



Climate and humans set the place and time of Proboscidean extinction in late Quaternary of South America



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ABSTRACT

The late Quaternary extinctions have been widely debated for a long time, but the varying magnitude of human vs. climate change impacts across time and space is still an unresolved question. Here we assess the geographic range shifts in response to climate change based on Ecological Niche Models (ENMs) and modeled the timing for extinction under human hunting scenario, and both variables were used to explain the extinction dynamics of Proboscideans during a full interglacial/glacial cycle (from 126 ka to 6 ka) in South America. We found a large contraction in the geographic range size of two Proboscidean species studied (*Cuvieronius hyodon* and *Notiomastodon platensis*) across time. The largest contractions of their geographical ranges occurred in the northern part of South America, where we previously reported no evidence of coexistence among earliest humans and non-sloth megafauna, including Proboscideans. Our results herein support a strong effect of climatic changes on geographical range dynamics of Proboscideans throughout late Quaternary, although this does not fully support climate change as the single cause of their extinctions. We show that both Proboscideans were narrowly distributed on scattered patches of suitable habitats (i.e., refugia) around 11 ka, period in which the earliest humans potentially arrived in South America, increasing the population density thereafter. Under this overall unsuitable climatic condition at 11 ka, both Proboscideans would be extinct after around 550 years of human hunting, but if climatic conditions were suitable like in Last Glacial Maximum (LGM), the time-for-extinction would be at least 3 times longer under the same human hunting pressures. Thus, our findings support the “Broken Zig-Zag” model and show that South American Proboscideans might have been completely extinct due to human impacts during periods of climate crisis. We conclude, in agreement with an increasing body of evidence in the recent literature, that the late Quaternary megafaunal extinction event was the result of additive effects from different stressors, and that the relative magnitude of these impacts vary across space and time. Indeed, climate changes set the place where the Proboscideans were extinct in South America, whereas the humans set the time of these extinctions.

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1. Introduction

Extinction events are recurrent in Earth's evolutionary history. Among them, late Quaternary extinctions (LQE) and their causes are one of the events most debated in the scientific literature (see Grayson, 1984 for a pioneering review). Those extinctions, which occurred in a time frame

encompassing the last 50,000 years, are primarily characterized by the disappearance of large-bodied animals (called megafauna) in all continents and many island systems, although in different magnitude and time periods, without subsequent ecological replacement. South America is the continent with the highest extinction rate for these large animals, and as many as 50 megafaunal genera were lost during the Quaternary (~83% of the genera; Koch and Barnosky, 2006). Moreover, many entire taxa of large-bodied mammals, such as the Proboscidea order, completely disappeared from South America. Although researchers, for a long time, hotly discussed the factors driving the late Quaternary extinctions (Koch and Barnosky, 2006; Haynes, 2009), a consensus seems so far to be reached (Grayson and Meltzer, 2003; Fiedel and Haynes, 2004; Grayson and Meltzer, 2004; Nogués-Bravo et al., 2010). Even so,

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an interaction of both humans and climate changes, rather than one or other single factor, is currently considered the most likely explanation for the megafauna extinction event at the end of the Pleistocene (Cione et al., 2003; Barnosky et al., 2004; Koch and Barnosky, 2006; Nogués-Bravo et al., 2008; Cione et al., 2009; Barnosky and Lindsey, 2010; Lorenzen et al., 2011; Prescott et al., 2012).

Following this idea, in a previous study (Lima-Ribeiro and Diniz-Filho, 2013a, 2013b) we meta-analyzed reliable radiocarbon dates describing first-appearance of humans and last-appearance of megafauna to test for the chronological coexistence between them in many regions across the entire New World. Our findings showed that non-sloth species, including Proboscideans, did not coexist with humans in northern South America; i.e., the non-sloths were most likely already extinct in northern South America when the earliest humans arrived in that region. Under this scenario, we proposed that only non-human causes (e.g., climate changes) could be envisaged for driving the non-sloth species to extinction in this region. Alternatively, both humans and climate changes might have caused the extinction of species in other regions of South America, such as mid-latitudes and Patagonia (although the Proboscideans reached only the northernmost Patagonia – latitude 42–43°S; see, e.g., Prado et al., 2005, 2012).

Theories about species extinctions rely on two different paradigms (Caughley, 1994) that consider either the factors contributing to the general decline of species before their populations become rare – the declining-species paradigm (Simberloff, 1986; Diamond, 1989) – or the genetic and demographic factors promoting the extinction of small populations – the small-population paradigm (Soulé and Wilcox, 1980). Under the declining-species paradigm, a large reduction in the availability of suitable climate conditions would be expected to cause a reduction in a species' realized distribution, thus contributing to a reduction of population size and a potential increase in extinction risk (Purvis et al., 2000). Using Ecological Niche Models – ENMs (see Araújo and Peterson, 2012; Peterson and Soberón, 2012), fossil record and paleoclimatic simulations we can estimate the size of the potential range of species through time (Nogués-Bravo, 2009; Svenning et al., 2011; Varela et al., 2011). We hypothesize, on the one hand, that if climate changes significantly exposed species to extinctions through late Quaternary, we should find large decreases in the species range size before they went extinct. On the other hand, if climate is not the single stressor driving species to extinction, then climatically suitable conditions must have never fully disappeared throughout late Quaternary. Yet, if humans hunted such animals, as suggested in literature from some empirical evidences (see examples in Surovell et al., 2005), then the extinction risk due to human hunting should be significantly higher during periods matching population declining than in periods of suitable conditions, in which large connected populations may be found. Thus, a synergy between climate and human impacts is expected to be the most likely cause of late Quaternary extinctions.

Here we test 1) whether geographic range shifts due to climate changes through the last interglacial/glacial cycle (from 126 ka to 6 ka) can fully account for the extinction of two species of South American Proboscideans (*Cuvieronius hyodon* and *Notiomastodon platensis*) using the dated fossil record, paleoclimatic simulations, and ENMs, 2) whether climate change impacts in megafauna had the same magnitude across the geographical ranges of both species, and 3) whether human hunting pressures needed to bring the species to extinction differ across times, taking into account the size and suitability of the species' geographic ranges modeled by ENMs. Given the large and recent increase of studies using ENMs to assess climate change impacts in late Quaternary biodiversity dynamics and the challenges that ENMs may face for paleobiological studies (Nogués-Bravo, 2009; Svenning et al., 2011; Varela et al., 2011), we intensively explore uncertainties in these models to illustrate a robust route for better understanding the outcome of ENMs in paleobiological studies.

2. Methods

2.1. Paleoclimatic simulations and climate predictors

The past climatic conditions were compiled from two coupled Atmosphere–Ocean General Circulation Models (AOGCMs), the Genesis2 and CCM1. The Genesis2 AOGCM (Thompson and Pollard, 1997) offers paleoclimatic simulations for last interglacial (126 ka), three glacial periods (42 ka, 30 ka, and 21 ka) and mid-Holocene (6 ka), whereas CCM1 provide paleoclimatic simulations between LGM and mid-Holocene (21 ka, 16 ka, 14 ka, 11 ka, and 6 ka). These AOGCMs provide then a fine temporal resolution from paleoclimatic simulations, which is a desirable feature to analyze the extinction dynamics through time. The CCM1 outputs were compiled from Paleoclimate Modeling Intercomparison Project Phase I (PMIP1) database available online at USA National Oceanic and Atmospheric Administration's – NOAA (<ftp://ftp.ncdc.noaa.gov/pub/data/paleo/gcmoutput/pmip/>). The 6 ka Genesis2 simulation is also from PMIP1 (Bonfils et al., 1998), and the 126 ka Genesis2 simulation is by Vavrus (2001).

Although there are new AOGCM's generations available currently (e.g., PMIP3 <<http://pmip3.lscce.ipsl.fr/>> and CMIP5 projects <<http://cmip-pcmdi.llnl.gov/cmip5/>>), they do not offer paleoclimatic simulations with temporal resolution as fine as Genesis2 and CCM1. Moreover, one of the biggest uncertainties in simulating LGM climates, for instance, is the reconstruction of the ice sheets (Abe-Ouchi et al., 2007; Peyaud et al., 2007). Although more recent ice sheet estimates are also available, there continues to be considerable uncertainty. Indeed, the protocols for PMIP3 have revised the ice sheet to make it more similar to PMIP1 (that we use) than the reconstruction for PMIP2 (Braconnot et al., 2012). Fortunately, studies such as Braconnot et al. (2007a,b) have also shown that the tropical climates are not quite sensitive to ice sheet reconstructions (see also Singarayer and Valdes, 2010) and hence we believe the paleoclimatic simulations used here are valid to assess extinction dynamics through time in South America.

We select three climate predictors from paleoclimatic simulations to map the past Proboscidean distribution: minimum temperature of the coldest month (tmin), maximum temperature of the warmest month (tmax) and annual precipitation (prec). These three climatic variables were chosen due to three main reasons: i) temperature and precipitation are the basic constituents of the climatic axis for any species niche space at long time intervals and broad spatial scales, and are direct surrogates of important resources to the species, such as water-energy availability; ii) the climatic modeling process generates many kinds of uncertainty no matter the AOGCM used in analysis (Randall et al., 2007), but temperature and precipitation are the climatic variables that present the lowest degree of uncertainty from any AOGCM (Braconnot et al., 2007a, 2007b); and iii) finally, these climatic variables capture the upper and lower temperature boundaries of the climatic niche of a species, then they are, conceptually, reliable predictors to assess the climate change role on the Proboscidean extinction at the end of the Pleistocene, which is our main goal in this study (see Franklin, 2009 for conceptual selection of model predictors). Previous studies on megafaunal extinctions have shown those climatic variables to be important determinants of species distribution ranges on broad-scale (Martínez-Meyer et al., 2004; Nogués-Bravo et al., 2008; Varela et al., 2010; Lorenzen et al., 2011). Furthermore, the addition of many predictors in species distribution modeling generally lead to overfitting of the models (i.e., reduces the predicted geographical range; see Nogués-Bravo, 2009, and Varela et al., 2011).

The variables were downscaled to a spatial resolution of 1° using kriging method, due to their originally coarse resolution from the original climatic outputs (2.5° × 3.75° latitude-longitude or higher), and extracted for a grid covering the entire South America (see area selection for modeling in Barve et al., 2011). We used the standard change-factor approach (Wilby et al., 2004), which interpolates the pre-

industrial climate (i.e. the current climatic scenario) from AOGCMs outputs and the difference between past and pre-industrial climate (i.e. climate change trends) for a same AOGCM instead of interpolating values directly from past climatic scenarios. Next, the past-interpolated climates are obtained adding the interpolated values of climate change trends to the interpolated pre-industrial ones. Because of the scale of variables values, we used absolute differences for temperatures, whereas for precipitation we used relative ones (see <http://www.worldclim.org/downscaling> for more details about this downscaling procedure; see also the use of this downscaling method in Martínez-Meyer et al., 2004, and Hijmans and Graham, 2006). This approach is taken to maintain higher resolution topography on the downscaled climate surfaces and to assure coherency of the climatic patterns across time (Hijmans and Graham, 2006).

2.2. Species data

2.2.1. Taxonomic background and nomenclature overview

The taxonomy of South American Proboscideans has a complex history since their first description by Georges Cuvier in 19th century (see Lucas, 2013 for a historic review of nomenclature). In short, after many taxonomic proposal and revisions, three taxa were recognized in the last decades for South American Proboscideans: one of Miocene age (*Amahuacatherium*), and two from Pleistocene (*Cuvieronius* and *Stegomastodon* = *Haplomastodon*). *Cuvieronius* is a genus with a single species (*Cuvieronius hyodon*) which occupied the highlands in Pleistocene South America and the west of Andes, whereas *Stegomastodon* was considered to have two lowlands species, one occupying the “northern” (*Stegomastodon waringi*) and another “southern” South America (*Stegomastodon platensis*) (Alberdi and Prado, 1995). However, Mothé et al. (2012), based on a recent morphological and phylogenetic analysis, concluded that two *Stegomastodon* species from South America have not enough morphological differences, nor represent a phylogenetically coherent taxon (i.e., a monophyletic group) if *Stegomastodon* species from North America are also considered (see also Mothé et al., 2013). The authors proposed then a new taxonomic revision, unifying *S. waringi* and *S. platensis* in a single species that was named to *Notiomastodon platensis* (*Notiomastodon* is a previous nomenclature, and has been recently accepted as a valid genus after later rejection of assigning any South American Proboscidean to *Stegomastodon*; see Ferretti, 2008; Mothé et al., 2012; Lucas, 2013). Thus, for the purpose of the present study, we followed the most recent classification of Mothé et al. (2012), such that all records attributed to any *Stegomastodon* species (= *Haplomastodon*) were considered to be *N. platensis*.

2.2.2. Fossil record sampling

The species occurrences were obtained from the dated-fossil remains of South American Proboscideans using multiple search criteria and several kinds of available information. We accessed key papers from primary literature reporting extensive lists of radiocarbon dates (e.g. Borrero, 2009), performed general internet searches (including the academic content's databases as ISI Web of Science, Jstor, PubMed, and Scielo), and from online radiocarbon databases and “gray literature” (i.e. papers from local libraries and meetings, PhD theses, research reports, technical notes) to complete our data sampling.

We found 31 dated-records with spatial location (i.e., with information about their latitude and longitude) for two South American species of Proboscideans, being 7 of *Cuvieronius hyodon* (hereafter, *Cuvieronius*) and 15 of *Notiomastodon platensis* (hereafter, *Notiomastodon*) within the glacial times (from 48,000 to 15,000 years BP; see Table S1). These localities were used as “training” data to build the ENMs (see Section 2.3). The remaining fossil records (5 for *Cuvieronius* and 4 for *Notiomastodon*) are dated at Pleistocene–Holocene boundary (~11,000 years BP; Table S1) and were used as “independent test” data to validate the ENM's projections at this interglacial period.

The majority of the fossil record (~80%) is dated from indirect associations (i.e., relating remains into a same dated layer) or by relative ones (i.e., assigning a relatively wide interval to that fossil occurrence, like late Pleistocene or Lujanian ages), and some records (~20%) were directly dated based on animal remains (e.g., bone; Table S1). Because of the small amount of fossil remains for both *Cuvieronius* and *Notiomastodon* in South America, we used all information available about fossil occurrences for modeling their past distributions. Further, we also used conservative criteria to link the fossil occurrences to the paleoclimatic simulations and then to model the past species distribution. Because we used two paleoclimatic simulations for OIS3 (oxygen isotope stage 3), 42 and 30 ka, and one for LGM (21 ka) representing the last glacial period for which the ENMs were built (see Section 2.3), each fossil locality was associated to the nearest temporal paleoclimatic simulation. Similarly, we used the same approach for fossil localities aged near to Pleistocene–Holocene boundary (11 ka), which were used as independent test data (see Section 2.4). The relatively-dated remains were linked to both 42 ka, 30 ka, and 21 ka paleoclimatic simulations, i.e. our working assumption is that the individual fossil dated as a late Pleistocene or Lujanian age might have survived in all those glacial periods.

We emphasize that the fossil record available for South American Proboscideans and used here to fit the ENMs might yield over- or under-estimate of their past potential distributions. However, we do not aim at fully describe the real locations where each Proboscidean species existed across the last interglacial/glacial cycle (i.e., realized distribution; for this we would necessity of a much better stratigraphic and taphonomic control for the fossil records), but rather to analyze how the potential geographical range size of these species shifted (expansion/contraction) through this period and if the climate changes may had drove they to extinction at the end of the Pleistocene (our first two hypotheses). Although the initial conditions might influence the models output over- or under-estimating the potential geographical ranges (Elith and Leathwick, 2009; Franklin, 2009), we consider that the change in the species potential distribution across time may be correctly assessed from the fossil records currently available for South American Proboscideans (Table S1).

We tested the assumption of stability of the climatic conditions occupied by species across time and then used the multi-temporal calibration approach to build the ENMs (see Section 2.3 for details). For instance, the South American Proboscideans occupied the same climatic space in 42 ka, 30 ka and 21 ka (see MANOVA tests in Section 2.3 and their results in Sections 3.1 and 4.1), then using the fossil occurrences from all these glacial periods to fit the ENMs (the multi-temporal calibration approach) ensures that the same modeling bias (if some) will occur in all time periods (the potential distribution will be over- or under-estimated in all periods). So, the dynamics of modeled potential distribution across time (i.e., increase/decrease of climatically suitable areas available to the Proboscidean survival from one time period to another) is not due to initial conditions related to fossil record uncertainty, but to climate changes through those time periods.

Further, we also evaluated the predictive performance and temporal transferability power of the ENM predictions using analytical procedures and independent test data and used only reliable models to develop our analyses (see Section 2.4 and online Supplementary Information for details about the leave-one-out test, which evaluate the sensitivity of range size estimates to fossil record uncertainty). We compared the modeled distributions with paleoecological reconstructions that used other techniques than ENMs (Sánchez et al., 2004; Prado et al., 2005; Marcon, 2008) to assess whether our models were able to get the main climatic preferences of both South American Proboscideans or not.

2.3. Mapping past Proboscidean distributions

To map the Proboscidean distributions across last interglacial/glacial cycle taking into account one of the most important ENM assumptions (i.e., the stability of climatic conditions occupied by species

through time), we performed a Multivariate Analysis of Variance (MANOVA) to test for differences between the climate conditions occupied by Proboscideans at 42 ka, 30 ka and 21 ka periods, all from Genesis2 AOGCM. In our case, significant p-values ($P > 0.05$, which were obtained from resampling test with 9999 permutations) indicate that the Proboscidean climate preferences did not differ among time periods (see Section 3.1), allowing us to use the multi-temporal calibration approach to build the ENMs, getting all species occurrence records from OIS3 and LGM (i.e., the glacial interval from 48,000 to 15,000 years BP) as training data to fit the ENMs (see Nogués-Bravo, 2009, and Svenning et al., 2011 for more details about reconstructing past geographical species ranges).

Next, the Proboscidean geographical ranges were modeled for 42 ka, 30 ka and 21 ka using Genesis2 paleoclimatic simulations, and then projected onto their climatic simulations for 126 ka and 6 ka. Regarding CCM1 AOGCM, the models were built for 21 ka, and then projected to all other periods for which paleoclimatic simulations exist (see Section 2.1). To deal with the uncertainties among predictions from different ENMs, we used different presence-only algorithms to model the past species distributions, such as the bioclimatic envelope (Bioclim), environmental distances (Euclidean, Gower), multivariate methods (Mahalanobis distance, ENFA), and machine learning algorithms (GARP, Maxent), all implemented in BioEnsembles software (Diniz-Filho et al., 2009; Terribile et al., 2012). Details about each algorithm are provided in online Supplementary Information).

In accordance to Varela et al. (2011), the presence-only algorithms should be preferred in paleobiogeographical studies due to technical concerns, limitations and conceptual features, such as: i) the sampling of absence data is impracticable for extinct species from fossil record (i.e., the absence of fossil records does not necessarily ensure species absence in a given region); ii) the species' absence mainly depends of non-climatic factors on narrower scales (e.g., dispersion, ecological interactions) which change through time; iii) the algorithms that require species presence and absence data tend to model the realized distributions instead of potential ones (see Jiménez-Valverde et al., 2008; Hortal et al., 2012; and Rangel and Loyola, 2012 for conceptual selection of ENMs; see also Soberón, 2007; Colwell and Rangel, 2009; and Soberón and Nakamura, 2009 for an wide theoretical discussion about species niche class and distributional features). However, the potential distribution modeling is suggested to evaluate the climate effect on the dynamic of the species geographic range specially in our paleobiogeographical context (Varela et al., 2011). Finally, iv) because the assumption of equilibrium species-climate assumed by correlative ENMs is difficult or even impossible to be tested from fossil data because it needs of absence data, simple algorithms are more appropriate in analyses of the dynamics of geographic ranges under climate change (Elith and Graham, 2009; Elith et al., 2010).

Except for Bioclim, we need to establish a threshold to transform continuous values of climatic suitability in binary species presence-absence maps. For this, we a priori selected five thresholds; i.e., four arbitrary thresholds such as 10th, 20th, 30th, and 50th percentiles and the Lowest Presence Threshold (LPT, the lowest predicted suitability value corresponding to a training data locality). Next, the suitable grid cells (i.e., those cells with suitability values higher than decision threshold) were classified in quartiles to map regions with different suitabilities to the Proboscideans, instead of only indicating their predicted presence-absence (the first quartile – Q1, indicates the most suitable regions, whereas the fourth quartile – Q4, indicates the less suitable ones). As Bioclim outputs do not yield continuous suitability values, we classified the grid cells in quartiles from each climatic variable and the worst result was assigned to each cell (i.e., if a cell was classified as Q1 for tmin, Q3 for tmax, and Q4 for prec, then this cell was finally assigned as Q4; see Nogués-Bravo et al., 2008 for a similar approach).

2.4. Assessing the models performance

The models predictive performance was evaluated for each decision threshold using the leave-one-out test because of the small number of species occurrence records for both *Cuvieronius* and *Notiomastodon*. This approach is described as a variation to the *k*-fold partitioning method on which a Jackknife sampling is imposed (see details in Pearson et al., 2007 and in online Supplementary Information).

Further, the models projections were independently validated thought time using the fossil records dated around 11 ka (Table S1) as independent test data. We validated the projections built only from the best-evaluated threshold (i.e., LPT; see Tables S2–S3 and text in Section 4). We computed how many fossil occurrences from 11 ka were predicted as species presence by projections at that time. To be more conservative, we consider reliable all those ENMs that accurately predicted at least half of independent test data. In accordance to Peterson et al. (2011), the independent validation is important to test the ability of models to accurately predict the species distribution in a different period of time (see also Fielding and Bell, 1997; Araújo et al., 2005; Nogués-Bravo, 2009). Nevertheless, because of the small number of fossil records available for 11 ka, we use only the ENMs showing reliable predictions from both evaluation approaches (i.e., traditional leave-one-out test and independent validation) to compute the geographical range shifts through time (see Section 2.5). Moreover, our independent validation approach may well be considered also as an adequate test for stability of climate conditions occupied by Proboscideans through time (see theoretical discussion in Nogués-Bravo, 2009, and practical examples in Martínez-Meyer et al., 2004, and Martínez-Meyer and Peterson, 2006; see also MANOVA test in Section 2.3).

2.5. Dealing with modeling uncertainties

We assessed the sources of uncertainty in our models built for 21 ka using a three-way Analysis of Variance (ANOVA) without replication (Zar, 1999), in which the predicted area (in number of grid cells) was the dependent variable and algorithms, AOGCMs and thresholds were factors. Again, we also calculated, for each grid cell, a hierarchical ANOVA such that previous quartile classification values from all ENMs were nested into time component. The latter analysis lead us a spatially explicit assessment of where each modeling component differs largely as to model predictions (these analyses were based on those proposed in Dormann et al., 2008; Diniz-Filho et al., 2009; and Terribile et al., 2012 to partitioning and mapping uncertainties from forecasting ENMs). All ANOVA's p-values were obtained from resampling test with 9999 permutations.

Finally, we combined the ENM predictions in an ensemble approaching to reduce the uncertainties in potential distribution of Proboscideans from each modeling algorithm (sensu Araújo and New, 2007). Since that Bioclim outputs yields in simple presence/absence classifications (i.e., do not yields in continuous suitability values), we used the previous classification of climatic suitability in quartiles to obtain our ensemble model. Also, to be more conservative and to model the ensemble potential distribution of South American Proboscideans, we assigned the better climatic suitability (the highest quartile) to each grid cell; i.e., if a cell was classified as Q1 for first model, Q3 for second model, and Q4 for third model, then this cell was finally assigned having Q1 suitability. So, our ensemble approach is a consensus in which the climatic suitability of each grid cell was predicted to be as high as that quartile assigned to it by at least one model with reliable predictions. We used the quartile classification only from LPT threshold and ENMs independently validated (except Maxent; see Sections 2.4 and 3.1 for details). Since both AOGCMs used here have climatic simulations for 21 ka, the climatic suitability for this time period was also ensemble from Genesis2 and CCM1 (note that all other climatic simulations used here come from single AOGCMs).

2.6. Assessing the geographical range size and extinction risk through time

We correlated the size of species geographical range from ensembled predictions (measured in number of grid cells with $1^\circ \times 1^\circ$ of resolution) against time, taking into account each quartile of suitability. Next, to test our main prediction on dynamics in geographical range size across the three South American archeological regions, as established by Lima-Ribeiro and Diniz-Filho (2013a), we calculated the difference between range size from glacial (maximum range size among 42 ka, 30 ka, or 21 ka) and present interglacial periods (range size of 11 ka) in northern South America, mid-latitudes and Patagonia, which we called of “range shift” (see Fig. 2 and Lima-Ribeiro and Diniz-Filho, 2013a for more details about the archeological regions).

We also assessed the sources of uncertainty related to range shift through time performing a two-way ANOVA without replication for each species (Zar, 1999) using the range shift (in number of grid cells) as dependent variable and algorithms and archeological regions as factors. However, we used only the most likely predictions from independently validated ENMs to analyze the changes in geographical range size taking into account the temporal transferability of their predictions (see Table 2 to check what algorithms were utilized for *Cuvieronius* and *Notiomastodon*). Following the principle of model selection based on theoretical expectations (Jiménez-Valverde et al., 2008; Franklin, 2009; Hortal et al., 2012; Rangel and Loyola, 2012), we exclude Maxent outputs of range shift analysis independently of their predictive performances. Maxent predicts different fraction into a distributional gradient from other presence-only algorithms (Jiménez-Valverde et al., 2008) and it is also very dependent of a priori chosen parameters (species prevalence, for example; see Elith et al., 2011 for a good explanation about Maxent). Then, to model the geographical range accurately under climate change, specially using fossil records of extinct species and paleoclimatic simulations, is not a simple (or reliable) task from Maxent model (Elith et al., 2011; see also Sections 2.3 and 3). However, Maxent algorithm was considered here to only analyze the sources of uncertainties from ecological niche modeling (see Section 2.4).

Next, we mapped the climatically stable areas through time (i.e. refugia) for both species and evaluated their extinction risk at the end of the Pleistocene using the classification schemes from IUCN red list criteria (<http://www.iucnredlist.org/>) (see also Lima-Ribeiro et al., 2012). IUCN criteria for threat classification rely on many aspects such as population dynamic and size, extent of occurrence and/or area of occupancy, and quantitative analyses (population viability). In our case, since ENMs yields in potential distributions (and not realized ones; see discussion in Section 2.2), the IUCN absolute cutoffs (e.g., extent of occurrence, in km^2 – criteria B – and population size, in number of individuals – criteria C and D) do not represent a fine estimate for extinction risk at the end of the Pleistocene. For our purpose, we believe that more plausible criteria should be based on relative estimates, such as the population decrease, in percentage, given by criterion A. So, the extinction risk from dynamics in geographical range was analyzed following other criteria than those from IUCN red list.

Using the IUCN criteria A3_{b,c} and estimates of projected population size (which can be obtained from geographical range size through

Table 2

Test of ENMs predictive performance from independent ‘test’ data. The values indicate the relative success rate in which the models projection for 11 ka truly predict the occurrence of fossil records at this time. The values in the parentheses correspond to proportion of the predicted presence area at 11 ka. Maxent was excluded (see Sections 2.3 and 2.5 for details).

Algorithm	<i>Cuvieronius</i>	<i>Notiomastodon</i>
Bioclim	0 (0.04)	0.5 (0.11)
ENFA	0.6 (0.33)	0.5 (0.20)
Euclidean	0.4 (0.21)	1 (0.65)
GARP	0.6 (0.26)	0.5 (0.23)
Gower	0.8 (0.29)	1 (0.40)
Mahal	0.4 (0.05)	1 (0.18)

time assuming a given fixed density), for instance, the Proboscideans should have been Critically Endangered (CR) at the end of the Pleistocene if impacts from climate changes yielded in a population decrease $\geq 80\%$, Endangered (EN) if $\geq 50\%$, Vulnerable (VU) if $\geq 30\%$, and unthreatened (Near Threatened – NT – or Least Concern – LC) in other cases. So, this approach indicates as much the climate changes throughout last interglacial/glacial cycle affected both species in South America at the end of the Pleistocene by constrain and fragment their geographical ranges, consequently decreasingly their populations, so raising their extinction risk.

2.7. Assessing the human hunting effects

The human impact on Proboscidean extinction risk was evaluated by estimating the time under hunting pressures needed to lead the species to extinction, called here of “time-for-extinction”. We used difference equations (Gotelli, 2008) and annual rates for simulating predator–prey dynamics (see details on demographical model in online Supplementary Information; see also Diniz-Filho, 2004a; Lima-Ribeiro and Diniz-Filho, 2013c). We then simulated in how long time a modest initial human population with 100 individuals arriving in South America around 11 ka (see Alroy, 2001) and growing at 1%/year, would drive each Proboscidean species to extinction. The initial population sizes (i.e., carrying capacity – K) of the Proboscideans were obtained by matching the predicted geographic range sizes from ENMs and estimated maximum population densities. The population densities and intrinsic rates of population increase (r) for the Proboscideans were estimated from allometric relationships by Brown (1995) using body size estimates of the species.

We then simulated the time-for-extinction under two initial conditions. First, we simulated the predator–prey dynamics using the predicted potential distributions at 11 ka to compute the population sizes. Since 11 ka is largely conservatively considered the time that humans firstly arrived in South America (Rothhammer and Dillehay, 2009), or at least achieved relatively high population densities, this modeling scenario is taken as “likely”; i.e., the scenario in which the human arriving in South America likely found the Proboscideans. However, to test our hypothesis about additive effects between human and climate changes, it is necessary to know the time-for-extinction if human had hunted Proboscideans during their most climatically suitable condition (i.e., with larger and well connected populations). For this, we used the geographical range sizes predicted at 21 ka to estimate the initial population size of the Proboscideans and then simulated the predator–prey dynamics. This is the “best-scenario”.

3. Results

3.1. Ecological niche modeling

The MANOVA tests showed that climate conditions occupied by the Proboscideans did not differ among the glacial periods – 42 ka, 30 ka and 21 ka (*Cuvieronius*: Wilks = 0.90, F = 0.29, GL = 6, 32, p = 0.94;

Table 1

Two-way ANOVA showing the variance in geographical range shift of *Cuvieronius* and *Notiomastodon* between glacial and present interglacial periods as predicted by different algorithms (ENMs) in three South American archeological regions (north, mid-latitudes and Patagonia, see Lima-Ribeiro and Diniz-Filho, 2013a). Such analyses were performed only with the independently validated ENMs, except Maxent in both cases (*Cuvieronius*: ENFA, GARP, Gower; *Notiomastodon*: all ENMs).

	<i>Cuvieronius</i>			<i>Notiomastodon</i>		
	SS	F	p-Value	SS	F	p-Value
Region	9.88e5	26.07	<0.001	2.84e6	374.15	<0.001
ENMs	1.35e3	0.04	0.94	6.44e5	33.98	<0.001
Region:ENMs	3.03e3	0.04	0.97	1.35e6	35.69	<0.001

Notiomastodon: Wilks = 0.88, $F = 0.53$, $GL = 6$, 48 , $p = 0.80$). Such results from MANOVA reinforce the adequacy of using all occurrence fossil records of glacial periods to fit the ENMs through time (called multi-temporal calibration approach; Nogués-Bravo, 2009; Svenning et al., 2011) and then to project the species climatic envelopes to other ones.

The built models at glacial periods (42 ka, 30 ka and 21 ka) showed different predictive performance from different thresholds (results showed in online Supplementary Information, Tables S2–S3). The arbitrary thresholds, such as 10th, 20th, and 30th percentiles, showed the worst fitted models, whereas the LPT generally presented well-fitted models for both Proboscideans, independently of algorithm and AOGCM. ENFA, GARP, and Gower algorithms were able to predict at least half of the *Cuvieronius* independent test data from their present interglacial projections (11 ka; Table 2). Therefore, the independent validation tests indicate that only these three models may be transferred to the other periods with some degree of confidence. For *Notiomastodon*, all ENMs presented high transferability power, since they correctly predicted at least half of their independent test data (Table 2).

Algorithms, thresholds and the interaction between them (Table 3) were the main factors adding the largest amount of variance to the predictive distribution maps of both Proboscideans at LGM (21 ka). Although statistically significant, the AOGCM factor and their interactions had lower influence on the models uncertainties (Table 3). More details are provided in online Supplementary Information, Figs. S1–S6 and Tables S1–S3.

3.2. Geographic range shift dynamics and human hunting effects

The geographical range size of both Proboscideans widely oscillated throughout the last interglacial/glacial cycle (Fig. 1). We found a wide contraction of the climatically suitable conditions for both Proboscideans through time (Fig. 1), as well as an increasingly fragmented distribution in the southern half of South America from glacial (42 ka, 30 ka, 21 ka) towards warmer present interglacial periods (11 ka and 6 ka). More than 85% of the most climatically suitable areas (i.e., those related to first quartile – Q1) of both Proboscidean species were lost between glacial and present interglacial (Fig. 1). However, *Notiomastodon*, the largest species (>6 tons) showed a more restricted potential distribution and small refugia than *Cuvieronius* (<4 tons). Overall, the population size at the ending Pleistocene was estimated to be around 50% lower than glacial times.

Following our expectations, the geographical range of both *Cuvieronius* and *Notiomastodon* showed a wide contraction in response to climate changes mainly in the northern region of South America, and minor shifts in mid-latitudes and Patagonia (Fig. 2). When we compared the magnitude of range shift (geographical range size of Pleniglacial periods minus present interglacial ones), the largest variance occurred just among the three South American archeological regions established in Lima-Ribeiro and Diniz-Filho (2013a), followed by algorithms and their interaction (Table 1).

Under these climate change effects, the “likely-scenario” of restricted and fragmented distributions at 11 ka shows both Proboscideans

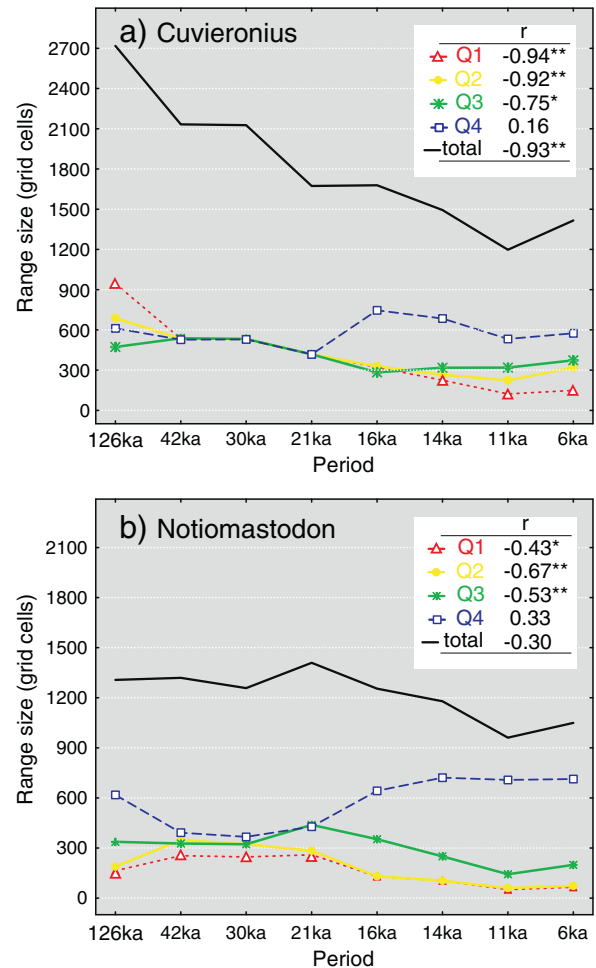


Fig. 1. Geographical range size (number of $1^\circ \times 1^\circ$ grid cells) of *Cuvieronius* (a) and *Notiomastodon* (b) across time. The color lines indicate the range size by quartiles of climatically suitable conditions in South America (the climatic suitability decrease from Q1, in red, to Q4, in blue) and black line indicates the full range size (sum of all quartiles). The r-values are their respective Pearson correlation coefficients (** < 0.05, *** < 0.001). Note the decrease in area and the strong negative relationship of the most suitable conditions for both Proboscideans through time.

would be extinct after around 550 years of human hunting, whereas under negligible climate effects (the “best-scenario”), the time-for-extinction was at least 3 times longer (Fig. 3).

4. Discussion

4.1. Maps of past Proboscidean distribution: are they reliable models?

Reconstructions of species range dynamics in the past periods are sensitive to the amount and quality of the fossil record, model algorithms, past climate simulations or ability to transfer climatic envelopes across different periods of time (Nogués-Bravo, 2009; Svenning et al., 2011; Varela et al., 2011). Therefore, the potential sources of uncertainty, including their magnitude across time and space, should be carefully assessed (Diniz-Filho et al., 2009; Diniz-Filho et al., 2010). In our study, in spite of relatively small amount of occurrence fossil records available to build the ENMs (especially for *Cuvieronius*), the MANOVA results together with model validation from inter-temporal projections, indicate stability of climatic conditions occupied by *Cuvieronius* and *Notiomastodon* through last glacial/interglacial cycle, which increase our confidence on the model predictions projected to different periods (Nogués-Bravo, 2009; Svenning et al., 2011; Varela et al., 2011). The results from

Table 3

Tree-way ANOVA showing the variance of the geographical range size of *Cuvieronius* and *Notiomastodon* as predicted for 21 ka by different algorithms (ENMs), thresholds (THRES), AOGCMs and their interactions. The degrees of freedom (Df) are equal to both genera. SS: sum of square.

	Df	<i>Cuvieronius</i>			<i>Notiomastodon</i>		
		SS	F	p-Value	SS	F	p-Value
ENMs	6	3.21	362.18	<0.001	2.92	3713.20	<0.001
THRES	4	2.12	298.44	<0.001	1.68	2675.20	<0.001
AOGCMs	2	0.01	3.09	0.049	0.003	10.40	<0.001
ENMs * THRES	21	0.87	24.56	<0.001	0.70	223.20	<0.001
AOGCMs * THRES	8	0.02	1.47	0.239	0.004	3.40	0.007
ENMs * AOGCMs	12	0.09	5.06	<0.001	0.004	2.80	0.012

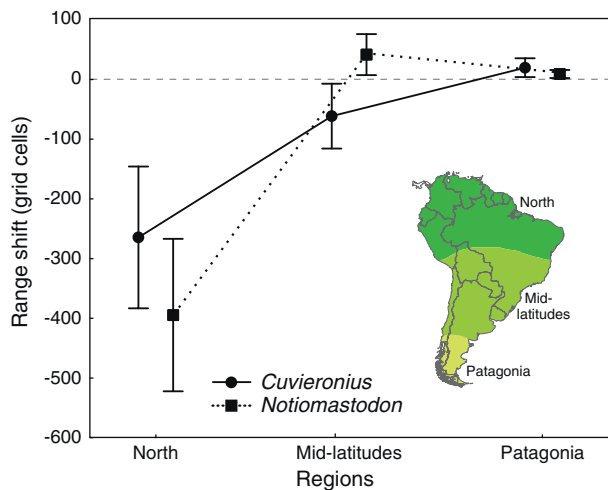


Fig. 2. Changes in geographical range size (in number of grid cells, ± 0.95 confidence interval) of *Cuvieronius* and *Notiomastodon* between glacial and interglacial periods in three South American archeological regions (see Lima-Ribeiro and Diniz-Filho, 2013a). The negative values indicate contraction of geographic range during this time slice, whereas positive values indicate range expansion. Note that an expressive range contraction occurs only in the northern region. See two-way ANOVA results from region factor in Table 1 for statistical significances.

independent validation show that species ecological niche modeled at glacial times (21 ka) were able to correctly predict their climatic preferences at interglacial one (11 ka) from many ENMs (see the discussion about environmental and geographical representations of ecological niche in Soberón, 2007; Colwell and Rangel, 2009; Soberón and Nakamura, 2009; Peterson et al., 2011). Therefore, we consider that potential distribution of South American Proboscideans, as predicted by ENMs used here, are accurate or at least represent a sounding approximation to evaluate the climate effects on the dynamics of geographical range sizes and shifts.

Moreover, our models show comparable predictions to those from paleoecological reconstructions using other techniques (Sánchez et al., 2004; Prado et al., 2005; Marcon, 2008). The predicted potential distribution of *Cuvieronius* shows its preference by temperate to cold climate (Prado et al., 2005) mainly because its widespread distribution in Patagonia and Andean cordilleran. Already *Notiomastodon*, a genus taken to explore warmer to temperate climates (Prado et al., 2005), was not predicted to occur on Andes and Patagonia at glacial times (42 ka, 30 ka, and 21 ka). Further, the predicted distribution of *Notiomastodon* is more continuous in the Amazonian lowland than *Cuvieronius* during

these glacial periods (Figs. S2–S3). In accordance to Sánchez et al. (2004), after the Great American Biotic Interchange, *Cuvieronius* utilized the Andes corridor for its dispersal in the South America, whereas *Notiomastodon* dispersed across the east route occupying warmer areas (see Alberdi et al., 2011 for a dispersion-vicariance analysis of Proboscids).

Our findings also corroborate those found in neoecological studies, in which the algorithms are the main source of variation regarding models predictions (in our case, geographical range size; Table 3; see also Dormann et al., 2008; Diniz-Filho et al., 2009, and Terribile et al., 2012 for other examples). These findings suggest that both a priori conceptual selection of ENM methods taking into account the goals of study (Jiménez-Valverde et al., 2008), and a posteriori model selection based on empirical validation (Fielding and Bell, 1997; Elith and Leathwick, 2009; Franklin, 2009), are important modeling features to reach reliable predictions, as well as that all well-evaluated model predictions should be combined in an ensembles approach (Araújo and New, 2007; Diniz-Filho et al., 2009). In neoecological studies, the AOGCMs were an important source of variation (Dormann et al., 2008; Diniz-Filho et al., 2009; Collevatti et al., 2013), but this did not occur here in the same magnitude.

The decision thresholds were also an important variance source in our models (Table 3), which corroborate with the theoretical concepts and suggestions to evaluate the ENM predictions from different decision thresholds and select the best one or consider their alternative predictions in the ensemble approach (see details in Nenzén and Araújo, 2011). In our case, the arbitrary thresholds propitiated the worst performances (Tables S2–S3). In accordance to Pearson et al. (2007), the arbitrary thresholds might lead the models to poorer predictive performances when evaluated by leave-one-out test because they tend to predict greater suitable areas than LPT. Thus, the models predictions do not differ of a random one, even when they show high success rates (i.e. predict correctly all ‘test’ data; Pearson et al., 2007). Moreover, the arbitrary thresholds are, by definition, very dependent of geographical extent of study area and willingness of researcher; i.e., the arbitrary thresholds are not ecologically-based on any robust concept. So, the arbitrary thresholds must be avoided or cautionary used in ENM context.

Moreover, our findings show that it is important also evaluate the spatial patterns of modeling uncertainties to know the reliability of their results. For instance, the largest variance for range size predictions comes from different ENMs (Table 3), indicating this factor a priori is an important source of uncertainty. However, the maps of uncertainties show ENMs predicted distinct potential distributions mainly in areas where the species were never expected to occur; i.e., areas outside of likely species range (Fig. S7). If high ENMs uncertainties were concentrated in regions where *Cuvieronius* (temperate and cold climates in Patagonia and Andean cordilleran) and *Notiomastodon* (warmer climates in Amazon basin) are expected to have occurred, respectively, then their predictions would be useless. The reliability of our ENM predictions is also showed by uncertainties from time component. Their spatial patterns indicate that climate changes through time was correctly predicted to affect both species in the areas where they are expected to have really occurred (see details on spatial interpretation of modeling uncertainties in Terribile et al., 2012).

4.2. Climate changes, human hunting, and extinction risk

Our findings clearly show the effects of the climate changes on extinction dynamics of South American Proboscideans over the last 126,000 years, in accordance to the global link recently found between climate change and late Quaternary extinctions (Nogués-Bravo et al., 2010). Our analyses reveal that the disappearance of about 85% of climatically suitable areas towards mid-Holocene is probably a key factor increasing the extinction risk of both Proboscideans at the transition between the Pleistocene and the Holocene (Purvis et al., 2000; Payne and Finnegan, 2007; Davies et al., 2009). Indeed, under the declining-species

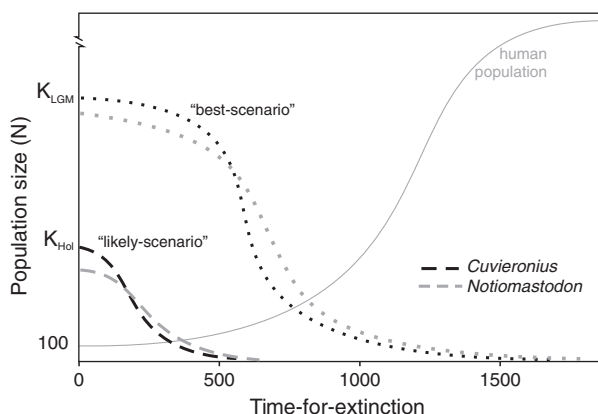


Fig. 3. Human hunting effects on *Cuvieronius* (<4 tons) and *Notiomastodon* (>6 tons) from both ‘‘likely-scenario’’ (dashed lines) and the ‘‘best-scenario’’ (dotted lines). The human population is represented by continuous tick line. See details about the model simulating predator–prey dynamic in online supplementary information.

paradigm (Simberloff, 1986; Diamond, 1989), the geographical range declining for a substantial portion of time is the main factor increasing the species extinction risk (Foote et al., 2007, 2008) because their populations might reach sizes below of minimum viable size (Diniz-Filho et al., 2005). For example, under the energetic equivalence rule (Damuth, 1981), the minimum viable population of large-bodied species must occupy wider geographic extents (therefore, lower densities) than small-bodied species, since the amount of energy per unit of area that each species use is independent of its body size (Kelt and Van Vuren, 2001). So, large-bodied species, when constrained to small range sizes, would have increasingly higher probabilities of extinction (Brown and Maurer, 1987, 1989, see also Diniz-Filho, 2004b). Besides, the extinction risk is still higher if these species have low population growing and reproductive rates (Isaac, 2009), as well as a wide gestation length and weaning age (Cardillo et al., 2005), which is the general case of large mammals (Johnson, 2002; Brook and Bowman, 2005). These characteristics will have an even amplified effect if these small ranges are scattered on a fragmented landscape (i.e., are restricted in refugia; Reed, 2004), as showed here for both Proboscideans toward warmer present interglacial (11 ka and 6 ka).

However, under this theoretical expectation and considering that the body size of *Notiomastodon* (>6 tons; Fariña, 1996; Fariña et al., 1998; Christiansen, 2004) is estimated to be at least one third larger than *Cuvieronius* (<4 tons; Smith et al., 2003; Christiansen, 2004; Smith and Lyons, 2011), this latter species should be less sensitive to climate impacts than the former one (see Polishchuk, 2010 for a power scaling of size selectivity of LQE), as supported by our results. First, the global range size predicted here is always smaller for *Notiomastodon* than for *Cuvieronius* at every paleoclimatic scenario (Fig. 1). Second, *Notiomastodon* presents greater range contraction through time in northern South America than *Cuvieronius* (Fig. 2). Third, the climatically suitable habitats became geographically more restricted and fragmented for *Notiomastodon* than for *Cuvieronius* toward the Holocene. Therefore, *Notiomastodon* should be restricted to one/two single populations during the early Holocene, which could increase its exposure to extinction. In other words, our results support that *Notiomastodon*, the largest-bodied species, would have higher extinction risk from climate impacts. On the contrary, *Cuvieronius*, the smallest-bodied species, should be less sensitive to fragmentation, therefore would have higher probabilities of survival to climate impacts. Indeed, the reliable last-appearance radiocarbon dates (i.e., the available age for taxa extinction) show that *Cuvieronius* became fully extinct around 1000 radiocarbon years later than *Notiomastodon* (see Table S1 and discussion about the reliability of last-appearance dates in Lima-Ribeiro and Diniz-Filho, 2013a).

Moreover, the large-bodied herbivores, like Proboscideans, are affected by climatic and ecological changes mainly from the nutritional stress induced by relatively rapid changes in plant communities (MacFadden, 2000a, but see a different point of view in Ripple and Valkenburgh, 2010). Thus, if the plant species are directly linked to climate conditions (Bond, 2008), so the specialist feeders are more prone to extinction than generalist ones, especially under global climate changes scenarios (Badgley et al., 2008; Janis, 2008) as in last interglacial/glacial cycle. In general, *Cuvieronius* and *Notiomastodon* were mixed-feeders (C3/C4 plants) through middle Pleistocene (Sánchez et al., 2004; Prado et al., 2005), probably exhibiting feeding strategies similar to those of modern African elephants (*Loxodonta africana*). These live in diverse habitats, are opportunists, and therefore are capable of living on nearly any dietary mixture (Bocherens et al., 1996). Their dietary characteristics, which ensure more efficient food use across multiple vegetational sources, were crucial for both Proboscideans to reach South America during the Great American Biotic Interchange, whereas their phylogenetically relative's mammoths and mastodonts (highly specialized feeders) remained restricted to North America (Sánchez et al., 2004). However, the South American Proboscideans presented more selective dietary adaptations toward the warm present interglacial. Some populations were exclusively C3-selective,

whereas others were C4-selective around latest Pleistocene/early Holocene (MacFadden, 2000b; Sánchez et al., 2003; Sánchez et al., 2004). These changes for more selective dietary certainly increased their extinction risks at that time. In this case, climate change likely was an important stressor for the South American Proboscideans because either the kind of plants they usually consumed during that phase of more specialized dietary disappeared toward the warmer Holocene (Sánchez et al., 2003; Sánchez et al., 2004) or at least because the proportion of C3/C4 plants changed through time in response to climate oscillation (MacFadden, 2000a; Hopley et al., 2007).

Under the scenarios delineated by our past geographic range size predictions, similar conclusions might also be supported by herd structures and population dynamics of Proboscideans. Following this idea, the biomass of herbivore communities is closely regulated by food availability (i.e. habitat's carrying capacity; see a study with African ungulates in Fritz and Duncan, 1994) and, in accordance with Mothé et al. (2010), the family structure of *Notiomastodon* is analogous to those from current African elephants (*Loxodonta africana*). Also, Thomas et al. (2008) show that summer home range (environmental requirements) of current African elephants is four times wider than its winter one. If we consider that environmental requirements of both Proboscideans (or at least *Notiomastodon*) during colder (i.e., LGM) and warmer (i.e., Holocene) climatic phases through late Quaternary follow those from *L. africana* at summer and winter seasons, respectively, our results point out that in warmer current interglacial (Holocene), period in which the species required habitats with larger carrying capacity, the extinction risk dramatically increased just because the climatically suitable areas and, consequently, food availability, were restricted on small patches in the South America at that time (Figs. S2–S3).

Nevertheless, the most evident insight of our analyses for disentangling climatic vs. human impacts is that the largest contraction of geographical range of both Proboscideans occurred just in the northern part of South America (see Fig. 2), the same region where Lima-Ribeiro and Diniz-Filho (2013a; Fig. 3) did not find evidences for human-megafauna (non-sloth taxa) coexistence. So, this finding greatly corroborates our main prediction, which states that the climate was a decisive stressor driving the megafaunal extinction in regions where humans did not coexist with it (see Lima-Ribeiro and Diniz-Filho, 2013a for details about human-megafauna coexistence). Further, we also show that Proboscideans were restricted in small and scattered refugia in the mid-latitudes and Patagonia regions (in latter, only *Cuvieronius*) at 11 ka, period in which the earliest humans reached South America.

In the terms used by the IUCN red list, the extinction risk of both Proboscideans imposed by climate changes at ending Pleistocene should undoubtedly be set as "Threatened", at least in its medium-risk subcategory called "Endangered" (i.e., an estimated population size reduction of >50% – A3b,c; see <http://www.iucnredlist.org/>). In this case, the endangered subcategory means that both Proboscideans were threatened, but not fully extirpated, by only climate changes (see similar interpretation for giant ground Sloths in Lima-Ribeiro et al., 2012). In other words, the refugee populations could subsequently expand when optimal climatic conditions broaden again (as seen in the last interglacial, 126 ka; Figs. 1, S2–S3). Since refugee populations of both Proboscideans did not expand throughout Holocene, just when they would disappear only after 550 years under human hunting pressure, we suggest that the synergistic action between climate and human impacts possibly drove their populations to full extinction in mid-latitudes and Patagonia regions (see Brook et al., 2008 for detail about synergies among extinction drivers and extinction risk; but see text below). This is also supported by the fact that none species went extinct during previous warm climates at last interglacial (126 ka) when there was no human in South America (i.e., by climate effects only), as well as because the time-for-extinction was at least 3 times longer under the "best-scenario" than "likely-scenario" of human hunting. Thus, the arrival of potential hunters just when the Proboscideans were narrowly distributed on refugia possibly was the decisive factor to their extinctions in South America.

Nogués-Bravo et al. (2008) also showed empirically that the geographical range of Eurasian woolly mammoths as predicted by ENMs collapsed towards mid-Holocene, and only then the increasing hunting pressure from human populations would be sufficient to extinct it as a 'coup de grâce' (see also Lorenzen et al., 2011 for other examples). In South America, Cione et al. (2003, 2009) also proposed a similar idea for megafaunal extinctions. Their "Broken Zig-Zag" hypothesis points an alternation of high and low biomass of South American megafauna (which they refer to as the Zig-Zag) due to the replacement between the open and close habitats (e.g., savanna–forest) from glacial and interglacial intervals, respectively, and that during the present interglacial, humans entered South America and broken the zig-zag by killing the larger herbivores during their less favorable periodic lapse (Cione et al., 2003; Cione et al., 2009). Our findings support then the Broken Zig-Zag hypothesis as a reliable model to disentangle the roles of multiple drivers and dynamics of late Quaternary extinctions, showing that Proboscideans would not be able to recuperate of climate crisis when humans arrived hunting them.

5. Concluding remarks

Historically, perhaps it have been more intuitive define primary causation for all late Quaternary extinctions thinking in single drivers, as pointed out by Surovell et al., 2005 about global evidence of primary causation debate for Proboscideans extinction. However, this is not always the most parsimonious alternative. Our findings reveal that the relative influence from climate and humans differ in distinct regions of the South America through time, so these factors may explain in an uncoupled way the place and time of extinctions. In northern South America, climate change was the primary (or possibly unique) stressor of Proboscideans extinction, whereas in mid-latitudes and Patagonia it was not. In these regions, the human hunting seems to be the decisive stressor driving the latest refugee populations to extinction. Therefore, the ecological niche modeling coupled with predator–prey dynamics performed here, together with other evidences from literature, support a synergetic effect between both humans and climate changes on extinction dynamic of South American Proboscideans across their entire geographical ranges throughout the last interglacial/glacial cycle. Thus, the long-term climate changes set the place (mid-latitudes and Patagonia), whereas sudden human impacts set the time (latest Pleistocene/earliest Holocene) of the Proboscidean extinction in South America. We hope that such comprehensive interpretation allows a better understanding on how these factors can be combined to explain late Quaternary megafaunal extinctions.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.palaeo.2013.10.008>.

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