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The relationship between mammal faunas and climatic instability since the Last Glacial Maximum: A Nearctic vs. Western Palearctic comparison

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A B S T R A C T

Climate has played a key role in shaping the geographic patterns of biodiversity. The imprint of Quaternary climatic fluctuations is particularly evident on the geographic distribution of Holarctic faunas, which dramatically shifted their ranges following the alternation of glacial-interglacial cycles during the Pleistocene. Here, we evaluate the existence of differences between climatically stable and unstable regions – defined on the basis of climatic change velocity since the Last Glacial Maximum – in the geographic distribution of several biological attributes of extant terrestrial mammals of the Nearctic and Western Palearctic regions. Specifically, we use a macroecological approach to assess the dissimilarities in species richness, range size, body size, longevity and litter size of species that inhabit regions with contrasting histories of climatic stability. While several studies have documented how the distributional ranges of animals can be affected by long-term historic climatic fluctuations, there is less evidence on the species-specific traits that determine their responsiveness under such climatic instability. We find that climatically unstable areas have more widespread species and lower mammal richness than stable regions in both continents. We detected stronger signatures of historical climatic instability on the geographic distribution of body size in the Nearctic region, possibly reflecting lagged responses to recolonize deglaciated regions. However, the way that animals respond to climatic fluctuations varies widely among species and we were unable to find a relationship between climatic instability and other mammal life-history traits (longevity and litter size) in any of the two biogeographic regions. We, therefore, conclude that beyond some biological traits typical of macroecological analyses such as geographic range size and body size, it is difficult to infer the responsiveness of species distributions to climate change solely based on particular life-history traits.

1. Introduction

Climate has played a key role in shaping current biodiversity patterns (see e.g. Currie, 1991; Hawkins et al., 2003). Distinguishing the relative importance of past and present climates on the geographic ranges of species is a fundamental question in biogeography. Hypotheses related to current climate have all been identified as plausible explanations of broad-scale patterns in species richness for birds and mammals (Hawkins et al., 2003; Torres-Romero and Olalla-Tárraga, 2014), while the imprint of past climates remains little explored. Several researchers have shown the relevance of climatic oscillations during the Pleistocene and the alternation of glacial-interglacial cycles throughout this geological epoch as a crucial factor to understand the geographic distribution of species nowadays (Hawkins and Porter, 2003; Svenning et al., 2015; Weigelt et al., 2016). In particular, most of the Holarctic region was covered by ice during the Last Glacial

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Maximum (LGM, 21 000 years ago), which caused dramatic changes in the distribution of organisms. The exposure of large areas to the LGM ice-sheets heavily impacted the climatically suitable areas for many species of terrestrial mammals in this biogeographic region, reducing their geographical ranges and increasing their vulnerability to extinction (Svenning et al., 2015).

Pleistocene glaciations left a legacy of high extinction rates and impoverished faunas, with those species highly sensitive to rapid climate variations either contracting their geographic ranges, on one hand, or catastrophically collapsing on the other (Johnson, 2002; Thuiller et al., 2005; Sandel et al., 2011). In the wake of climatic amelioration Pleistocene ice sheets retreated and favorable habitats expanded, and species consequently recolonized these habitats and expanded their distribution range (Provan and Bennett, 2008). Glacial refugia may have played a major role for the survival of animal and plant species during unfavorable Pleistocene environmental conditions, and as sources of post-glacial recolonization (Hewitt, 2000). According to the post-glacial recolonization hypothesis (Hewitt, 1999, 2000), highly vagile species could more rapidly spread northwards and recolonize newly exposed areas, whereas geographic range expansions for the majority of (less vagile) species would have been slower. This scenario is also coincident with the observation that climatic stability over time in the Holarctic tends to be associated with higher species diversity in mammals and birds (Hawkins and Porter, 2003).

The climatic stability hypothesis predicts that climatically stable areas – compared to unstable regions – are associated with high levels of richness, endemism and intraspecific genetic diversity (Fjeldsa and Lovett, 1997; Jansson, 2003). While climate stability favors species persistence and speciation, the climatically unstable areas increase extinction risk, and species adaptability to instability becomes essential to predict which species are most likely to survive under global climate change (Dynesius and Jansson, 2000; Sandel et al., 2011). Many studies have explored how the distributional ranges of plants and animals may be affected by long-term historic climatic fluctuations (see. e.g. Lima-Ribeiro et al., 2010; Werneck et al., 2012; Terribile et al., 2012). Nonetheless, there is less evidence on the specific life-history traits (such as body size, geographic range size, litter size and a suite of reproductive traits) that determine the responsiveness of species to survive under such climatic variability scenarios (but see. e.g. Isaac, 2009; Tafani et al., 2013; González-Suarez and Revilla, 2012). Possible individual responses of species to better cope with climate change include (among others) (i) the ability to survive longer (and thus integrate the effects of change across a longer lifespan), (ii) flexibility in migration patterns or expansions of geographic ranges, and (iii) change in seasonal and circadian rhythms to enter hibernation, torpor, aestivation, latency, and use of burrows (see e. g. Morris et al., 2008; Ozgul et al., 2010; Turbill et al., 2011). Understanding the historical adaptive value of these life-history traits is fundamental to better predict the response of species to future global climate change (see. e.g. Winkler et al., 2002; Both and Visser, 2005). Indeed, the extent to which a life-history trait mitigates the impact of environmental fluctuation stress on fitness is perhaps the most robust gauge of its adaptive value (Stahler et al., 2013). Here, we evaluate if any differences exist between climatically stable and unstable areas (defined as a measure of the local rate of displacement of climatic conditions since the LGM) in the geographic distribution of some biological attributes of extant Holarctic terrestrial mammal faunas. Specifically, we use a broad-scale macroecological approach to assess the dissimilarities in species richness, range size, body size, longevity and litter size of extant mammal species that inhabit regions with contrasting histories of climatic stability (since the LGM). Typically, ecogeographical ‘rules’ have been used to attempt to generalize the responses of the Earth's faunas and floras to the influences of environmental factors (McDowall, 2008). Beyond the well-known latitudinal diversity gradient ¬ the general decrease in species richness towards seasonal macroclimatic regimes (Hawkins et al., 2003; Hillebrand, 2004) – some other ecogeographical rules also predict varying biological traits between climatically stable and unstable regions. For instance, Rapoport's rule describes a positive relationship between the geographic range size of species with increasing latitude and elevation (Stevens, 1992; Gaston et al., 2008), whereas Bergmann's rule refers to a general pattern of increasing body size with decreasing temperature (Bergmann, 1847; Diniz-Filho, 2008).

Our contribution to this question focusses on climatic stability. Our first goal was to determine differences (if any) among climatically stable and unstable areas in species richness and life history traits –range size, body size, longevity, and litter size – for Nearctic and Western Palearctic regions. We hypothesize (1) climatically unstable areas will be inhabited by less species, and (2) species in climatically unstable areas will have broader geographic distributions, larger body sizes, greater longevities, and smaller litter sizes than those inhabiting climatically stable environments. Thus, we predict that mammal fauna in climatically stable areas will be dominated by those species with range-restricted, small-bodied, and short-lived (Araújo et al., 2008; Graham et al., 2010; Lyons et al., 2010). To test whether these differences are robust among continents, our second goal is to identify differences between mammalian orders and biogeographic region (i.e. Nearctic vs. Palearctic) and conduct separate analyses in each case. If Quaternary climatic fluctuations have had a significant effect on the geographic distribution of terrestrial mammals, these should mostly be evident in the Holarctic (Davies et al., 2009).

2. Materials and methods

2.1. Geographical distribution, life-history traits and climatic data

Mammal range maps were compiled from the IUCN Red List (http://www.iucnredlist.org, accessed in March 2015). All islands were excluded to avoid possible island effects (Whittaker and Fernández-Palacios, 2007). Overall, we compiled information for a total of 563 and 259 mammal species (with 15 species shared in both regions) that occur in the Nearctic and Western Palearctic (until the Ural Mountains) region respectively. We used ArcGIS 10.0 to calculate geographical range sizes (hectares) for each mammal species.

We gathered information on four life-history traits that are commonly used as predictors of extinction risk in terrestrial mammals (Collen et al., 2011; Murray et al., 2011; González-Suarez and Revilla, 2012): geographic range area, adult body size, longevity, and litter size. Data were primarily obtained from “Pantheria” (Jones et al., 2009), which contains more than 5416 species records, complemented with “AnAge” (online database, http://genomics.senescence.info/species/-maintained by De Magalhães and Costa, 2009) and “MoM v4.1” data (Smith et al., 2003). We confirm our data with the taxonomy of Wilson and Reeder (2005) to avoid taxonomic discrepancies. To minimize the effects of the typically right-skewed distribution of body sizes, longevity as well as range size, the records were log-10 transformed.

Following Sandel et al. (2011), we based our analysis around the geographical patterns in duration of climate stability, defined by major climatic shifts during the Late Quaternary climate-change, and measured as the mean annual temperature velocity since the Last Glacial Maximum (21 000 year ago). Climate-change velocity is thus defined as the local rate of displacement of climatic conditions