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Towards a Middle Pleistocene terrestrial climate reconstruction based on herpetofaunal assemblages from the Iberian Peninsula: State of the art and perspectives

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The pattern of the varying climatic conditions in southern Europe over the last million years is well known from isotope studies on deep-ocean sediment cores and the long pollen records that have been produced for lacustrine and marine sedimentary sequences from Greece, Italy and the Iberian margin. However, although relative glacial and interglacial intensities are well studied, there are still few proxies that permit quantitative terrestrial temperature and precipitation reconstruction. In this context, fauna-based climate reconstructions based on evidence preserved in archaeological or palaeontological sites are of great interest, even if they only document short windows of that climate variability, because (a) they provide a range of temperature and precipitation estimates that are understandable in comparison with present climate; (b) they may allow the testing of predicted temperature changes under scenarios of future climate change; and (c) quantitative temperature and precipitation estimates for past glacials and interglacials for specific regions/latitudes can help to understand their effects on flora, fauna and hominids, as they are directly associated with those cultural and/or biological events. Moreover such reconstructions can bring further arguments to the discussion about important climatic events like the Mid-Bruhnes Event, a climatic transition between moderate warmths and greater warmths during interglacials. In this paper we review a decade of amphibian- and reptile-based climate reconstructions carried out for the Iberian Peninsula using the Mutual Ecogeographic Range method in order to present a regional synthesis from MIS 22 to MIS 6, discuss the climate pattern in relation to the Mid-Bruhnes Event and the thermal amplitude suggested by these estimates and finally to identify the chronological gaps that have still to be investigated.

1. Introduction

Since Buffon, in his *Époques de la Nature* (1778), suggested that the climate of Western Europe must have been much warmer in the past to support the elephants, hippos, big cats and rhinos that were found as fossils, the vertebrate record has been understood to provide information on past climatic conditions, via the use of analogy with modern representatives. At first, studies of fossil vertebrates involved only counting the number of taxa and organisms present in an archaeological or palaeontological excavation and interpretation of these data was done in a qualitative and descriptive way only. Since then there have been many advances in both the methods used for analysis of fossil vertebrate remains and

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a great increase in scope of the questions. They have been used to address quantitative palaeoenvironmental reconstructions (e.g. Chaline et al., 1995; Lyman and O'Brien, 2005; Villa et al., 2010; Lopes et al., 2013), effect of climatic variability on vertebrates (e.g. Blois and Hadly, 2009; Blois et al., 2010, 2013; Bryson et al., 2010; McDonald and Bryson, 2010), changes in the vertebrate communities over time (e.g. Stewart, 2008, 2009; Hofreiter and Stewart, 2009), determination of refuge area (e.g. Stewart and Lister, 2001; Stewart and Cooper, 2008; López-García et al., 2010a), extinction and speciation processes (e.g. Lister, 2004; Nogués-Bravo et al., 2008; Gillespie et al., 2012), impact of vertebrates on flora (e.g. Johnson, 2009a; b; Gill et al., 2009, 2012; Faith, 2011; Brault et al., 2013), evolution of the ecological niches over time (e.g. Martínez-Meyer et al., 2004; Rödder et al., 2013) and finally the most advanced of these approaches involves quantitative reconstruction of palaeoclimatic conditions.

Methods for the quantitative inference of palaeoclimate using vertebrates dates back to the pioneering work of Brattstrom (1953, 1956), followed in the 1990's by an abundant literature (e.g. Markwick, 1994, 1998; Kay and Maden, 1996; Motuzco and Ivanov, 1996; Montuire et al., 1997; Aguilar et al., 1999; Montuire, 1999). The most commonly used vertebrates for palaeoclimatic reconstructions are mammals (of which small mammals dominate over herbivorous megafauna), followed by reptiles and amphibians. The parameters which can be reconstructed using vertebrate remains are principally temperature and precipitation (Table 1).

Methods for palaeoclimatic reconstructions based on vertebrates have increased both in number and accuracy in recent decades. However the application of most of these methods is restricted to a period or a biome/geographical location, is limited by the availability of a particular proxy or ecometric and in most cases does not permit a reconstruction of both temperature and rainfall. For example, in the case of palaeoclimatic reconstructions with thermal ecology (Brattstrom, 1956; Markwick, 1994, 1998; Böhme et al., 2006; Böhme at al., 2008) and the relation size-temperature-metabolic rate (Denny et al., 2009; Makarieva et al., 2005; Sniderman, 2009; Head et al., 2009a, b, 2013), only temperature parameters can be inferred. In the case of reconstructions based on hypsodonty (Fortelius et al., 2002, 2006; Damuth et al., 2002; Eronen and Rook, 2004; Eronen et al., 2010b, 2011) it is only possible to infer precipitation, a factor that is always subject to large uncertainties for the past (Porch, 2010). Another limitation of some of these methods is that they can only be applied to a species that presents the necessary ecometric, such as the large size of *Titanoboa* (Head et al., 2009a), *Beelzebufo* (Makarieva et al., 2009) and *Barbaturex* (Head et al., 2013) or to a taxon that is restricted today to tropical environments such as Crocodylia (Markwick, 1994, 1998).

Finally, there are other methods that can only be used for more recent periods, such as the Mutual Ecogeographic Range (Martínez-Solano and Sanchiz, 2005; Blain et al., 2009, 2016a), a variant of the numerous methodologies for climate reconstruction which use the modern distribution of species such as the Mutual Climatic Range and the Modern Analogue Technique (see Birks et al., 2010 for a synthesis and comparison), due to the fact that it is necessary to have extant representatives for the species recovered from archaeological sites. This method has been applied mainly to the late Middle and Late Pleistocene-Holocene for small-mammals (e.g. López-García et al., 2008, 2010b; 2011a; b; c; d; 2013a; b; Bañuls-Cardona et al., 2012, 2013; 2014; Fernández-García and López-García, 2013; Fernández-García, 2014; Rey-Rodríguez et al., 2016; Fagoaga et al., 2017, 2018) and back to the earliest Pleistocene for herpetofauna (e.g. Martínez-Solano and Sanchiz, 2005; Blain, 2005, 2009, 2012–14; Blain et al., 2007, 2008a; 2009, 2010a,b; 2011a; b; 2012a; b, 2013a, b, c, 2014a, b, c, 2015, 2016a, 2017a, b, 2018; Blain and Corchón Rodríguez, 2017; Agustí et al., 2009; Marquina et al., 2017; Villa et al., 2018a; b). Using this method in older periods with extinct taxa (especially mammals) and relating them to their closest current representatives could increase the error in palaeoclimatic reconstruction since the extinct taxon may not necessarily have had the same niche as its current representatives (Rödder et al., 2013), and during the past the biological communities were not necessarily analogous with present ones (Williams and Jackson, 2007; Semken et al., 2010; Urban et al., 2012; Correa-Metrio et al., 2012) and this disparity increases further back in time (Stewart, 2008). The presence of non-analogous or disparate communities is also a problem when reconstructions are based on current biomes or ecoregions, as in the case of the transfer function method (Hernández-Fernández, 2001, 2006; Hernández-Fernández and Peláez-Campomanes, 2003, 2005; Hernández-Fernández and Vrba, 2006; Hernández-Fernández et al., 2007) and the variant of the mutual climate range method of Polly and Eronen (2011), as in the past these biomes or ecoregions did not necessarily exist as today.

The Mutual Ecogeographic Range (MER) has been applied, under different names (see Lyman, 2016), to fossil amphibians and reptiles at a regional level (Catalonia) or for some Spanish provinces (Granada, Murcia, Burgos, Castellón and Valencia) by Blain (2005, 2009) and at a peninsular scale first by Martínez-Solano and Sanchiz (2005) and since then by Blain et al. (2009) and subsequent publications. According to Birks et al. (2010), the Mutual Climatic Range is part of indicator-species approaches (based on the "presence/absence of one or few taxa") whereas Modern Analogue Technique is part of assemblage approaches (based on the "presence/absence of many taxa"). As a bioclimate envelope approach is not generated for each taxon, MER seems to be closest to a Modern Analogue Technique. Moreover in contrast to the indicator species approaches, the assemblage approach considers the fossil assemblage as a whole (as we do, even if we are aware that generally a very few ecologically strong indicator species have more weight in such reconstruction than other more ubiquitous ones) and the relative abundances of all the different fossil taxa. In contrast to Modern Analogue Technique it is assumed (as in Mutual Climatic Range approaches) that a taxon has an equal probability of occurrence anywhere within its climate range (Hupper and Solow, 2004; Horne and Mezquita, 2008) even if this has been shown not to be true in many empirical studies.

Assuming niche conservatism, MER involves finding the modern sample(s) that is (are) most similar to the fossil assemblage. Then the past climatic conditions are inferred from the climate variable(s) for the analogous modern sample(s). Application of MER to the Spanish fossil record is possible because most of the fossil Pleistocene amphibians and reptiles belong to extant species, with only a few exceptions (see Blain et al., 2016b for a recent review). The climate reconstruction is then based on the mean of the whole analogous modern samples (expressed here as 10×10 km UTM squares) without any weighting as usually the distribution of the obtained values is normal (see for example Martínez-Solano and Sanchiz, 2005). Such a method, based only on absence/presence (and not abundance), is consequently free from taphonomical bias and over-representation of some species in the fossil assemblages that may be more linked with the diet preference of the agent of accumulation or to the close proximity of a particular environment (rocky areas for karst sites or water biotopes for lake sites) than with climate.

Lobo et al. (2016) verified the assumption that current ecological niches for amphibians represent a reliable inference tool for past environmental conditions. This assumption can also certainly be extended to reptiles. Lobo et al. (2016) also demonstrate that for direct raw inferences, the combined taxa sets do not improve in