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Bigger kill than chill: The uneven roles of humans and climate on late Quaternary megafaunal extinctions

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ABSTRACT

Starting around 50,000 years ago, most large terrestrial animals went extinct in most continents. These extinctions have been attributed either to climatic changes, impacts of human dispersal across the world or a synergy among both. Most studies regarding these extinctions, however, have focused on particular continents or used low-resolution analyses. We used recent advances in fossil dating and past climatic models in a high-resolution quantitative analysis, comparing the explanatory power of the hypotheses at global scale. The timing of human arrival to each region was the best explanation for the extinctions. Climatic effects, where present, were additive rather than synergistic with human arrival. While climatic variation was a contributory cause that helped explaining the process, anthropogenic impacts were the necessary cause that drove it.

1. Introduction

Since the 19th century, when science became aware of the sudden and geologically recent disappearance of many large-bodied animals, the late Quaternary Extinctions (LQE) have remained a great and controversial matter (Grayson, 2008). Starting around 50,000 years ago, about two thirds of all large terrestrial animal genera went extinct in a sequence that affected most continents (Koch and Barnosky, 2006). For a long time, two main hypotheses – attributing these extinctions either to climatic changes during the last glacial event or to the impacts of modern man's dispersal across the world – have divided the academic community. Many researchers also came to defend a synergy between both factors as a more plausible scenario for the extinctions (Barnosky, 2004; Nogués-Bravo et al., 2008; Lorenzen et al., 2011; Prescott et al., 2012; Lima-Ribeiro and Diniz-Filho, 2013), although controversies about the balance of climate and humans as extinction drivers still remain (Lima-Ribeiro et al., 2012; Prescott et al., 2012).

The late Quaternary megafaunal extinctions were a global phenomenon and we believe that a global approach is the best way to understand causal mechanisms. This would bring the full range of temporal and geographical variation in extinction times to bear, allowing one to disentangle the overall signal from regional trends. Most studies, however, have focused on particular continents and taxa (e.g. Alroy, 2001; Diniz-Filho, 2004; Johnson, 2006; Nogués-Bravo et al., 2008). A few global analyses have been presented (Lyons et al., 2004; Gillespie, 2008; Prescott et al., 2012; Sandom et al., 2014); but innovative and insightful as these studies have been, they carry some problems. While some works lack quantitative analyses of the proposed extinction causes (e.g. Lyons et al., 2004; Gillespie, 2008), others are based on crude and often unrealistic scenarios of human arrival and megafaunal extinction (Prescott et al., 2012; see Lima-Ribeiro et al., 2012 for details). Both Prescott et al. (2012) and Sandom et al. (2014) include non-quantitative variables in their models, as their hominin paleogeography variable is based on discrete human arrival scenarios. The most recent global analysis (Sandom et al., 2014) is based on global databases on extinct (and extant) mammals' distributions that are bound to be incomplete and/or to contain a proportion of untrustworthy data (as shown by the inclusion on the analysis of Africa and Southern Asia, regions with poor paleontological

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records). Additionally, their approach lacks a comparison of extinction dates with human arrival and climatic change focused on chronology (rather than geography).

Fossil dating allows the establishment of synchrony between extinction events and their potential drivers. In the last years, a growing number of dates have been published and reviewed around the world (see Supplementary References). Improved climatic models have been developed for the last 122,500 years (Andersen et al., 2004). These advances made a once unfeasible chronological global analysis of climatic changes, human arrival to each region and extinction of megafaunal taxa a concrete possibility, opening a promising path for resolving the extinction debate.

In light of these new chronometric advances, we performed an exhaustive gathering of data for human first appearance dates (HFADs) and last appearance of megafaunal genera (MLADs) on nineteen regions across the globe, together with climatic variation through the late Quaternary, to provide the first high-resolution chronological analysis of the LQE extinctions. We tested the hypotheses that human arrival or climate variance would be responsible for the extinction of megafaunal genera. This more detailed approach should advance the extinction debate, providing the first quantitative chronological test of the roles of anthropogenic impacts and climatic variation on the demise of the world's megafauna.

2. Materials and methods

2.1. Data

The predictions of both hypotheses were compared in order to evaluate them. The environmental hypothesis predicts that extinctions would have occurred during or following intense climatic changes through the late Quaternary. The human impact hypothesis, on the other hand, predicts that extinctions would have followed human colonization of each landmass across the planet.

First, last appearance dates of megafauna (MLADs) species and first appearance dates of anatomically modern humans (HFADs) on several landmasses were gathered from all published scientific sources that could be assessed (see Supplementary Tables 1 and 2). These landmasses included South America, North America, Caribbean islands, Northern and Western Eurasia, Australia, Tasmania, Madagascar, New Zealand and Japan. Climate variation in the North hemisphere through the last millennia of the Quaternary was assessed by the North Greenland Ice Core Project (NGRIP) data on the variation of oxygen isotopic composition in ice cores (Andersen et al., 2004). This database comprises $\delta^{18}O$ data from the last 122,500 years, with ^{18}O values for every 50 years. For the South hemisphere we used the European Project for Ice Coring in Antarctica (EPICA) database, which comprises data on the variation of deuterium concentrations ($\delta^{2}H$) at irregular but frequent intervals along the last 800,000 years. We used EPICA data for the last 122,500 years only, to cover an interval similar to the one provided by NGRIP. Both $\delta^{18}O$ and $\delta^{2}H$ are proxies for temperature conditions for their respective hemispheres. Their use in our analysis assumes that although changes along the glacial cycle differed among regions, times of intense global temperature variation within each hemisphere would be reflected as regional changes of increased magnitude (Walker, 2005). We opted for this approach, instead of assuming any finer regionalization, because actual global reconstructions of past climatic conditions are few and punctual across time, and do not necessarily reflect periods when megafaunal extinctions took place. Environmental proxies with high spatial resolution, including phytophysiognomical reconstructions based on pollen data, are available for just a few regions across the world, which precludes their use in global models (Gill et al., 2009, 2013; Rule et al., 2012). Considering such limitations, we believe that high-resolution chronological data for each hemisphere can be more informative than a crude and possibly misleading interpolation of past climatic scenarios in a geological period when climate undergone many rapid changes.

To allow comparisons between the hypotheses' predictions, data reliability was assessed through a scoring system. Paleontological and archaeological dates are sensitive to methodological errors (Walker, 2005). Sample contamination, poor materials, stratigraphic misinterpretations, inadequate dating methods and other problems can seriously jeopardize a date's accuracy. To identify reliable data, many authors have used different quantitative scales based mainly on sample material, stratigraphic associations and the type of equipment and logistics used in a given study (Mead and Meltzer, 1984; Burney et al., 2004; Barnosky and Lindsey, 2010; Iwase et al., 2012). Dates from articles and books that passed through such scrutiny were collected without further appraisal. In most cases, however, dates lacked any sort of accuracy determination, making data filtering a necessity. For radiocarbon based dates, this filtering was achieved using the Mead-Meltzer Scale (Mead and Meltzer, 1984) modified by Barnosky and Lindsey (2010), applying strict criteria: for paleontological and archaeological dates to be accepted, they had to reach at least ranks 11 (out of a maximum rank of 12) and 13 (out of a maximum rank of 17) respectively (following Barnosky and Lindsey, 2010). Still, most datings performed in Oceania over the extinctions period are based on different methods, mainly U/Th (Uranium—-Thorium dating), OSL (Optically Stimulated Luminescence dating) and ESR (Electron Spin Resonance dating). As there are no scoring systems capable of evaluating the accuracy of dates obtained by these methods, ranked scales along the lines of the Mead-Meltzer Scale were designed to assess the reliability of U/Th and OSL dates (Supplementary Table 3). The new scales do not include ranks associated with archaeological remains, because human dates were always based on radiocarbon methods. ESR dating involves a more complex set of techniques, making its dates harder to fit into a simple scoring system. So, only sources that utilized CSUS-ESR (Closed System U-Series ESR), a more accurate variant of the ESR method, were considered in the following analyses (Grün et al., 2008, 2010).

After the data filtering, date calibration was performed. Radiocarbon datings are based on the $^{14}C/^{12}C$ ratio of tested samples; as base concentrations of both isotopes fluctuate through time in the atmosphere, calibration is necessary to transform ‘radiocarbon years’ on actual ‘years before present’. Dates were calibrated using the software Calib 6.0, using the IntCal09 curve for every sample. Even though this calibration curve was originally designed for the northern hemisphere, it is the only one that encompasses the whole span of the extinction event.

As a last precaution, we tested bootstrapping corrections over the paleontological dates of South America (using the Cueva del Milodon, in Argentina, as the well sampled site) to avoid possible biases caused by the Signor-Lipps effect, following the methodology established by Barnosky and Lindsey (2010). This method has been criticized by Johnson et al. (2013) for not accounting adequately for the uncertainties and biases that affect the estimation of MLAD and HFAD. Regarding the nature of the expected bias, using uncorrected MLAD and HFAD would underestimate the coexistence between humans and megafauna. Anyway, the use of corrected data did not significantly affect the results, thus we opted for using uncorrected data to perform all analyses described in the following section, keeping in mind that this could make our analyses conservative against finding an association between human arrival and megafaunal extinction.

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