



The influence of climate on species distribution over time and space during the late Quaternary



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ABSTRACT

Understanding the effect of climate on the composition of communities and its change over time and space is one of the major aims in ecology and paleoecology. Herein, we tackled on this issue by studying late Quaternary large mammal paleocommunities of Eurasia. The late Quaternary was a period of strong environmental instability, especially characterized by the occurrence of the last glacial maximum (LGM). We used community phylogenetics and joint species distribution models in order to understand the factors determining paleocommunity composition in the late Quaternary. Our results support the existence of strong climatic selection operating on the LGM fauna, both through the disappearance of warm-adapted species such as *Elephas antiquus*, *Hippopotamus amphibius*, and *Stephanorhinus hemitoechus*, and by setting the stage for the existence of a community characterized by cold-adapted large mammals. Patterns of abundance in the fossil record, co-occurrence between species pairs, and the extent of climatic forcing on faunal composition, differ between paleocommunities, but not between extinct and extant species, which is consistent with the idea that climate change, rather than the presence of humans, exerted a major effect on the survival of the late Quaternary megafauna.

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1. Introduction

Understanding the influence that climate change has on the distribution of individual species and ecological communities over time and space is one major goal in ecology (Ovaskainen et al., 2013; Parmesan and Yohe, 2003; Walther et al., 2002). Many accounts focus on whether species with similar environmental tolerances react as an integrated community, or show individualistic responses either, to change (Burns et al., 1996; Lorenzen et al., 2011; Parmesan, 2006; Villalobos et al., 2016a). These approaches mostly focus on short-term species reactions. However, this could be misleading as deep time climatic events are known to have influenced the structuring of current communities (Davis and Shaw, 2001; Svenning et al., 2015; Valiente-Banuet et al., 2006). Hence, increasing attention is now being devoted to methods apt to integrate such deep time information in studies dealing with the ecological effects of climate change at the community level, either

by explicitly modeling the paleobiogeography of the fossil record (Villalobos et al., 2016b), or by relying on the evidence stored in phylogenetic trees (Diniz-Filho and Bini, 2007; Diniz-Filho et al., 2013).

The paleoecological approach to the study of community composition and change over time (i.e. temporal turnover) is obviously marred by the issues of diachrony and the incompleteness of the fossil record (Alroy, 1998; Raia et al., 2009). Fortunately, several statistical methods are now able to account for these sampling biases (Fernández and Vrba, 2005; Raia et al., 2006; Wagner and Marcot, 2013), and to apply modern ecological tools to fossil communities (Barnosky, 2005; Blois et al., 2014; Cano et al., 2014; Cantalapiedra et al., 2011; Raia, 2010). As pertains to the influence of climate change on community composition and its evolution, several reports now clearly indicate that Quaternary fauna temporal turnover increased during periods of environmental turmoil (Barnosky, 2010; Blois et al., 2014; Blois and Hadly, 2009; Faith and Behrensmeyer, 2013; Prothero, 2012; Raia et al., 2005), suggesting that species co-occurring in time should also have comparable climatic tolerances (Burns et al., 1996; Raia, 2010; but see Villalobos et al., 2016b). Rates of speciation and extinction

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similarly affect community composition, and many studies link such rates to the climatic unrest that characterized the Quaternary period (Barnosky, 2005; Dynesius and Jansson, 2000; Kozak and Wiens, 2010; McPeck, 2008) still pointing to a large effect of climate on the identity of species within communities.

The late Quaternary was a period of extraordinarily intense environmental change (Dawson, 2013). By the end of this period, the last glacial maximum (LGM) marked one of Earth's most extreme moments of climatic variability (Clark et al., 2009). The intense, global sway in climate greatly affected terrestrial faunas, causing long-distance species movement (Raia et al., 2012), decreasing species endemism, and possibly increasing extinction rate in small-ranged species (Davis and Shaw, 2001; Sandel et al., 2011), and in small mammals (Blois et al., 2010). As for large mammals, LGM faunas in Eurasia were characterized by steppe specialists such as the woolly mammoth, saiga, woolly rhino, musk-ox and steppe bison, forming a no longer existent ecosystem known as the mammoth steppe (Dale Guthrie, 2001; Zimov et al., 2012). The demise of such ecosystem is usually viewed as part of the late Pleistocene megafaunal extinction (Koch and Barnosky, 2006), and attributed either directly to the effect of climate change (Grayson, 1977; Grayson and Meltzer, 2003; Lima-Ribeiro et al., 2014; Meltzer, 2015; Wroe et al., 2013), or to human overkill (Alroy, 2001; Brook and Bowman, 2005; Surovell et al., 2016). Although a number of warm-adapted, middle to late Pleistocene species went extinct before the LGM (e.g. hippopotamus, straight-tusked elephant, cave hyena) several components of the LGM steppe megafauna are still alive today (e.g. saiga antelope, musk-ox, reindeer). Other LGM species already occur in the warm last interglacial (LIG) preceding the LGM (e.g. woolly mammoth, steppe bison, woolly rhino). Finally, a number of species co-occurring geographically to the mammoth steppe megafauna, such as the Irish elk, red deer, and wolf, were not steppe specialists. Such idiosyncrasies suggest that neither the identity of the mammoth steppe megafauna, nor its demise were necessarily or solely controlled by the extraordinarily harsh LGM climate. Here, we ask whether climate change had any discernible effect on megafauna distribution over time and space, by using climate-explicit approaches to study species co-occurrence patterns in paleo-communities spanning in age from the last interglacial (LIG) to the beginning of the Holocene (thus encompassing the LGM). We tested whether climate shaped the composition and turnover of megafauna communities during LIG, LGM and Early Holocene discrete temporal intervals. This question also takes indirectly on the issue of whether humans, rather than climate, caused the extirpation of the megafauna at the end of the LGM. If humans had a major impact, we expect LGM faunal composition to bear little or no signature of climatic effects, since the incidence of species in the LGM fossil record would be more influenced by human hunting pressure than by the prevailing environmental conditions.

To such aim, we applied joint species distribution models and community phylogenetics techniques. The former allow identifying the climatic conditions individual species lived in, and how much species with similar climatic requirements tend to co-occur in space. With this, it is possible to ascertain how large the effect of climate was on patterns of geographic co-occurrence (Hui et al., 2015; Pollock et al., 2014). Community phylogenetics offers the opportunity to understand the factors affecting community composition, telling the effects of competition apart from those of habitat filtering (Godoy et al., 2014; Kembel, 2009). Habitat filtering is commonly associated with phylogenetic clustering since closely related species tend to show similar climatic tolerances. Conversely, high levels of interspecific competition lead to phylogenetic overdispersion because niches of closely related species tend to overlap consistently, so that they settle apart from each other (in space) in

order to reduce interspecific competition. Under habitat filtering, evolutionary convergence originates phylogenetic overdispersion because species from different branches of the tree tend to converge on similar climatic tolerance. Finally, under intense competition and in the presence of convergence the community structure shows a random dispersion or phylogenetic clustering either (Cavender Bares et al., 2004; Cavender-Bares et al., 2009; Ndiribe et al., 2013; Swenson et al., 2006; Webb et al., 2002). Community phylogenetics was successfully extended to the study of fossil faunas (Raia, 2010). Herein, we statistically defined the paleocommunities first (Raia et al., 2009, 2006), then tested species co-occurrence patterns as explained by climate by using JSDMs (Hui et al., 2015; Pollock et al., 2014). Eventually, we applied community phylogenetics to test whether the paleocommunity composition was influenced by climate, or by ecological interactions either. Our goal was to compare LGM to pre- and post-LGM communities to understand the effect of climate change on patterns of co-occurrence in these fossil assemblages.

2. Material and methods

2.1. Setting the database of fossil occurrences and feeding categories

We prepared a database including 6462 Eutherian mammals fossil occurrences distributed over 947 fossil localities for 161 extinct and living species. This database geographically spans over Eurasia and ranges in age from 0.130 to 0.005 Mya. We collected the information about fossil localities and their faunal lists from the following databases: the paleobiodb database (<https://paleobiodb.org/#/>), the NOW database (<http://www.helsinki.fi/science/now/>) integrated to the databases provided in Raia et al. (2009) and Carotenuto et al. (2010, 2015). In order to assess the influence of species ecology on community composition, we assigned each species to distinct feeding categories after Price et al. (2012), Meloro et al. (2008) and Raia et al. (2010) (see Supplementary Table 1 for species attributions). When compiling the dataset, we discarded species with uncertain classification and fully revised them for synonyms. The dataset includes both biochronological and radiometric estimates as localities age. For localities with dubious estimates, we used the ages provided in Carotenuto et al. (2010), which were computed by using spectral ordering (Fortelius et al., 2006). Under this procedure, Fiedler eigenvector scores are computed in order to collate the fossil localities in time, depending on the similarity of their faunal lists. Then scores are regressed against radiometric age estimates to obtain the mathematical relationship between scores and ages. The formula is eventually applied to those localities which lack a reliable age estimate. With a very high R^2 (0.98) between Fiedler scores and localities with radiometric age estimation (Raia et al., 2009), this method proved to be very successful to obtain age references for fossil localities of uncertain age.

We divided the database into three temporal intervals, according to the most important climatic events of the Quaternary: from 0.130 to 0.115 Mya (a temporal range including the Last Interglacial, here LIG); from 0.022 to 0.0145 Mya focusing on LGM, and from 0.009 to 0.005 Mya (around the Holocene Climatic Optimum, here epitomized simply as “Holocene”, HOL).

2.2. Identifying paleo-communities (PCOMs)

Paleo-communities (PCOMs sensu Raia et al., 2006) are statistically discrete groups of fossil localities (Raia et al., 2009, 2005). To identify LIG, LGM and HOL PCOMs we used bootstrapped cluster analyses (BCA), as in (Raia et al., 2009, 2005). BCA works by performing a single cluster analysis (the reference clusters) based on

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