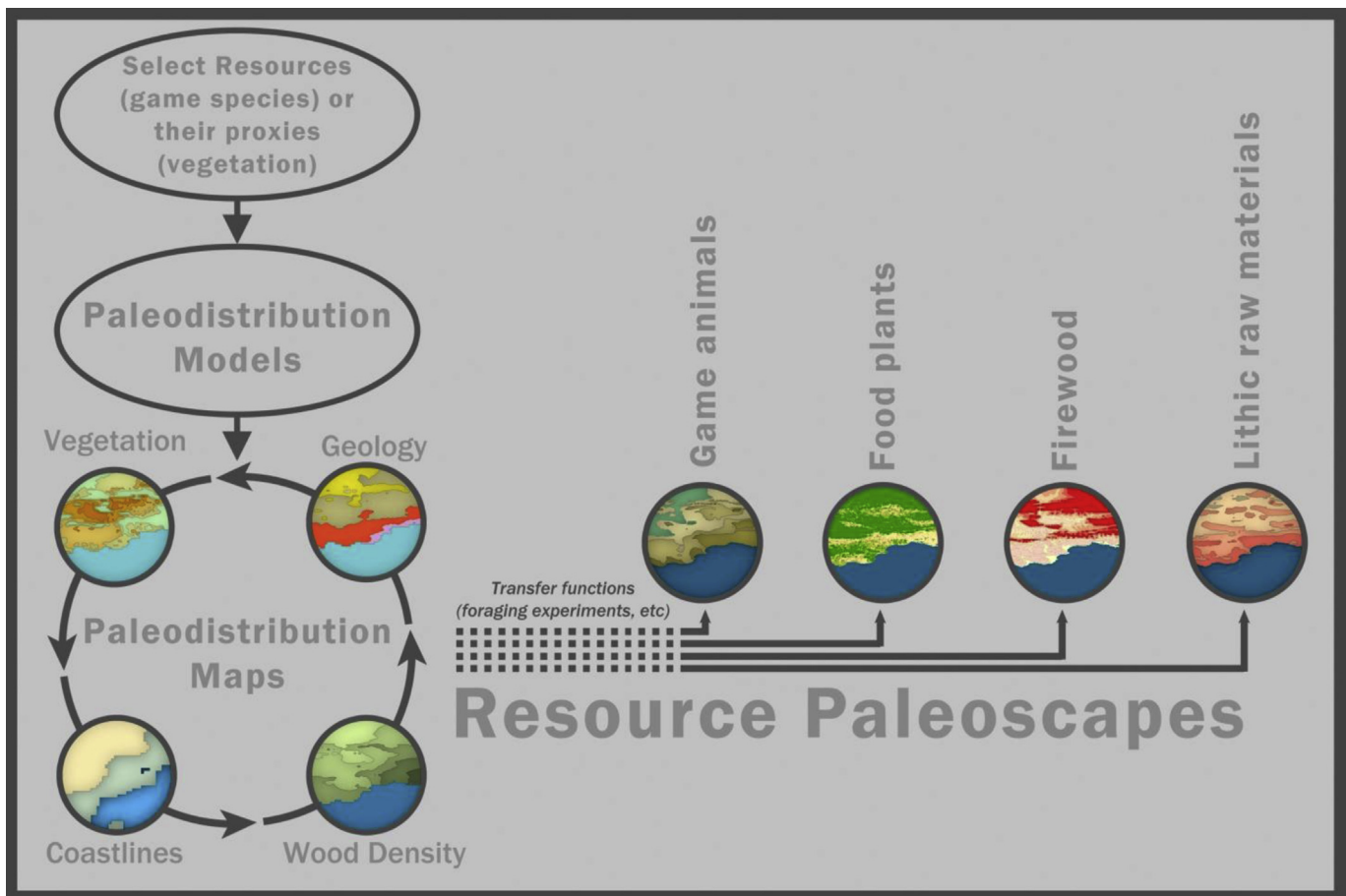


#### 4. Hindcasting resource landscapes

Reconstructing the paleoscape at the time of occupation is challenging but informative because it supports the spatially and temporally explicit investigation of how prehistoric people dually used their landscape and how their behaviors were influenced by it (Fig. 5). Many authors have used terms such as “ancient landscape” and “paleo-landscapes”, but we prefer “paleoscape” because features like coastlines and oceans, often changing in position, are important components. 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 modeled in a formal (analytical, statistical or simulation) manner (Fisher et al., 2010; Marean, 2010). An early example of a similar but informal modeling approach attempted to predict “affordances and landscape facets” during lower Bed II times at Olduvai Gorge. These “affordances and landscape facets” were defined as resources (carcasses, stone tool raw material, etc.) and hazards such as carnivore hot spots. The model was built from empirical observations in the field that led to habitat reconstructions, which then were assigned affordance and hazard characteristics through analogy to modern environments (Peters and Blumenschine, 1995; Blumenschine and Peters, 1998).

The study of coastline distance and configuration highlights the efficacy of quantitative models for archaeology and paleoanthropology in general. As noted in the previous section, studies of the South African coastline (Fig. 4) suggest that many of the coastal cave sites there, that contain important records informing our understanding of modern human evolution, were occasionally far inland during glacial periods due to lower global mean sea levels (van Andel, 2002; Fisher et al., 2010). Distance to coast is a crucial environmental variable to hunter–gatherers, and is readily predicted from sea level and topography. The utility of the model has already been demonstrated by several studies. The results of the coastline model supported the hypothesis of Jacobs et al. (2006) that the distance between the coast and Blombos cave influenced the type and amount of shellfish that was collected and brought back to the site (Fisher et al., 2010). Evidence of shellfish collecting is absent at times when the coast is far away (Jerardino, 2011). Coastline distance was shown to correlate to measures of occupation intensity at the site Pinnacle Point 13B. It was argued that the coast is the richest source of food in that environment, thus the highest ranked habitat type, and therefore drove site occupation intensity which waxed and waned as the distance to the coast reduced and increased (Marean, 2010).

A key part of the paleoscape concept is that climate and environmental change can affect more than just food availability,



**Fig. 5.** A framework for modeling resource paleosciapes. Key resources used by hunter–gatherers (animals, plants, stone materials), or their proxies (vegetation type, landform, coastline), are identified. Distribution models are developed for these resources or proxies based on modern distributions and environments (Fig. 1) and hindcast to past environmental states for time periods of interest (Figs. 2–4) in order to generate a set of paleodistribution maps. By developing a “transfer function” linking one or more paleodistribution maps to key resources (for example through resource acquisition experiments or ethnographic observations), a set of resource paleosciapes can be modeled (game animals, food plants, lithic raw materials, and potentially many others).

including those things that form the foundations of hunter–gatherer technology such as resins, wood suitable for fires and making bows and spears, poisons, and stone suitable for making tools (Fig. 5). Along the south coast of South Africa, most stone tools are manufactured either from quartzite collected as beach cobbles or silcrete that must be heat treated to be made appropriate for stone tool manufacture. Thus the cost of quartzite is partially a function of distance to coast and the cost of silcrete is partially a function of wood fuel availability (Brown et al., 2012). Brown (2011) argued that modeled coastline distance explained the changing abundance of quartzite versus silcrete with people switching to silcrete as the coast withdrew. Regional shifts in seasonality of rainfall patterns during MIS5 and 4 as reconstructed from speleothem isotopes were hypothesized by Bar-Matthews et al. (2010) to have driven an expansion of summer rain onto the south coast during MIS4, while during the inter-glacial MIS5 the area would have received greater proportions of winter rain. In the Cape, the regions with stronger winter rain are dominated by C<sub>3</sub> grass and shrub vegetation and rather depauperate in trees (Cowling, 1992). Such an expansion of summer rain could have brought with it greater amounts of C<sub>4</sub> grass, which is reflected in the speleothem isotopes, along with the tree flora of the seasonal tropics, such as acacias, which make excellent fuel for fires. (Alternatively, the shift from C<sub>3</sub> to C<sub>4</sub> could be explained by muted temperature decline and lower atmospheric carbon dioxide levels during glacials.) During MIS4, Brown and Marean (2010) observed changes in lithic technology at site Pinnacle Point PP5-6 from coastal cobble quartzite to fine-grained silcrete that is heat treated. They argued that the changing availability of wood fuel altered the costs of heat treatment such that heat treatment was energetically favored when summer rains were stronger and trees more abundant, explaining the prominence of silcrete during MIS4. Paleodistribution modeling could help sort out alternative hypotheses of resource distributions.

Species or ecological communities representing these various types of important resources can be identified from archaeological materials or other sources (ethnographic, etc.). Modern species and habitat localities (from biodiversity databases, species trait databases, vegetation maps) can then be associated with current climate and other environmental variables by developing distribution models, and this relationship can be applied to paleoclimate reconstructions to hindcast biotic distributions to time periods contemporaneous with the archaeology (as in Fig. 3). In contrast with paleo-SDM as used in paleobiology, where the objective is to understand the paleodistributions of the species themselves, in this case the purpose is to characterize important components of the resource paleoscape (emphasizing the use of plant and animal species by people) available to that human population (Fig. 5).

In the review by Verhagen and Whitley (2012, p 62), they noted GIS has been used to create other spatial models of land use from an agency perspective. As an example they cite a study of Neolithic agriculture in Italy, in which geomorphic (landform) classes were classified and ranked for their prehistoric agricultural potential (Robb and Van Hove, 2003). Verhagen and Whitley also described an example from their own work on the Georgia (USA) coast model. Faunal and floral assemblages from archaeological sites were used to directly interpolate the spatial distribution of different food resources at endpoints of time periods of occupation (i.e. without correlating the distributions with contemporaneous environmental data). These distributions were summed to produce a calorie landscape and least-cost path distances were calculated for these calorie-scapes. Aside from these few intriguing examples (and see Section 2), we are aware of few other instances of hindcasting resource paleoscaping in archaeology and paleoanthropology. The improvements in climate models, paleodistribution data and

modeling methods required to effectively model resource paleoscaping are discussed in the next section.

## 5. Improved paleodistribution modeling for archaeology and paleoanthropology

Both paleoenvironmental reconstruction and predictive modeling have been widely used in archaeology and paleoanthropology. They overlap in their objectives, methods and data requirements with SDM. SDM has become widely used across a range of biological fields, yet has not been used as extensively in archaeology and paleoanthropology. SDM offers rigorous methods for analyzing complex multivariate data, and robust approaches to dealing with biased and incomplete sampling. On the other hand, paleoenvironmental reconstruction and SDM both rely on similar assumptions that may only be weakly supported (Birks et al., 2010). Reconstructing past climates/environments from modern species–climate/environment associations relies on assumptions that observed species distributions are strongly limited by climate and that species–climate correlations are conserved over time. Non-analog climates, combinations of climate conditions that occurred in the past but not the present (Jackson and Overpeck, 2000), are not easily addressed in this framework.

Furthermore, paleoenvironmental reconstruction and predictive modeling are both based on empirical (statistical) methods that depend on reliable distributional and climate data and that are unreliable for predicting outside the range of conditions used to estimate those models, e.g., for novel (non-analog) climates or species assemblages (Jackson et al., 2000; Jackson and Williams, 2004). Different approaches to understanding paleoenvironments, and species paleodistributions, have in common that they can benefit from: a) improved paleoclimate models, b) improved paleoclimate proxy and species paleodistribution data for model validation, with attention to scale issues, and c) rigorous modeling methods for multidimensional problems, including mechanistic models. If these challenges can be addressed, distribution modeling of resource paleoscaping provides a strong link between SDM methods and important research questions about the paleoenvironment in archaeology and paleoanthropology.

### 5.1. Improved paleoclimate models and downscaling

The success of distribution models projected onto altered climate states of different time periods is dependent on the accuracy of the modeled climate. Climate models have been steadily improving, especially as concern about climate change has grown, as such models offer a means to predict potential changes (Stocker et al., 2013). For example, global climate models are now routinely coupled with complex oceanography models and vegetation models (and typically referred to as coupled atmosphere–ocean general circulation models – AOGCMs), and are thereby becoming increasingly integrated across the primary drivers of climate. Despite this, uncertainty remains in the climate modeling simulations. Different AOGCMs that perform equally well for the present-day routinely produce differing responses when projecting away from present (Collins et al., 2013; Flato et al., 2013; Gavin et al., 2014). There are over 20 different general circulation models that are being used to simulate paleoclimates in a comparative manner through the Paleoclimate Modeling Intercomparison Project (PMIP, Braconnot et al., 2011) which is now in its third stage of development (PMIP3; <https://pmip3.lsce.ipsl.fr/>). The focus of PMIP3 has been on a limited range of time periods, primarily on the mid-Holocene (6 ka) and the Last Glacial Maximum (21 ka), but also some simulations for the Last Interglacial (early Eemian, mid-Eemian and glacial inception) and the abrupt cooling event at 8.2

ka. With the growing climate modeling capacity, coordinated efforts between modeling groups and validation against current and past climates, we can expect that the climate predictions of past and future are set to be continuously improving.

AOGCM simulations are conducted on a scale unsuitable for species distribution modeling (usually 1° cells or larger) and thus need to undergo a downscaling procedure to incorporate regional and local scale climate variability (Beaumont et al., 2008). This downscaling may also introduce a new array of uncertainty, errors and/or biases in the final climate output used for projecting SDMs (e.g., Wilby et al., 1998).

Methods used to perform downscaling fall into two broad categories: statistical or dynamical (Wilby and Wigley, 1997). Within statistical downscaling, two approaches are commonly used: the delta method and pattern scaling (also called weather typing). The delta method is fairly simplistic and involves – for a given variable – determining the difference between simulations for the time period of interest and the pre-industrial period (anomalies), converting this to a high resolution (using some sort of spatial interpolation), and then applying this difference to baseline observed current climate. The baseline climate widely used is the high resolution WorldClim database ([www.worldclim.org](http://www.worldclim.org)) that represents an interpolated average of conditions from 1950 to 2000 (Hijmans et al., 2005). In addition, extrapolation may be necessary to extend these high-resolution climate surfaces to exposed terrestrial areas during periods of lowered sea level (Sakaguchi et al., 2010; Buckley et al., 2010b; Huntley et al., 2013). Pattern scaling, in contrast, aims to first match regional weather patterns with local weather events and then to identify these weather patterns in the AOGCM simulations. This method reconstructs local climates by finding analogous large-scale weather fields in the historical record that matches those observed in the AOGCM simulations. Thus, climates are reconstructed based on repeating weather patterns. This has been shown to greatly improve the downscaling skill (i.e. accuracy) when compared with the delta method (e.g., Flint and Flint, 2012).

Dynamical downscaling usually involves nesting a regional climate model within the output simulations from a global model, thereby allowing the AOGCM to provide the large scale climate state and the regional climate model to focus on local landscape level forcings, e.g., topography (Hawkins and Sutton, 2009). This provides high resolution climate simulations that cover a limited area of the globe. This approach maintains the use of comprehensive physics-based models to characterize the climate of a region. There are also a number of complex hybrid approaches that combine dynamical and statistical downscaling (Fuentes and Heimann, 2000; Busch and Heimann, 2001).

Statistical downscaling methods are widely used, especially the delta method, as they generally are easier to implement and have far lower computational requirements than dynamical downscaling. At present, there is no universally superior downscaling technique and different methods can yield different results (Vrac et al., 2007; Barsugli et al., 2013). Statistical downscaling includes a set of assumptions that may or may not hold for past or future climates. The delta method, for example, assumes that changes in climate vary only over large distances (which are captured at the scale of the AOGCM cells), and that the relationships between climate variables and the baseline are stationary through time (Barsugli et al., 2013). With pattern scaling, the basic premise assumes that there are no novel weather systems that influence local climate under the altered climate state. These problematic assumptions of downscaling have even led some to suggest that downscaled climate model projections should not be used in paleo-SDM and that researchers should use coarse-grained climate projections or wait for regional climate models to be developed (Varela et al., 2011). Regional climate modeling downscaling is also not

problem free and often require bias corrections (e.g., Christensen et al., 2008).

Climate modeling is a complex and advancing science. The primary focus has been on producing AOGCMs, with downscaling to scales necessary for biological applications, such as SDM, being of secondary concern. This is changing, however, and paleo-SDM studies can start to include projections onto climate layers produced by a range of AOGCMs and different downscaling procedures (Gavin et al., 2014). This will enable some assessment of the uncertainty introduced by the climate modeling on the final predicted distribution (i.e. ensemble modeling sensu Araújo and New, 2007).

## 5.2. Paleoclimate and distribution data for validation

Improved paleoclimate proxy and species paleodistribution data are required for validation of the modeled paleoclimates and hindcast species distributions. As noted in Section 2.2, paleodistribution data become increasingly useful for model validation when they are aggregated into regional databases as they have been for fossil pollen data in the northern hemisphere, and this is underway for a growing number of taxonomic groups and time periods (Brewer et al., 2012). Examples include mammals in Quaternary North America (<http://www.ucmp.berkeley.edu/faunmap/>), Miocene mammals of the western United States (<http://www.ucmp.berkeley.edu/miomap/>), and all taxa and time periods, globally, in the Paleobiology Database (<http://paleobiodb.org>) to name a few. Paleoclimatology datasets are also increasingly being compiled into libraries and databases (<http://www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets>).

Paleoenvironmental data sample the environment with different spatial and temporal resolutions depending on the type of data (e.g., faunal remains, pollen, isotopes, charcoal) and the site taphonomic conditions. Further, paleoenvironmental archives formed by environmental processes (e.g., pollen deposition) differ in their patterns of accumulation from those formed by human actions (transport of materials). This presents a scaling challenge when relating paleoenvironmental proxy data from point locations to paleoenvironmental reconstructions from models. Predictive and process-based paleodistribution models are, in fact, upscaling methods that use environmental maps to model phenomena at larger spatial scales (Schlummer et al., 2014). The challenge of spatially up-scaling sufficient quantities of independent paleoenvironmental data for model validation can be addressed by collecting additional data and by aggregating point data into regional archives. The comprehensive review by Schlummer et al. (2014) describes five approaches for upscaling from points to areas in archaeological research based on terrestrial archives. These approaches are: a) pattern recognition, b) spatial interpolation, c) predictive modeling, d) process-based modeling and e) implicit upscaling to map units. Most of these methods can be applied to data from terrestrial archives ranging from landform evolution, soil fertility, soil erosion, and pollen, to Paleolithic sites. However, their review does not explicitly address temporal scaling problems and solutions across those domains.

A major challenge remaining is that temporal sampling in paleoenvironmental archives, whether formed by environmental or human processes, can be much coarser than modeled distributions. This issue is well known in paleosciences as time-averaging where, for example, a faunal assemblage from a site may in fact represent taxa that were temporally segregated and did not coexist as an ecological community because the remains were accumulated over a long period of time – centuries or millennia rather than seasons or years (Kowalewski, 1996; Roy et al., 1996). This temporal mismatch can be addressed through paleo-species distribution modeling of individual taxa rather than communities or

assemblages, and by aggregating species, climate and paleoclimate data to a temporal resolution matching the paleoarchives available for validation.

Temporal sampling and scaling issues also affect SDM (although on shorter time scales) and have been addressed in a number of ways (reviewed on pp. 73–74 in Franklin, 2010a). Matching species occurrence data with contemporaneous climate and other environmental data from historical time periods can improve models based on natural history collections and other species types of observations that span decades and centuries (Kremen et al., 2008). Distribution models have been developed for different seasons of the year for species that are migratory and use habitats differently, for example for breeding versus non-breeding (Suarez-Seoane et al., 2008). In wildlife ecology, methods have been developed specifically to address the fact that species do not occupy all suitable habitat, and also that species differ in their ability to be detected by observers during monitoring surveys. Occupancy modeling methods use data from repeated surveys to correct estimates of site occupancy (proportion of surveyed sites occupied by a species) for imperfect detection (MacKenzie et al., 2002; MacKenzie, 2005). Occupancy modeling has been used as a species distribution modeling method when replicated survey data are available for estimating detection probability (Tyre et al., 2003; Wintle et al., 2004). The challenge remains to adapt methods such as temporal matching and occupancy modeling to the time scales associated with paleoarchives.

As we suggested in Section 3, a recursive approach of modeling distributions using modern species locality and climate data, hindcasting biotic distributions using paleoclimate models, and validating hindcast distributions with zooarchaeological and archaeobotanical data from the paleoarchives will provide a clearer picture of past resource paleoscapes associated with human occupation. Furthermore, the hindcast record can be used to test parameters of models used to make forecasts in reaction to climate change. This then would allow us to more confidently use these models to predict future species distributions in reaction to climate change and thus add greater confidence to forecasts that have exceptionally important social value. Such recursive studies should be carried out within the same region in order to avoid extrapolating to non-analog combinations of environmental conditions. An ideal research model might employ a computationally intensive regional climate model to hindcast a climate stage of interest, which is then used to drive a regional distribution model that hindcasts species, which can then be directly validated with a regional archaeological and paleontological record. Such a narrow recursive strategy would then lend predictive power to the use of that model for forecasting regional climate and environmental change (Marean et al., *in press*).

### 5.3. Distribution modeling methods

SDM is widely used for predicting current and future distributions and therefore modeling methods are under rapid development; paleodistribution modelers can take advantage of these developments. Rigorous modeling methods already exist for analyzing multidimensional data, addressing multicollinearity, testing for variable importance, estimating response curves, associating response variables with multiple predictors, and mitigating or at least understanding effects of sample size and sample bias (Elith and Leathwick, 2009; Franklin, 2010a; Braunisch et al., 2013; Elith and Franklin, 2013). Methods are also being developed to help identify non-analog environments – combinations of different climate and other variables that did not occur in a different time period – in order to identify where and why model projections may be highly uncertain (Fitzpatrick and Hargrove, 2009; Elith et al.,

2010; Mesgaran et al., 2014). Finally, frameworks are being identified for dealing with uncertainty in forecasting or hindcasting using SDM stemming from choice of modeling method, predictors, climate scenarios, shape of response functions and other modeling decisions (Araújo et al., 2005; Buisson et al., 2010; Elith et al., 2010; Synes and Osborne, 2011; Webber et al., 2011).

The best practices available for using correlative models calibrated from modern distributions cannot overcome the problem of hindcasting to periods where the biota included many extinct taxa (“non-analog biota”). In this case, models of feeding guilds, functional types, “nearest living relative” or ecological community types may still be able to depict the distribution of key resources in the paleoscape. Further, mechanistic models, including dynamic vegetation models (Cramer et al., 2001; Sitch et al., 2003; Scheiter and Higgins, 2009; Snell et al., 2014), may be used to hindcast the distributions and dynamics (Henne et al., 2013) of physiognomically-defined vegetation, such as open versus closed habitats (forest, woodland, savannah, grassland, desert), under various climate forcings. While the ecosystem categories may be very general, these process-based models take into account effects of fire, carbon dioxide concentration in the atmosphere, competition between species, and so forth, in addition to climate.

## 6. Resource paleoscapes

The goal of our review is to identify for archaeologists and paleoanthropologists how SDM approaches may significantly advance their goals of better understanding the environmental context of hominin evolution. The standard approach in archaeology and paleoanthropology is typical of paleoenvironmental studies in general; site and locality-based environmental proxies (such as pollen, faunal remains, isotopes) are used to extrapolate landscape-level inferences – or concoct narratives – about past environmental conditions. Given the similarity of approaches, our message is relevant to all paleoscientists involved in paleoenvironmental reconstruction. We advocate an approach where SDM is used to hindcast various aspects of the paleoenvironment, and then point-based (site and locality) empirical evidence is used to validate these models. In other words, we recommend a hypothetico-deductive approach. SDM methods and the required paleoclimate models have advanced to the point where this is not only feasible, but we argue is now, for several reasons, a preferred research strategy.

This explicitly deductive strategy generates predictions grounded in strong theoretical understandings of the relation between species, habitat distributions and climate that have been developed through statistical and mechanistic studies of modern species distributions. Hindcasting ‘resource paleoscapes’ using SDM methods offers a more powerful approach than direct paleoenvironmental reconstructions because we can rely on spatially extensive and accessible information about the current distribution of species, functional types or communities (habitats) and their concurrent climate/environments to develop these models. This moves our research agenda away from inductive paleoenvironmental reconstructions generated from a selection of sites, to using our sites to test hypothesized paleoscape reconstructions generated from theoretically and empirically grounded models.

The paleo-SDM approach makes spatial predictions of continuous distributions across the paleoscape. This is crucial because people exploited paleoscapes and moved across them to forage for resources (Janssen and Hill, 2014), so the space between our sites is as important as the site itself. If we are trying to understand hunter–gatherer mobility in the past, then we need to have projections of the resource base between the sites that provide our observations. In archaeology and paleoanthropology our goals are to understand where hominins would have foraged for plants and

animals for food, where they needed to go to get wood for fires, where trees that were good sources of resin for binding would be found, and so forth. Paleodistribution models, hindcast using paleoclimate models, provide a way to generate theoretically grounded projections of an integrated paleoscape in which our people of the past moved and foraged.

A higher-order goal of the paleosciences has always been to develop paleoecologies or understandings of the ecosystems of the past (Gifford, 1981; Behrensmeier et al., 1992). To do so we first need spatially explicit reconstructions of the diversity and abundance of plants and animals. These have remained frustratingly elusive, and as a result our ability to develop paleoecologies has been stymied. The approach advocated here using paleo-SDM to create paleoscaping provides a significant step toward that goal of understanding past ecosystems.

In contrast, archaeological and non-cultural sites that harbor paleoenvironmental data can be as rare as hen's teeth and therefore usually comprise an inadequate sample for developing quantitative models that can be used for spatial prediction. They are also plagued by the spatial and temporal sampling issues discussed in the previous section. Because there are strong biases regarding what is preserved in the deposits, hindcasting SDM resource-scapes may provide alternative lines of evidence of resource availability, and then how to translate this into resource use.

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## References

- Alfano, M.J., Barron, E.J., Pollard, D., Huntley, B., Allen, J.R., 2003. Comparison of climate model results with European vegetation and permafrost during oxygen isotope stage three. *Quat. Res.* 59, 97–107.
- Anderson, R., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29, 129–151.
- Araújo, M.B., Luoto, M., 2007. The importance of biotic interactions for modelling species distributions under climate change. *Glob. Ecol. Biogeogr.* 16, 743–753.
- Araújo, M.B., New, M., 2007. Ensemble forecasting of species distributions. *Trends Ecol. Evol.* 22, 42–47.
- Araújo, M.B., Whittaker, R.J., Ladle, R.J., Erhard, M., 2005. Reducing uncertainty in projections of extinction risk from climate change. *Glob. Ecol. Biogeogr.* 14, 529–538.
- Austin, M., 2007. Species distribution models and ecological theory: a critical assessment and some possible new approaches. *Ecol. Model.* 200, 1–19.
- Austin, M.P., 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecol. Model.* 157, 101–118.
- Austin, M.P., Van Niel, K.P., 2011. Improving species distribution models for climate change studies: variable selection and scale. *J. Biogeogr.* 38, 1–8.
- 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. *J. Anthropol. Archaeol.* 30, 359–374.
- Banks, W.E., d'Errico, F., Peterson, A.T., Kageyama, M., Colombeau, G., 2008a. Reconstructing ecological niches and geographic distributions of caribou (*Rangifer tarandus*) and red deer (*Cervus elaphus*) during the Last Glacial Maximum. *Quat. Sci. Rev.* 27, 2568–2575.
- Banks, W.E., d'Errico, F., Peterson, A.T., Kageyama, M., Sima, A., Sánchez-Goni, M.-F., 2008b. Neanderthal extinction by competitive exclusion. *PLoS One* 3, e3972.
- Banks, W.E., d'Errico, F., Dibble, H.L., Krishtalka, L., West, D., Olszewski, D.L., Peterson, A.T., Anderson, D.G., Gillam, J., Montet-White, A., 2006. Eco-cultural niche modeling: new tools for reconstructing the geography and ecology of past human populations. *PaleoAnthropology* 4, 68–83.
- Bar-Matthews, M., Marean, C.W., Jacobs, Z., Karkanas, P., Fisher, E.C., Herries, A.I.R., Brown, K., Williams, H.M., Bernatchez, J., Ayalon, A., Nilssen, P.J., 2010. A high resolution and continuous isotopic speleothem record of paleoclimate and paleoenvironment from 90 to 53 ka from Pinnacle Point on the south coast of South Africa. *Quat. Sci. Rev.* 29, 2131–2145.
- Barron, E., Pollard, D., 2002. High-resolution climate simulations of oxygen isotope Stage 3 in Europe. *Quat. Res.* 58, 296–309.
- Barsugli, J.J., Guentchev, G., Horton, R.M., Wood, A., Mearns, L.O., Liang, X.Z., Winkler, J.A., Dixon, K., Hayhoe, K., Rood, R.B., 2013. The practitioner's dilemma: how to assess the credibility of downscaled climate projections. *Eos Trans. Am. Geophys. Union* 94, 424–425.
- Beaumont, L.J., Hughes, L., Pitman, A.J., 2008. Why is the choice of future climate scenarios for species distribution modelling important? *Ecol. Lett.* 11, 1135–1146.
- Behrensmeier, A.K., Damuth, J.D., DiMichele, W.A., Potts, R., Sues, H.-D., Wing, S., 1992. *Terrestrial Ecosystems Through Time: Evolutionary Paleoecology of Terrestrial Plants and Animals*. University of Chicago Press, Chicago.
- Bettridge, C.M., Dunbar, R., 2012. Modeling the biogeography of fossil baboons. *Int. J. Primatol.* 33, 1278–1308.
- Birks, H.B., Heiri, O., Seppä, H., Bjune, A.E., 2010. Strengths and weaknesses of quantitative climate reconstructions based on late-Quaternary biological proxies. *Open Ecol. J.* 3, 68–110.
- Blois, J.L., Williams, J.W., Fitzpatrick, M.C., Ferrier, S., Veloz, S.D., He, F., Liu, Z.Y., Manion, G., Otto-Bliesner, B., 2013a. Modeling the climatic drivers of spatial patterns in vegetation composition since the Last Glacial Maximum. *Ecography* 36, 460–473.
- Blois, J.L., Williams, J.W., Fitzpatrick, M.C., Jackson, S.T., Ferrier, S., 2013b. Space can substitute for time in predicting climate-change effects on biodiversity. *Proc. Natl. Acad. Sci. U. S. A.* 110, 9374–9379.
- Blumenshine, R.J., Peters, C.R., 1998. Archaeological predictions for hominid land use in the Paleo-Olduvai basin, Tanzania, during lowermost Bed II times. *J. Hum. Evol.* 34, 565–607.
- Booth, T.H., Nix, H.A., Busby, J.R., Hutchinson, M.F., 2014. BIOCLIM: the first species distribution modelling package, its early applications and relevance to most current MaxEnt studies. *Divers. Distrib.* 20, 1–9.
- Braconnot, P., Harrison, S.P., Otto-Bliesner, B., Abe-Ouchi, A., Jungclauss, J., Peterschmitt, J.-Y., 2011. The paleoclimate modeling intercomparison project contribution to CMIP5. *CLIVAR Exch.* 56, 15–19.
- Braunisch, V., Coppes, J., Arletaz, R., Suchant, R., Schmid, H., Bollmann, K., 2013. Selecting from correlated climate variables: a major source of uncertainty for predicting species distributions under climate change. *Ecography* 36, 971–983.
- Brewer, S., Jackson, S.T., Williams, J.W., 2012. Paleoecoinformatics: applying geo-historical data to ecological questions. *Trends Ecol. Evol.* 27, 104–112.
- Brown, K., Marean, C., 2010. Wood Fuel Availability for Heat Treatment Drives the Rise and Fall of Silcrete as a Raw Material in the Middle Stone Age of South Africa. Abstracts of the PaleoAnthropology Society Meetings, pp. A0001–A0040.
- Brown, K.S., 2011. *The Sword in the Stone: Lithic Raw Material Exploitation in the Middle Stone Age at Pinnacle Point Site 5-6, Southern Cape, South Africa* (Ph.D. dissertation). Anthropology. University of Cape Town, Cape Town, South Africa.
- Brown, K.S., Marean, C.W., Jacobs, Z., Schoville, B.J., Oestmo, S., Fisher, E.C., Bernatchez, J., Karkanas, P., Matthews, T., 2012. An early and enduring advanced technology originating 71,000 years ago in South Africa. *Nature* 491, 590–593.
- Bruch, A.A., Sievers, C., Wadley, L., 2012. Quantification of climate and vegetation from Southern African Middle Stone Age sites – an application using Late Pleistocene plant material from Sibudu, South Africa. *Quat. Sci. Rev.* 45, 7–17.
- Buckley, L.B., Urban, M.C., Angilletta, M.J., Crozier, L.G., Rissler, L.J., Sears, M.W., 2010a. Can mechanism inform species' distribution models? *Ecol. Lett.* 13, 1041–1054.
- Buckley, T.R., Marske, K., Attanayake, D., 2010b. Phylogeography and ecological niche modelling of the New Zealand stick insect *Clitarchus hookeri* (White) support survival in multiple coastal refugia. *J. Biogeogr.* 37, 682–695.
- Buisson, L., Thuiller, W., Casajus, N., Lek, S., Grenouillet, G., 2010. Uncertainty in ensemble forecasting of species distribution. *Glob. Change Biol.* 16, 1145–1157.
- Busch, U., Heimann, D., 2001. Statistical-dynamical extrapolation of a nested regional climate simulation. *Clim. Res.* 19, 1–13.
- Carnaval, A.C., Moritz, C., 2008. Historical climate modelling predicts patterns of current biodiversity in the Brazilian Atlantic forest. *J. Biogeogr.* 35, 1187–1201.
- Christensen, J.H., Boberg, F., Christensen, O.B., Lucas-Picher, P., 2008. On the need for bias correction of regional climate change projections of temperature and precipitation. *Geophys. Res. Lett.* 35, L20709. <http://dx.doi.org/10.1029/2008GL035694>.
- Clark, J.S., 1998. Why trees migrate so fast: confronting theory with dispersal biology and the paleorecord. *Am. Nat.* 152, 204–224.
- Clark, J.S., Bell, D.M., Kwit, M.C., Zhu, K., 2014. Competition-interaction landscapes for the joint response of forests to climate change. *Glob. Change Biol.* 20, 1979–1991.
- Collins, M., Knutti, R., Arblaster, J., Dufresne, J.-L., Fichefet, T., Friedlingstein, P., Gao, X., Gutowski, W.J., Johns, T., Krinner, G., Shongwe, M., Tebaldi, C., Weaver, A.J., Wehne, M., 2013. Long-term climate change: projections, commitments and irreversibility. In: Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M. (Eds.), *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 1029–1136.
- Conolly, J., Manning, K., Colledge, S., Dobney, K., Shennan, S., 2012. Species distribution modelling of ancient cattle from early Neolithic sites in SW Asia and Europe. *Holocene* 22, 997–1010.
- Cowling, R.M., 1992. *The Ecology of Fynbos: Nutrients, Fire and Diversity*. Oxford University Press, Southern Africa.

- Cramer, W., Bondeau, A., Woodward, F.I., Prentice, I.C., Betts, R.A., Brovkin, V., Cox, P.M., Fisher, V., Foley, J.A., Friend, A.D., Kucharik, C., Lomas, M.R., Ramankutty, N., Sitch, S., Smith, B., White, A., Young-Molling, C., 2001. Global response of terrestrial ecosystem structure and function to CO<sub>2</sub> and climate change: results from six dynamic global vegetation models. *Glob. Change Biol.* 7, 357–373.
- Deacon, H.J., 1995. Two Late Pleistocene-Holocene archaeological depositories from the southern Cape, South Africa. *South Afr. Archaeol. Bull.* 50, 121–131.
- Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36, 027–046.
- Dormann, C.F., Schymanski, S.J., Cabral, J., Chuine, I., Graham, C., Hartig, F., Kearney, M., Morin, X., Römermann, C., Schröder, B., Singer, A., 2012. Correlation and process in species distribution models: bridging a dichotomy. *J. Biogeogr.* 12, 2119–2131.
- Duker, R., Cowling, R.M., du Preez, D.R., van der Vyver, M.L., Weatherall-Thomas, C.R., Potts, A.J., 2015. Community-level assessment of freezing tolerance: frost dictates the biome boundary between Albany subtropical thickets and Nama-Karoo in South Africa. *J. Biogeogr.* 42, 167–178.
- Elith, J., Franklin, J., 2013. Species distribution modelling. In: Levin, S. (Ed.), *Encyclopedia of Biodiversity*, second ed. Academic Press, Waltham, MA, pp. 692–705.
- Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M., Peterson, A.T., Phillips, S.J., Richardson, K., Scachetti-Pereira, R., Schapire, R.E., Soberon, J., Williams, S., Wisz, M.S., Zimmermann, N.E., 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29, 129–151.
- Elith, J., Kearney, M., Phillips, S., 2010. The art of modelling range-shifting species. *Methods Ecol. Evol.* 1, 330–342.
- Elith, J., Leathwick, J.R., 2009. Species distribution models: ecological explanation and prediction across space and time. *Annu. Rev. Ecol. Syst.* 40, 677–697.
- Ferrier, S., Guisan, A., 2006. Spatial modelling of biodiversity at the community level. *J. Appl. Ecol.* 43, 393–404.
- Ferrier, S., Manion, G., Elith, J., Richardson, K., 2007. Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. *Divers. Distrib.* 13, 252–264.
- Fisher, E.C., Bar-Matthews, M., Jerardino, A., Marean, C.W., 2010. Middle and Late Pleistocene paleoscape modeling along the southern coast of South Africa. *Quat. Sci. Rev.* 29, 1382–1398.
- Fitzpatrick, M.C., Hargrove, W.W., 2009. The projection of species distribution models and the problem of non-analog climate. *Biodivers. Conserv.* 18, 2255–2261.
- Flato, G., Marotzke, J., Abiodun, B., Braconnot, P., Chou, S., Collins, W., Cox, P., Driouech, F., Emori, S., Eyring, V., 2013. Evaluation of climate models. In: Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M. (Eds.), *Climate Change: the Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 741–866.
- Flint, A.L., Flint, L.E., 2012. Downscaling future climate scenarios to fine scales for hydrologic and ecologic modeling and analysis. *Ecol. Process.* 1 <http://dx.doi.org/10.1186/2192-1709-1-2>.
- Ford, A., Clarke, K.C., Raines, G., 2009. Modeling settlement patterns of the late classic Maya civilization with Bayesian methods and geographic information systems. *Ann. Assoc. Am. Geogr.* 99, 496–520.
- Franklin, J., 1995. Predictive vegetation mapping: geographic modeling of bio-spatial patterns in relation to environmental gradients. *Prog. Phys. Geogr.* 19, 474–499.
- Franklin, J., 2010a. *Mapping Species Distributions: Spatial Inference and Prediction*. Cambridge University Press, Cambridge, UK.
- Franklin, J., 2010b. Moving beyond static species distribution models in support of conservation biogeography. *Divers. Distrib.* 16, 321–330.
- Fuentes, U., Heimann, D., 2000. An improved statistical-dynamical downscaling scheme and its application to the Alpine precipitation climatology. *Theor. Appl. Climatol.* 65, 119–135.
- Gavin, D.G., Fitzpatrick, M.C., Gugger, P.F., Heath, K.D., Rodríguez-Sánchez, F., Dobrowski, S.Z., Hampe, A., Hu, F.S., Ashcroft, M.B., Bartlein, P.J., 2014. Climate refugia: joint inference from fossil records, species distribution models and phylogeography. *New Phytol.* 204, 37–54.
- Gifford, D.P., 1981. Taphonomy and paleoecology: a critical review of archaeology's sister disciplines. *Adv. Archaeol. Method Theory* 4, 365–438.
- Graves, D., 2011. The use of predictive modelling to target Neolithic settlement and occupation activity in mainland Scotland. *J. Archaeol. Sci.* 38, 633–656.
- Guisan, A., Thuiller, W., 2005. Predicting species distributions: offering more than simple habitat models. *Ecol. Lett.* 8, 993–1009.
- Guisan, A., Rahbek, C., 2011. SESAM—a new framework integrating macroecological and species distribution models for predicting spatio-temporal patterns of species assemblages. *J. Biogeogr.* 38, 1433–1444.
- Hampe, A., 2004. Bioclimate envelope models: what they detect and what they hide. *Glob. Ecol. Biogeogr.* 13, 469–471.
- Hastie, T., Tibshirani, R., Friedman, J., Hastie, T., Friedman, J., Tibshirani, R., 2009. *The Elements of Statistical Learning*. Springer.
- Hawkins, E., Sutton, R., 2009. The potential to narrow uncertainty in regional climate predictions. *Bull. Am. Meteorol. Soc.* 90, 1095–1107.
- Henne, P.D., Elkin, C., Colombaroli, D., Samartin, S., Bugmann, H., Heiri, O., Tinner, W., 2013. Impacts of changing climate and land use on vegetation dynamics in a Mediterranean ecosystem: insights from paleoecology and dynamic modeling. *Landsc. Ecol.* 28, 819–833.
- Hernandez, P.A., Graham, C.H., Master, L.L., Albert, D.L., 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography* 29, 773–785.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* 25, 1965–1978.
- Hijmans, R.J., Graham, C.H., 2006. The ability of climate envelope models to predict the effect of climate change on species distributions. *Glob. Change Biol.* 12, 2272–2281.
- Hilbert, D.W., Ostendorf, B., 2001. The utility of artificial neural networks for modelling the distribution of vegetation in past, present and future climates. *Ecol. Model.* 146, 311–327.
- Hufford, M.B., Martinez-Meyer, E., Gaut, B.S., Eguiarte, L.E., Tenaillon, M.I., 2012. Inferences from the historical distribution of wild and domesticated maize provide ecological and evolutionary insight. *PLoS One* 7, 11. <http://dx.doi.org/10.1371/journal.pone.0047659>.
- Huntley, B., Allen, J.R., Barnard, P., Collingham, Y.C., Holliday, P.R., 2013. Species distribution models indicate contrasting late-Quaternary histories for Southern and Northern Hemisphere bird species. *Glob. Ecol. Biogeogr.* 22, 277–288.
- Hutchinson, G.E., 1957. Concluding remarks. *Cold Springs Harbour Symp. Quant. Biol.* 22, 415–427.
- Hutchinson, G.E., 1959. Homage to Santa Rosalia or why are there so many kinds of animals? *Am. Nat.* 93, 145.
- Jackson, S.T., Overpeck, J.T., 2000. Responses of plant populations and communities to environmental changes of the late Quaternary. *Paleobiology* 26, 194–220.
- Jackson, S.T., Webb, R.S., Anderson, K.H., Overpeck, J.T., Webb III, T., Williams, J.W., Hansen, B., 2000. Vegetation and environment in eastern North America during the last glacial maximum. *Quat. Sci. Rev.* 19, 489–508.
- Jackson, S.T., Williams, J.W., 2004. Modern analogs in Quaternary paleoecology: here today, gone yesterday, gone tomorrow? *Annu. Rev. Earth Planet. Sci.* 32, 495–537.
- Jacobs, Z., Duller, G.A., Wintle, A.G., Henshilwood, C.S., 2006. Extending the chronology of deposits at Blombos Cave, South Africa, back to 140ka using optical dating of single and multiple grains of quartz. *J. Hum. Evol.* 51, 255–273.
- Janssen, M.A., Hill, K., 2014. Benefits of grouping and cooperative hunting among Ache hunter-gatherers: insights from an agent-based foraging model. *Hum. Ecol.* 42, 823–835.
- Jerardino, A., 2012. What archaeology can tell us about sustainability and climate change: a South African west coast perspective. *J. Mar. Sci. Res. Dev.* 1:105 <http://dx.doi.org/10.4172/2155-9910.1000105>.
- Kearney, M.R., Porter, W.P., 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecol. Lett.* 12, 334–350.
- Kowalewski, M., 1996. Time-averaging, overcompleteness, and the geological record. *J. Geol.* 104, 317–326.
- Kozak, K.H., Graham, C.H., Wiens, J.J., 2008. Integrating GIS-based environmental data into evolutionary biology. *Trends Ecol. Evol.* 23, 141–148.
- Kremen, C., Cameron, A., Moilanen, A., Phillips, S.J., Thomas, C.D., Beentje, H., Dransfield, J., Fisher, B.L., Glaw, F., Good, T.C., Harper, G.J., Hijmans, R.J., Lees, D.C., Louis, E., Nussbaum, R.A., Raxworthy, C.J., Razafimanahana, A., Schatz, G.E., Vences, M., Vieites, D.R., Wright, P.C., Zjhra, M.L., 2008. Aligning conservation priorities across taxa in Madagascar with high-resolution planning tools. *Science* 320, 222–226.
- Kvamme, K.L., 2012. Spatial information technologies and landscape archaeology: past problems and future directions. *eTopoi J. Anc. Stud.* 3, 335–340.
- MacKenzie, D.I., 2005. What are the issues with presence-absence data for wildlife managers? *J. Wildl. Manag.* 69, 849–860.
- MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, A., Langtimm, C.A., 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83, 2248–2255.
- Mackey, B.G., Lindenmayer, D.B., 2001. Towards a hierarchical framework for modeling the spatial distribution of animals. *J. Biogeogr.* 28, 1147–1166.
- Marean, C.W., 2010. Pinnacle Point Cave 13B (Western Cape Province, South Africa) in context: the Cape Floral Kingdom, shellfish, and modern human origins. *J. Hum. Evol.* 59, 425–443.
- Marean, C.W., Anderson, R.J., Bar-Matthews, M., Braun, K., Cawthra, H.C., Cowling, R.M., Engelbrecht, F., Esler, K.J., Fisher, E., Franklin, J., Hill, K., Janssen, M., Potts, A.J., Zahn, R., 2014. A new research strategy for integrating studies of climate, environment, and paleoanthropology. *Evol. Anthropol. (in press)*.
- Marra, M., Smith, E., Shulmeister, J., Leschen, R., 2004. Late Quaternary climate change in the Awatere Valley, South Island, New Zealand using a sine model with a maximum likelihood envelope on fossil beetle data. *Quat. Sci. Rev.* 23, 1637–1650.
- Martinez-Meyer, E., Peterson, A.T., Hargrove, W.W., 2004. Ecological niches as stable distribution constraints on mammal species, with implications for Pleistocene extinctions and climate change projections for biodiversity. *Glob. Ecol. Biogeogr.* 13, 305–314.
- McCoy, M.D., Ladefoged, T.N., 2009. New developments in the use of spatial technology in archaeology. *J. Archaeol. Res.* 17, 263–295.

- McEwan, D.G., 2012. Qualitative landscape theories and archaeological predictive modelling— a journey through No Man's Land? *J. Archaeol. Method Theory* 19, 526–547.
- McGuire, J.L., Davis, E.B., 2013. Using the palaeontological record of *Microtus* to test species distribution models and reveal responses to climate change. *J. Biogeogr.* 40, 1490–1500.
- Mesgaran, M.B., Couzens, R.D., Webber, B.L., 2014. Here be dragons: a tool for quantifying novelty due to covariate range and correlation change when projecting species distribution models. *Divers. Distrib.* 20, 1147–1159.
- Moriondo, M., Trombi, G., Ferrise, R., Brandani, G., Dibari, C., Ammann, C.M., Lippi, M.M., Bindi, M., 2013. Olive trees as bio-indicators of climate evolution in the Mediterranean Basin. *Glob. Ecol. Biogeogr.* 22, 818–833.
- Mosbrugger, V., Utescher, T., 1997. The coexistence approach — a method for quantitative reconstructions of Tertiary terrestrial palaeoclimate data using plant fossils. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 134, 61–86.
- Nix, H., Busby, J., 1986. BIOCLIM, a Bioclimatic Analysis and Prediction System. Annual report CSIRO. CSIRO Division of Water and Land Resources, Canberra.
- Nogués-Bravo, D., 2009. Predicting the past distribution of species climatic niches. *Glob. Ecol. Biogeogr.* 18, 521–531.
- Ohmann, J.L., Gregory, M.J., Henderson, E.B., Roberts, H.M., 2011. Mapping gradients of community composition with nearest-neighbor imputation: extending plot data for landscape analysis. *J. Veg. Sci.* 22, 660–676.
- Ovaskainen, O., Hottola, J., Siitonen, J., 2010. Modeling species co-occurrence by multivariate logistic regression generates new hypotheses on fungal interactions. *Ecology* 91, 2514–2521.
- Ovaskainen, O., Soininen, J., 2011. Making more out of sparse data: hierarchical modeling of species communities. *Ecology* 92, 289–295.
- Pearman, P.B., Randin, C.F., Broennimann, O., Vittoz, P., van der Knaap, W.O., Engler, R., Le Lay, G., Zimmermann, N.E., Guisan, A., 2008. Prediction of plant species distributions across six millennia. *Ecol. Lett.* 11, 357–369.
- Pearson, R.G., Dawson, T.P., 2003. Predicting the impacts of climate change on the distribution of species: are bioclimatic envelope models useful? *Glob. Ecol. Biogeogr.* 12, 361–371.
- Peters, C.R., Blumenshine, R.J., 1995. Landscape perspectives on possible land use patterns for Early Pleistocene hominids in the Olduvai Basin, Tanzania. *J. Hum. Evol.* 29, 321–362.
- Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. *Ecol. Model.* 190, 231–259.
- Phillips, S.J., Dudík, M., 2008. Modeling of species distributions with MaxEnt: new extensions and a comprehensive evaluation. *Ecography* 31, 161–175.
- Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J., Ferrier, S., 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecol. Appl.* 19, 181–197.
- Politis, G.G., Prates, L., Merino, M.L., Tognelli, M.F., 2011. Distribution parameters of guanaco (*Lama guanicoe*), pampas deer (*Ozotoceros bezoarticus*) and marsh deer (*Blastoceros dichotomus*) in Central Argentina: archaeological and paleoenvironmental implications. *J. Archaeol. Sci.* 38, 1405–1416.
- Polly, P.D., Eronen, J.T., 2011. Mammal associations in the Pleistocene of Britain: implications of ecological niche modelling and a method for reconstructing palaeoclimate. In: Ashton, N., Lewis, S., Stronger, C. (Eds.), *The Ancient Human Occupation of Britain*. Elsevier, UK, pp. 279–304.
- Porch, N., 2010. Climate space, bioclimatic envelopes and coexistence methods for the reconstruction of past climates: a method using Australian beetles and significance for Quaternary reconstruction. *Quat. Sci. Rev.* 29, 633–647.
- Potts, A.J., Hedderson, T.A., Cowling, R.M., 2013a. Testing large-scale conservation corridors designed for patterns and processes: comparative phylogeography of three tree species. *Divers. Distrib.* 19, 1418–1428.
- Potts, A.J., Hedderson, T.A., Franklin, J., Cowling, R.M., 2013b. The Last Glacial Maximum distribution of South African subtropical thicket inferred from community distribution modelling. *J. Biogeogr.* 40, 310–322.
- Pound, M.J., Haywood, A.M., Salzmann, U., Riding, J.B., Lunt, D.J., Hunter, S.J., 2011. A Tortonian (late Miocene, 11.61–7.25 Ma) global vegetation reconstruction. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 300, 29–45.
- Robb, J., Van Hove, D., 2003. Gardening, foraging and herding: Neolithic land use and social territories in Southern Italy. *Antiquity* 77, 241–254.
- Roy, K., Valentine, J.W., Jablonski, D., Kidwell, S.M., 1996. Scales of climatic variability and time averaging in Pleistocene biotas: implications for ecology and evolution. *Trends Ecol. Evol.* 11, 458–463.
- Sakaguchi, S., Sakurai, S., Yamasaki, M., Isagi, Y., 2010. How did the exposed seafloor function in postglacial northward range expansion of *Kalopanax septemlobus*? Evidence from ecological niche modelling. *Ecol. Res.* 25, 1183–1195.
- Scheiter, S., Higgins, S.I., 2009. Impacts of climate change on the vegetation of Africa: an adaptive dynamic vegetation modelling approach. *Glob. Change Biol.* 15, 2224–2246.
- Schlummer, M., Hoffmann, T., Dikau, R., Eickmeier, M., Fischer, P., Gerlach, R., Holzkämper, J., Kalis, A.J., Kretschmer, L., Lauer, F., 2014. From point to area: upscaling approaches for Late Quaternary archaeological and environmental data. *Earth-Sci. Rev.* 131, 22–48.
- Sitch, S., Smith, B., Prentice, I.C., Arneeth, A., Bondeau, A., Cramer, W., Kaplan, J.O., Levis, S., Lucht, W., Sykes, M.T., Thonicke, K., Venevsky, S., 2003. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Glob. Change Biol.* 9, 161–185.
- Skidmore, A.K., Franklin, J., Dawson, T.P., Pilesjö, P., 2011. Geospatial tools address emerging issues in spatial ecology: a review and commentary on the Special Issue. *Int. J. Geogr. Inf. Sci.* 25, 337–365.
- Snell, R., Huth, A., Nabel, J., Bocedi, G., Travis, J., Gravel, D., Bugmann, H., Gutiérrez, A., Hickler, T., Higgins, S., 2014. Using dynamic vegetation models to simulate plant range shifts. *Ecography* 37, 1184–1197.
- Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M., 2013. *Climate Change 2013. The Physical Science Basis. Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change-Abstract for decision-makers.* Groupe d'experts intergouvernemental sur l'évolution du climat/Intergovernmental Panel on Climate Change-IPCC, C/O World Meteorological Organization, 7bis Avenue de la Paix, CP 2300 CH-1211 Geneva 2 (Switzerland).
- Suarez-Seoane, S., de la Morena, E.L.G., Prieto, M.B.M., Osborne, P.E., de Juana, E., 2008. Maximum entropy niche-based modelling of seasonal changes in little bustard (*Tetrax tetrax*) distribution. *Ecol. Model.* 219, 17–29.
- Svenning, J.-C., Flojgaard, C., Marske, K.A., Nogués-Bravo, D., Normand, S., 2011. Applications of species distribution modeling to paleobiology. *Quat. Sci. Rev.* 30, 2930–2947.
- Synes, N.W., Osborne, P.E., 2011. Choice of predictor variables as a source of uncertainty in continental-scale species distribution modelling under climate change. *Glob. Ecol. Biogeogr.* 20, 904–914.
- Teodoridis, V., Mazouch, P., Spicer, R.A., Uhl, D., 2011. Refining CLAMP — investigations towards improving the Climate Leaf Analysis Multivariate Program. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 299, 39–48.
- Thuiller, W., 2004. Patterns and uncertainties of species' range shifts under climate change. *Glob. Change Biol.* 10, 2020–2027.
- Tyre, A.J., Tenhumberg, B., Field, S.A., Neejalk, D., Parris, K., Possingham, H.P., 2003. Improving precision and reducing bias in biological surveys: estimating false-negative error rates. *Ecol. Appl.* 13, 1790–1801.
- van Andel, T.H., 2002. The climate and landscape of the middle part of the Weichselian glaciation in Europe: the Stage 3 Project. *Quat. Res.* 57, 2–8.
- van Huissteden, K., Vandenbergh, J., Pollard, D., 2003. Palaeotemperature reconstructions of the European permafrost zone during marine oxygen isotope Stage 3 compared with climate model results. *J. Quat. Sci.* 18, 453–464.
- VanDerWal, J., Shoo, L.P., Williams, S.E., 2009. New approaches to understanding late Quaternary climate fluctuations and refugial dynamics in Australian wet tropical rain forests. *J. Biogeogr.* 36, 291–301.
- Varela, S., Lobo, J.M., Hortal, J., 2011. Using species distribution models in paleobiogeography: a matter of data, predictors and concepts. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 310, 451–463.
- Verhagen, P., Whitley, T.G., 2012. Integrating archaeological theory and predictive modeling: a live report from the scene. *J. Archaeol. Method Theory* 19, 49–100.
- Vrac, M., Stein, M., Hayhoe, K., Liang, X.Z., 2007. A general method for validating statistical downscaling methods under future climate change. *Geophys. Res. Lett.* 34, L18701. <http://dx.doi.org/10.1029/2007GL030295>.
- Waltari, E., Guralnick, R.P., 2009. Ecological niche modelling of montane mammals in the Great Basin, North America: examining past and present connectivity of species across basins and ranges. *J. Biogeogr.* 36, 148–161.
- Webber, B.L., Yates, C.J., Le Maitre, D.C., Scott, J.K., Kriticos, D.J., Ota, N., McNeill, A., Le Roux, J.J., Midgley, G.F., 2011. Modelling horses for novel climate courses: insights from projecting potential distributions of native and alien Australian acacias with correlative and mechanistic models. *Divers. Distrib.* 17, 978–1000.
- Wiens, J.A., Stralberg, D., Jongsomjit, D., Howell, C.A., Snyder, M.A., 2009. Niches, models, and climate change: assessing the assumptions and uncertainties. *Proc. Natl. Acad. Sci. U. S. A.* 106, 19729–19736.
- Wilby, R.L., Wigley, T., 1997. Downscaling general circulation model output: a review of methods and limitations. *Prog. Phys. Geogr.* 21, 530–548.
- Wilby, R.L., Wigley, T., Conway, D., Jones, P., Hewitson, B., Main, J., Wilks, D., 1998. Statistical downscaling of general circulation model output: a comparison of methods. *Water Resour. Res.* 34, 2995–3008.
- Wintle, B.A., McCarthy, M.A., Parris, K.M., Burgman, M.A., 2004. Precision and bias of methods for estimating point survey detection probabilities. *Ecol. Appl.* 14, 703–712.
- Wis, M.S., Hijmans, R.J., Li, J., Peterson, A.T., Graham, C.H., Guisan, A., NCEAS Predicting Species Distributions Working Group, 2008. Effects of sample size on the performance of species distribution models. *Divers. Distrib.* 14, 763–773.
- Wis, M.S., Pottier, J., Kissling, W.D., Pellissier, L., Lenoir, J., Damgaard, C.F., Dormann, C.F., Forchhammer, M.C., Grytnes, J.A., Guisan, A., 2013. The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biol. Rev.* 88, 15–30.