# Constraint envelope analyses of macroecological patterns reveal climatic effects on Pleistocene mammal extinctions

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## ABSTRACT

Quantitative analysis of macroecological patterns for late Pleistocene assemblages can be useful for disentangling the causes of late Quaternary extinctions (LQE). However, previous analyses have usually assumed linear relationships between macroecological traits, such as body size and range size/range shift, that may have led to erroneous interpretations. Here, we analyzed mammalian datasets to show how macroecological patterns support climate change as an important driver of the LQE, which is contrary to previous analyses that did not account for more complex relationships among traits. We employed quantile regression methods that allow a detailed and fine-tuned quantitative analysis of complex macroecological patterns revealed as polygonal relationships (i.e., constraint envelopes). We showed that these triangular-shaped envelopes that describe the macroecological relationship between body size and geographical range shift reflect nonrandom extinction processes under which the large-bodied species are more prone to extinction during events of severe habitat loss, such as glacial/interglacial transitions. Hence, we provide both a theoretical background and methodological framework to better understand how climate change induces body size-biased species sorting and shapes complex macroecological patterns.

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## Introduction

During a geological instant encompassing the last 50,000 yrs of the late Quaternary, hundreds of species of large-bodied animal, which were mostly mammals but also included birds and reptiles, died out in an extinction event on all continents and certain island systems when the climate changed through the last ice age and modern humans spread out of Africa. Because of the chronological coincidence among events at a global scale, climate change and human impacts have been proposed as the main causes of the late Quaternary extinctions (the LQE) (see the state-of-the-debate in Koch and Barnosky, 2006).

The climatic hypothesis (see Grayson, 1984, for a pioneering review) suggests that such extinctions occurred because: 1) large-bodied animals were not able to adapt to new climatic conditions during the last deglaciation (a top-down effect) (Guthrie, 2003); 2) viable populations were no longer supported because suitable conditions were reduced (a bottom-up effect) (Graham and Lundelius, 1984; Nogués-Bravo et al., 2010; Rawlence et al., 2012; but see Robinson et al., 2005 and Gill et al., 2009 for contrary evidence); or 3) both. Based on the theories of current species extinction (Caughley, 1994), a top-down effect would promote the extinction of small populations due to genetic and demographic

factors, which is known as the small-population paradigm (Soulé and Wilcox, 1980), whereas the climate dynamics in a bottom-up effect would increase the extinction risk through a contribution to the general decline of populations, which is known as the declining-species paradigm (Simberloff, 1986; Diamond, 1989; see Purvis et al., 2000 for empirical evidence). Moreover, climate change also causes shifts in geographical distribution of species that have severe implications for population persistence (see Jansson and Dynesius, 2002).

The anthropogenic hypothesis, however, assumes that the human range expansion was the underlying cause of the LQE, and its effects can be either direct (hunting) or indirect (competition for resources or disturbance to habitats). Human hunting is the most accepted stressor, and it became popular after the publication of Martin's overkill hypothesis for the Americas in the late 1960s (Martin, 1967, 1973) and has been reinforced with a global model (Martin, 1984). The overkill hypothesis argues that early humans were big game hunters and caused the extinction of large-bodied mammals by overkilling much of their prey as modern humans spread out of Africa (Martin, 1984). Disturbance to habitats, an indirect effect, is considered to have had the most severe effects in insular environments (Grayson and Meltzer, 2003).

Although valid arguments are provided for both hypotheses, climate change and human impacts have often been presented as competing hypotheses, and a consensus about the causes of the LQE appears unlikely as indicated by the contradictory views among different authors

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(e.g., Grayson and Meltzer, 2003, 2004; Fiedel and Haynes, 2004). An important point against the climatic hypothesis, for instance, is that glaciations were recurrent throughout the Quaternary, but species went extinct only during the most recent glaciation (Koch and Barnosky, 2006; but see a defense by Wroe et al., 2013). Regarding anthropogenic hypothesis, empirical evidence is scarce for direct human exploitation of large-bodied mammals such as kill sites (Meltzer, 1986; Borrero, 2009; but see Surovell and Waguespack, 2008 and Surovell and Grund, 2012 for a different interpretation) and the coexistence between the earliest humans and now-extinct species is still questioned in certain regions of the world (Lima-Ribeiro and Diniz-Filho, 2013a, 2013b).

Contrary to the two single causes being competing, support for a synergetic interaction of these two main extinction drivers has been increasingly accepted as the most likely explanation for the megafauna extinction event at the end of the Pleistocene (Koch and Barnosky, 2006; Barnosky and Lindsey, 2010; Lorenzen et al., 2011; Lima-Ribeiro et al., 2012a, 2012b; Prescott et al., 2012; Lima-Ribeiro and Diniz-Filho, 2013a). This synergetic hypothesis suggests that increasing human impacts to large-bodied species that were in decline as a result of the collapse of climatically suitable areas were more likely the final thrust that set the place and time of megafauna extinctions (Cione et al., 2003, 2009; Nogués-Bravo et al., 2008; Lima-Ribeiro et al., 2013).

The evaluation of each hypothesis has been hampered by a lack of reliable fossil data for many species in several parts of the world and by challenges in using robust methodological approaches enabling quantitative analyses and syntheses (see comments in Lima-Ribeiro and Diniz-Filho, 2013a, 2013b). Recently, advances in quantitative analysis regarding the causes of the LQE have been proposed by using a macroecological framework (Lyons, 2003; Lyons and Smith, 2010; Lyons et al., 2010; Grund et al., 2012). By characterizing the body size of Pleistocene mammals, for instance, Smith et al. (2003) were able to conduct quantitative comparisons of the body size distributions and test such hypotheses at continental scales (Smith and Lyons, 2011). However, macroecological patterns are often complex and improper methods and invalid assumptions have often been used to explain such complexity. An important consequence from such analyses is that the resulting conclusions are likely to be biased and tend to reinforce the competitive debate by moving away from recent evidence for the multiple-driver nature of the LQE.

For instance, following the species-decline paradigm from climate effects, Grund et al. (2012) and Lyons et al. (2010) assumed that if climate change was an important driver of the LQE, then the large-bodied species (or extinct mammals) should present, on average, smaller Pleistocene range sizes and larger range shifts than small-bodied species. Although the LQE was certainly selective toward large-bodied species (Smith and Lyons, 2011), this assumption is challenged by the complexity of the macroecological patterns arising from the relationship between body size and range size/range shifts (Brown and Maurer, 1987). Hence, the studies by Grund et al. (2012) and Lyons et al. (2010) do not support climate change inducing body size-biased species sorting. By exclusion, their conclusions support only human impacts as a driver of the LQE.

Here, we re-analyze the quantitative dataset from Grund et al. (2012: Fig. 3), which is part of a dataset from Lyons (2003) and Lyons et al. (2010), and show that the macroecological pattern from the relationship between body-size and range-shift supports climate change as an important driver of the LQE, which is in contrast to their original conclusions. Further, we advanced both the theoretical background and methodological framework to better understand how climate change can shape macroecological patterns. We employed quantile regression methods that allow a detailed and fine-tuned quantitative analysis that accounts for the complex macroecological patterns revealed by such relationships. Therefore, we suggest a new interpretation by highlighting a key mechanism from range-shift dynamics inducing body size-biased species sorting, with important implications for the role of climate change on the LQE.

## Constraint envelopes and extinction risks: theoretical and methodological issues

### Theoretical background

Every aspect of the biology of a species is often influenced by and reflected in its body size. Body size can easily be obtained from living individuals or fossil data and is a key component in macroecological analysis (Peters, 1983), from which other species traits or attributes can be estimated by allometric scaling relationships (Brown, 1995; Silva and Downing, 1995). However, different macroecological or macroevolutionary processes affect the evolution of body size across taxa and space (Cooper and Purvis, 2009, 2010; Diniz-Filho et al., 2009), and the resulting macroecological patterns are often complex (see examples in Jones et al., 2011). A relatively common and complex macroecological pattern involving body size as a predictor is represented by a polygonal relationship (resembling a triangular shape) instead of a linear relationship. In a bivariate space ($X$–$Y$ plan), the triangular-shaped relationships arise because many species attributes, often represented along the $Y$-axis, present heterogeneous variance throughout the body-size gradient, often represented along the $X$-axis (Fig. 1). In macroecology, these triangular-shaped relationships are commonly referred to as "constraint envelopes".

Constraint envelopes are well known in the macroecological literature (Brown and Maurer, 1987, 1989; Brown, 1995; Gaston and Blackburn, 2000; Blackburn and Gaston, 2001, 2002; Agosta and Bernardo, 2013), particularly from the study of the relationship between body size and geographical range size (a complete review encompassing other relationships can be found in Blackburn and Gaston, 2001). The underlying prediction for these envelopes is that if macroecological or macroevolutionary processes impose absolute functional constraints on the species level traits, including emergent traits such as geographic range size and shift or population density, then the resulting patterns should reflect those constraints (Maurer et al., 2004; see also Blackburn and Gaston, 2001; Smith et al., 2010).

When analyzing constraint envelopes, the limiting factor should be the macroecological factor that affects the long-term persistence of the species. In this sense, Brown and Maurer (1987, 1989) proposed that the size of the minimum viable population of each species is the key limiting factor shaping the constraint envelope of the geographical range-size/body-size relationship. The minimum viable population can be defined as the population size below which the time to extinction for a given species is considerably shorter than expected by the average lifespan of their phylogenetic relatives (Blackburn and Gaston, 2001). This definition allows a mechanistic prediction to be made for the origin of constraint envelopes that follows the energetic equivalence rule (Damuth, 1981), which states that the amount of energy per unit of area that each species is able to use is independent of its body size (Kelt and Van Vuren, 2001). This implies that large-bodied species must maintain lower population densities and occupy wider areas than small-bodied species to maintain their minimum viable populations. As a result, species with larger body sizes require larger range sizes to persist for substantial time periods (Brown and Maurer, 1987). In contrast, small-bodied species can present geographical ranges that are either narrow, with populations surviving in high local densities in a few spatially localized habitat patches, or wide, with populations occupying many small but spatially scattered patches (Fig. 1; see also Foote et al., 2008 for details about range size and taxa duration).

These differential and area-dependent extinction thresholds generate the process by which constraint envelopes arise for body-size/range-size relationships across assemblages. The probability of extinction usually increases when large-bodied species become constrained to small geographical ranges because their populations will easily decrease below their minimum viable population size (Brown and Maurer, 1987, 1989; Brown, 1995; Blackburn and Gaston, 2001, 2002).