

CLIMATE PREDICTORS OF LATE QUATERNARY EXTINCTIONS

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Between 50,000 and 3,000 years before present (BP) 65% of mammal genera weighing over 44 kg went extinct, together with a lower proportion of small mammals. Why species went extinct in such large numbers is hotly debated. One of the arguments proposes that climate changes underlie Late Quaternary extinctions, but global quantitative evidence for this hypothesis is still lacking. We test the potential role of global climate change on the extinction of mammals during the Late Quaternary. Our results suggest that continents with the highest climate footprint values, in other words, with climate changes of greater magnitudes during the Late Quaternary, witnessed more extinctions than continents with lower climate footprint values, with the exception of South America. Our results are consistent across species with different body masses, reinforcing the view that past climate changes contributed to global extinctions. Our model outputs, the climate change footprint dataset, provide a new research venue to test hypotheses about biodiversity dynamics during the Late Quaternary from the genetic to the species richness level.

KEY WORDS: Body size, climate change, climate footprint, genetic diversity, global extinctions, Late Quaternary, phylogeography, refugia, species richness.

During the last 50,000 years the global climate became colder and drier reaching full glacial conditions in the Last Glacial Maximum, 21 kyr BP (21,000 years before present). Because then, the climate has become warmer (Ruddiman 2000). These climatic changes promoted drastic alterations in biome types and their locations (e.g., Williams et al. 2004). Warming also created opportunities for colonization of new regions by anatomically modern humans, which triggered profound alterations in world ecosystems (e.g., Barnosky 2008). Coincident with climatic changes and the expansion of humans, 101 mammalian megafaunal gen-

era went extinct (e.g., Barnosky et al. 2004). For more than a century, researchers have hotly debated the relative importance of climate change versus human impacts as drivers of Late Quaternary extinctions (e.g., Martin 1973; Grayson 1984; Guthrie 1984; Barnosky 1986; Alroy 2001; Brook and Bowman 2002; Stuart et al. 2004; Nogués-Bravo et al. 2008; Pushkina and Raia 2008). Hypotheses supporting humans as the main cause of Late Quaternary extinctions encompass a variety of different impacts, including overharvesting, biological invasions, habitat transformation, and human-induced diseases (see Burney and Flannery

2005, but see also Wroe et al. 2006, and Koch and Barnosky 2006). The climate change hypothesis proposes that reductions in climatically suitable areas for species would have caused a reduction in their geographical ranges, thus increasing their vulnerability to extinctions. Support for this hypothesis stems from the coincidence between the climatic changes and pulses of extinctions mainly in Eurasia and North America (Stuart et al. 2004; Guthrie 2006). The first pulse of extinctions, during increasingly glacial conditions between 45 and 21 kyr BP, included species that were adapted to warm environments, such as straight-tusked elephants, hippopotami, hemionid horses, and short-faced bears. During the second pulse of extinctions, with decreasing glacial conditions between 21 and 3 kyr BP, cold-adapted species such as woolly mammoths, giant Irish deer, or caballoid horses disappeared. The climate change hypothesis has been mainly investigated by comparing the temporal agreement between dates of fossil records with climatic/vegetation changes, but this has been done for specific regions of the world (Stuart et al. 2004) making generalizations for other regions difficult.

We test the climate change hypothesis for Late Quaternary extinctions using estimated extinctions from the literature, global climate change simulations, and a recently proposed spatially explicit framework for investigating biodiversity risk from an analysis of climate variables alone (Ohlemüller et al. 2006, Williams et al. 2007; see also Fig. S1).

Theoretical Model and Predictions

It is commonly accepted that population size affects extinction probability (e.g., Purvis et al. 2000) and that dispersal is one of the most powerful strategies for the adaptation of species under climate change (e.g., Anderson et al. 2009). It follows that if one accepts that the quantity of potential habitat available for species correlates with population size through local abundances (Andreawartha and Birch 1954; see Borregaard and Rahbek 2010 for a recent review on geographic distributions and species abundances), then changes in the size of species-climate envelopes can be used as a coarse-scale surrogate for population size (e.g., Thomas et al. 2004; but see Thuiller et al. 2004 and Araújo et al. 2005). In a similar vein, challenges to species dispersal could be estimated by measuring the distances required to migrate between analogous climate conditions in different time periods (Fig. S1). Given these two indicators of risk, one can make the starting assumptions that if Late Quaternary extinctions were associated with climate changes, then (1) continents with higher levels of extinctions should have witnessed a greater loss of their original climate envelopes, and (2) distances required to track analogous climate envelopes should have been larger. Here, we test this idea by globally modeling the two climate-based indicators of risk

for two different periods in the last 50 kyr (Fig. S1). For each location (grid cell), we calculate the area of and the distance to climatically analogous areas within a radius of 4000 km. Next we combine these two indicators to develop an index of risk from climate change during the Late Quaternary (herein termed the climate footprint) from 42 to 21 kyr BP and from 21 to 0 kyr BP (Figs. S2 and S3). Finally, we compare the climate footprint values with estimated extinctions in the last 50 kyr from the literature (Barnosky et al. 2004 and Koch and Barnosky 2006).

We divided the n dimensional climatic space (e.g., n_1 and n_2) for the emerged lands into different types of analogous climate envelopes (see Supplementary Information for further details). All these climatically analogous conditions are then mapped into a geographical space. Each of the 2° grid cells belongs to a type of climatic condition (see Fig. S1). For each (target) grid cell, we calculate the area and the average distance for a time period t (i.e., the sum of the area of grid cells with analogous climate envelopes within a 4000 km radius at 42 kyr BP) to all grid cells with analogous climatic conditions within a radius of 4000 km. The area of grid cells was calculated after taking into account the curvature of the Earth (Zar 1989). We finally measured the change in area and average distance in analogous climate envelopes between t_0 , t_1 and t_2 (i.e., $t_0 = 42$ kyr BP, $t_1 = 21$ kyr BP; or $t_1 = 21$ kyr BP, $t_2 = 0$ kyr BP). Analogous climate envelopes could undergo a small change in their area and geographical location due to a small climatic change. When this is the case the potential risk of extinction for species is considered to be low. On the contrary, large climatic changes could reduce the area and considerably shift the geographical location of a climate envelope. In such cases, the potential risk of extinction is considered to be high. Further details on data, analytical procedures, and supplementary results are given in the Supporting Information.

Potential Climate-Induced Extinction Risk

Areas characterized by cold and dry climates in both North America and Eurasia decreased between 1 and 4 million km², since the Last Glacial Maximum (Fig. 1; see SI for changes between 42 kyr BP and 21 kyr BP periods). For the same period, analogous climate envelopes shifted by more than 1500 km in North America and Eurasia (70 m per year) (Fig. S2). In some regions, Alaska, Yukon and Central Arctic Siberia, analogous climate envelopes migrated by more than 3000 km (140 m per year; Fig. S2). These results match pollen analyses and biome reconstructions, which also indicate large declines of biomes in these continents (Williams et al. 2004). Modeled shifts in analogous climate envelopes are consistent with documented range shifts of mammals in North America, on average between 1200 and 1400 km, during

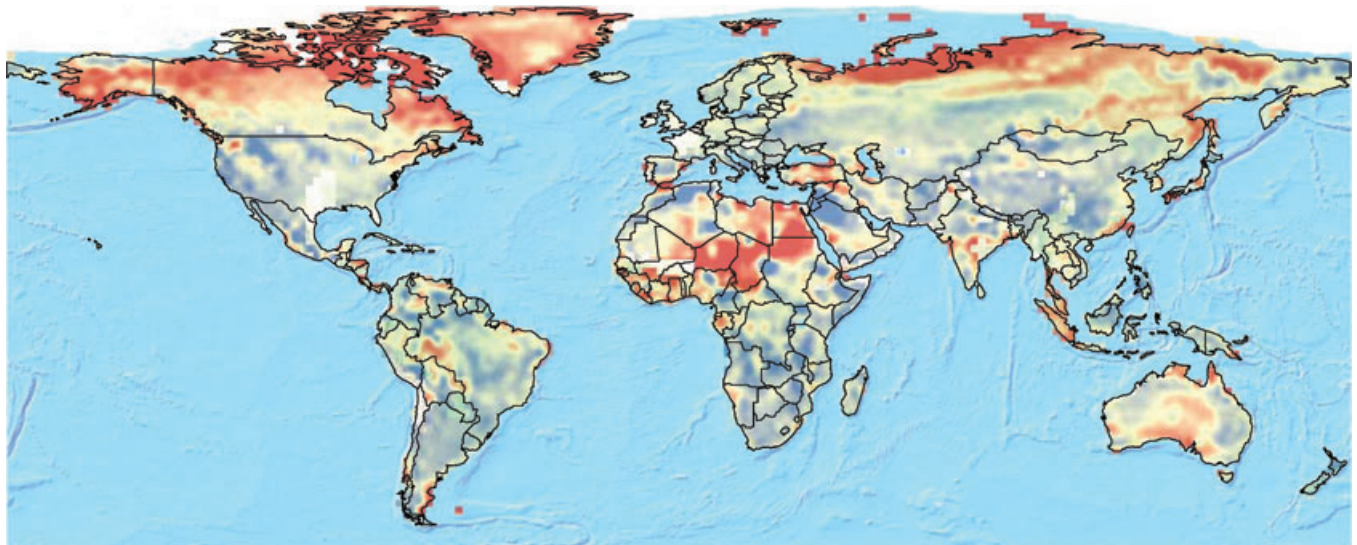


Figure 1. The footprint of Late Quaternary climate changes on global megafauna extinctions in terrestrial ecosystems. The exposure of different regions to species extinctions due to climate change during the Late Quaternary (values range from 0, in blue, indicating lowest exposure, to 1 in red, indicating the highest exposure). This map summarizes the changes in area of and distance to analogous climate envelopes from 42 kyr BP to 21 kyr BP and from 21 kyr BP to 0 kyr BP. We resample the raw footprint map using a cubic convolution method for a better visualization.

the late Pleistocene (Lyons 2003). Similarly, pollen analyses indicate that tree populations responded to postglacial warming by migrating northwards in North America about 100–1000 m per year (Davis 1981), although molecular evidence indicate slower migration rates (McLachlan et al. 2005). The area of analogous climate envelopes decreased by between 1 and 3 million km² since the Last Glacial Maximum in South America (Fig. S2), although analogous climate envelopes generally did not shift by more than 500 km (17 m per year). In the same period, analogous climate envelopes in central and southern Africa suffered gains or losses, on average, between 0 and 1 million km², and they shifted by less than 500 km (17 m per year; Fig. S2). In contrast, grid cells within the Sahel and the Sahara lost around 3 million km² of Last Glacial Maximum-analogous climate envelopes. Finally, most of Australia suffered losses of Last Glacial Maximum-analogous climate envelopes of between 3 and 4 million km², with shifts of less than 500 km (17 m per year).

Comparing Potential with Actual Mammal Extinctions

Our results provide evidence that continents with the highest climate footprint values, in other words, with climate changes of greater magnitudes during the Late Quaternary, witnessed more extinctions than continents with lower climate footprint values (Fig. 2 left plot), although the scarce number of cases in our analysis constrains our ability to provide more robust statistical analyses. The continental rank of extinct megafaunal genera is led

by South America, followed by North America, Eurasia (above 45°) and Africa. The continental rank of continents by footprint values is led by North America, followed by Eurasia, Africa, and South America. According to estimates of extinctions of mammalian megafauna during late Pleistocene (Barnosky et al. 2004 and Koch and Barnosky 2006), 86% and 76% of genera went extinct in South America and North America, respectively. The average climate footprint values for these continents are 0.13 and 0.33, respectively. Thirty-six percent of the megafaunal genera went extinct in Eurasia, which shows an average footprint value of 0.31. Eighteen percent of megafaunal genera in Africa went extinct and its footprint value is 0.18. Finally, 88% of mammalian megafaunal genera, 21 genera, went extinct in Australia during the late Pleistocene. However, of these 21 extinct megafauna genera, at least 18 disappeared before the time periods that we have used to measure the footprint of climate changes. Therefore, neither discussions nor conclusions about climate change impacts on Australian megafauna extinctions can be drawn from our results.

If climate change, rather than only a selective pressure from anatomically modern humans, had a key role in the extinctions of species, then there should be evidence of large impacts on small mammals in addition to the megafauna. Thus, we also compare climate footprint against the number of extinct small mammals using, similarly to the previous analysis at the genera level, continental rank-orders by number of species extinctions and climate footprint. We use a recent estimation of extinct mammal species by continent across body mass groups (see supplementary table 2 in Koch and Barnosky 2006). First, we divide mammals in two

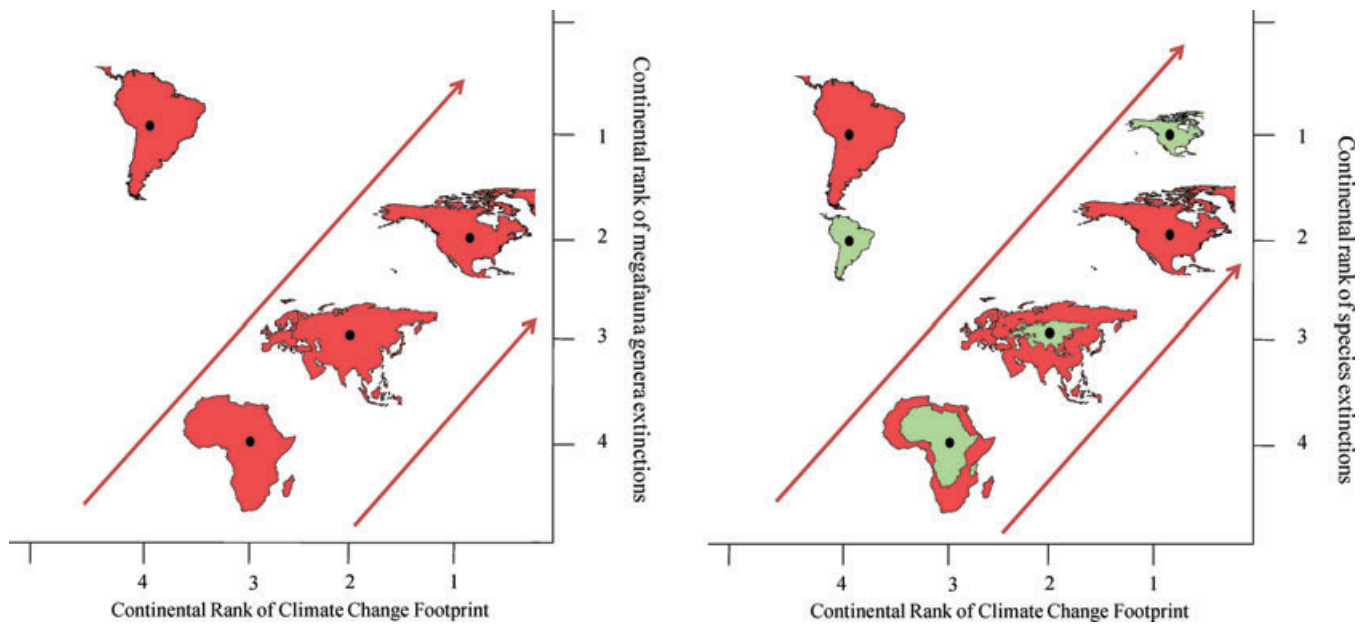


Figure 2. Rank of continents by climate footprint and extinctions. Left plot. Continents ranked by number of extinctions at the genera level. Right plot. Continents ranked by number of mammal extinctions at the species level. Species were divided in two groups: Green and small shapes of continents show the rank-order of extinctions for “small mammals,” body mass < 4.5 (log₁₀ gm). Red and large shapes of continents show the rank-order of extinctions for “large mammals,” body mass > 4.5 (log₁₀ gm).

groups by body mass. “Large mammals” are those with a body mass higher than 4.5 (log₁₀ gram) and “small mammals” are those with body mass lower than 4.5. Results show that the higher the climate footprint in each continent, the larger the number of both small and large mammal species that went extinct and vice versa (Fig. 2 right plot). South America is the only exception to this general trend, because it has high levels of extinctions but the lowest rank of climate footprint. Finally, we compute the rank Spearman correlation between the percentages of actual extinctions and the continental climate footprint values for the nine body mass groups combined (see Supporting Information; see also the pattern of species extinctions, in %, by body mass and continental climate footprint in Fig. S5), showing that the percentage of extinct species by continent increases with the magnitude of climate change predicted by our index after excluding South America ($n = 24$, $\rho = 0.44$, P -value < 0.05). In other words, the continents with large climate changes suffered more extinctions and vice versa, again with the exception of South America (including South America $n = 33$, $\rho = 0.13$ P -value > 0.05).

Discussion

Our results suggest that the continents exposed to Quaternary climate changes of greater magnitude have also witnessed higher extinctions and vice versa. Results are consistent across species with different body masses, reinforcing the view that past climate changes might have contributed to global extinctions. However,

South America departs from this general pattern as it displayed high extinction levels even though it has been exposed to moderate climate changes.

Evidence reviewed in recent studies (Barnosky et al. 2004 and Koch and Barnosky 2006) supports the view that climate was not the main cause of extinctions in North America although the extinction of megafaunal species without intense human presence in Alaska is consistent with a stronger role for climate at the edges of species’ geographic ranges. Our results that the highest potential risk for mammal extinctions from climate change is found in the northern parts of Canada and Alaska supports the latter idea. Although the quality and resolution of the paleo-record and paleo-climates should caution against literal interpretations of small differences in our analyses, it is noteworthy that climatic footprints in Eurasia were slightly lower than in North America but that numbers of extinctions were much reduced. When considering the view that humans played a role in Quaternary extinctions, as suggested for example in the case of the woolly mammoth (Nogués-Bravo et al. 2008), further comparative analyses between Eurasia and North America including human densities, differences in technological and cultural stages, and other proxies allowing understanding of the potential human impacts, might clarify the different levels of extinctions between these two continents. The previous reviews (Barnosky et al. 2004 and Koch and Barnosky 2006) also highlighted the existence of insufficient data to clarify the causes of extinctions in Africa and South America. Our results provide new quantitative insight into the potential role

of large-scale climatic changes in Late Quaternary Extinctions in Africa. Indeed, a low climatic footprint might be interpreted as indicating a reduced effect of climate on extinction levels, which, if true, should contribute to the low levels of species extinctions in this continent. Different hypotheses were suggested to explain the “African anomaly,” such as the long coevolution between humans and their prey (Martin 1984; Lyons et al. 2004), or low human population densities in Africa (Koch and Barnosky 2006). We suggest that small climatic changes and the long coevolution between humans and their prey should not be seen as mutually exclusive but complementary factors explaining the low proportion of genera that went extinct in this continent. Our predictions do not match the extremely high levels of recorded extinctions in South America, suggesting that nonclimatic factors are more likely to have driven extinctions there. However, it should be noted that in South America most of the known extinctions occurred in the southern part of the continent. The average footprint value of the land below 40°S is 0.48, a value that our model also predicts in areas of continents such as North America that suffered high levels of extinctions (Fig. 1). The average climate footprint value for the South American lands below 40°S is indeed—three to four times higher than the average climate footprint for South America as a whole. The climate footprint dataset will provide an apt arena for further research on climate change and Late Quaternary extinctions relationships at regional scale.

Our results support the view that climate change might have been a meaningful extinction driver during the Late Quaternary. However, extinctions of species are usually not the consequence of a single cause (e.g., Brook et al. 2008). Most often they are a consequence of synergetic mechanisms leading to population declines, which are then followed by population extinction. Indeed, more ancient Quaternary glacial–interglacial cycles were not sufficient to cause large extinctions of mammalian fauna. The main difference between the previous cycles and the last one was that modern humans, a global force altering the Earth’s biota (Barnosky 2008), emerged and dispersed across the world. If extinctions occur when novel threats outside the evolutionary experience of species appear (Brook et al. 2008), humans are potential suspect for Late Quaternary extinctions. We suggest that both stressors, climate change acting in combination with human impacts, and their varying magnitude across geographical space determined the number of species that went extinct across different regions and continents. A small magnitude of one of these stressors, as is the case of the low climate footprint in Africa or the low and late presence of modern humans across the islands in the Siberian Arctic, likely prevented and delayed extinctions. On the contrary, in other areas, the interaction of these two stressors at high magnitudes during the Late Quaternary likely drove many species to a point leading to irreversible population declines and extinctions.

We acknowledge that the low number of cases in our analysis on the effects of climate change in Late Quaternary extinctions, four continents or just three when we exclude South America, constrains our ability to provide more robust statistical analyses. The probability that, for example, Africa, Eurasia, and North America were ranked just by chance in the order showed in Figure 2 is 0.33. However, the consistency of the results across different body sizes (Fig. 2 Right) reinforces the view that climate change likely exerted an influence on Late Quaternary extinctions.

The debate about extinctions in the Late Quaternary has usually been polarized by views supporting a single and global “killer,” that is, humans versus climate change. However, our findings caution against overly simple explanations and call for investigation of the potential synergisms between human- and climate-change induced extinctions (e.g., Wroe et al. 2004). Advancing our understanding of the Late Quaternary extinctions will require an investigation of the interactions among mechanisms that might have contributed to final extinctions. Progress in the Late Quaternary extinctions debate will also enhance our knowledge about future extinction crises when factors such as humans and climatic change come together.

Outlook

Climatic changes during the Pleistocene might have played a key role to shape current biodiversity patterns. Here, we have assessed the role of climatic changes in mammal extinctions, but our spatially explicit predictions could also be used to test hypotheses about biodiversity from the genetic to the species richness level. Here, we provide four potential avenues for further research.

First, changes in genetic diversity. Climatic changes and human impacts at the end of the Pleistocene likely affected extinct and also extant species (e.g., Alroy 2001; Brook and Bowman 2002; Hofreiter and Stewart 2009). For example, recent analyses show that surviving species may also have experienced losses in terms of genetic and ecological diversity (Hofreiter 2007). Plotting the geographical trends of extant species’ genetic diversity or population size changes along time using ancient DNA in the geographical space and testing these trends against our predictions would further clarify the impacts of climatic changes in genetic diversity.

Second, distribution and origin of past biodiversity refugia. The literature on Late Quaternary extinctions has largely acknowledged the effect of modern humans in population declines and species extinctions. Surprisingly, phylogeographical and paleoecological research has usually interpreted that Late Quaternary refugia are a matter of climatic conditions (Bennett and Provan 2008, but see Stewart et al. 2009). If the combined effect of

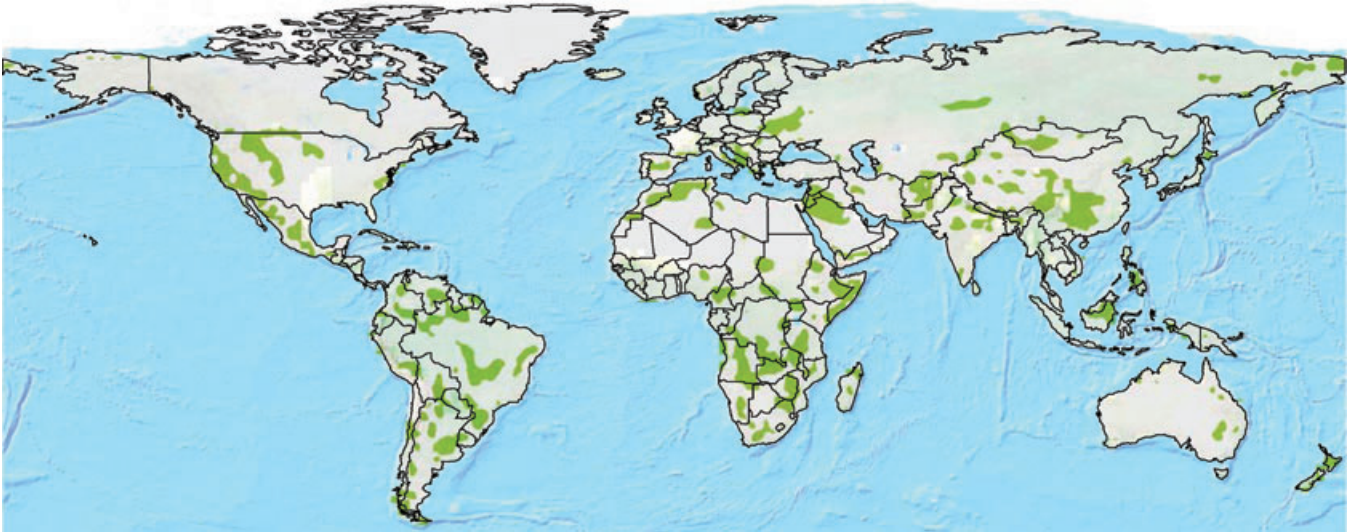


Figure 3. Climatic refugia during the Late Quaternary. Regions in green are hypothesized climatic refugia. These areas were selected from the climate footprint map and they represent the lowest 10% climate footprint values. These areas represent climatic stable regions with the lowest levels of potential risk of extinction along the Late Quaternary.

humans and climate drove population declines and local extinctions, then we need to rethink our perception about the factors shaping biodiversity refugia. One potential way to deal with this issue is to use the climate footprint to map climatic refugia. For example, those areas with the lowest values of climate footprint may well be considered climatic refugia (Fig. 3). Compiling the location of refugia across the phylogeographical and paleoecological literature and comparing them against these climatic refugia would clarify whether the location of biodiversity refugia deviates from the climatic ones. It would also provide clues as to whether Late Quaternary refugia had a climatic and/or human origin.

Third, the signal of extinctions in current species richness patterns. The species richness debate is mainly focused on contemporary factors to explain species richness patterns (i.e., current climate), avoiding the evolutionary perspectives of speciation, extinction, and dispersal as the main factors shaping species richness (but see Jansson 2003 for plants or Araujo et al. 2008 for reptiles). Testing whether climate footprint, as a proxy to exposure to extinctions, shaped the current patterns of global species richness will provide evolutionary insights into the factors behind species richness.

Finally, extinctions and climatic changes at regional scale. We acknowledge that our study is constrained by the broad resolution of species extinctions data (continental scale) and by the broad spatial and temporal resolution of our paleoclimatic reconstructions. A promising research venue would be estimating number of past extinctions within regions with similar geographical areas across the world (for making results comparable and providing at the same time a larger sample size for statistical ana-

lyses) and to relate them to a new generation of high-resolution climate footprint datasets.

We have made our spatial predictions, the “footprint dataset,” freely available (it can be downloaded from Supporting information) to favor novel and integrative lines of research in phylogeography, evolutionary biology, and global change biology to advance our understanding of climate change-biodiversity relationships.

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Supporting Information

The following supporting information is available for this article:

Figure S1. The footprint of Late Quaternary climate changes on global megafauna extinctions in terrestrial ecosystems.

Figure S2. Climate change indicators of extinction risk.

Figure S3. Climate change indicators of extinction risk from the 42 kyr period, and the 21 kyr period.

Figure S4. Frequency distribution, numbers of grid cells, of climate change footprint values by continent.

Figure S5. Species extinctions (in %) by body mass and continental climate footprint.

Table S1. Tolerance ranges used for five climate variables.

Result S1. The ecological meaning of the footprint of Late Quaternary climate changes on global megafauna extinctions.

Result S2. Changes in area and average distance between two different climatic tolerance ranges.

Supporting Information may be found in the online version of this article.

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