Evolutionary Ecology Research, 2017, **18**: 97–121

Climate change, human overkill, and the extinction of megafauna: a macroecological approach based on pattern-oriented modelling

Matheus S. Lima-Ribeiro[1] and José Alexandre F. Diniz-Filho[2]

[1]PaleoMACRO-ecology Lab, Instituto de Biociências, Regional Jataí, Universidade Federal de Goiás, Jataí, GO, Brazil and [2]Departamento de Ecologia, ICB, Universidade Federal de Goiás, Goiânia, GO, Brazil

ABSTRACT

Background: The debate on Late Quaternary extinctions (LQE) has long been centred on the contrast between climatic and human-related explanations, with no consensus being reached. Here we propose a macroecological approach to study LQE that combines niche and demographic models to determine the ecological mechanisms behind the megafauna extinction.

Question: Is the overkill hypothesis plausible and realistic when assessing the ecological mechanisms behind LQE? What is the range of population parameters for both human and now-extinct animals that is consistent with the actual extinction pattern?

Features of model: Ecological niche models (ENMs) are used to assess climate impact on population viability, whereas density-dependent population models with reciprocal feedback between humans and their prey are used to simulate human hunting pressure. The feasibility of predicted extinction scenarios and explored parameter space is ordered based on a pattern-oriented modelling (POM) approach. We illustrate the usefulness of our framework using the extinct South American ground sloth *Megatherium* as an example.

Methods: We built ENMs by using fossil occurrences records and palaeoclimatic simulations from the last glacial cycle and projected their predictions to the Holocene. Population modelling was based on 4000 random samples of ENM ensembles, from which prey density was estimated using a Gaussian central–peripheral abundance model. For each ensemble, a plausible range of demographic parameters (e.g. growth rate, carrying capacity, mortality of human population, meat consumption) was set across 100 random repetitions, giving 400,000 models simulating *Megatherium*'s extinction dynamics.

Results: The macroecological approach highlighted many plausible mechanistic extinction scenarios capable of reproducing a wide range of hypotheses about the LQE. Most models (51%) simulating a vigorous human population with unrealistic growth rates ($r_h > 1.3\%$ per year) and intense over-exploitation of prey (individual meat-consumption-rate – $CI > 100$ g per day from one prey only) produced scenarios of rapid extinction as predicted by the overkill hypothesis. However, such overkill scenarios unrealistically predicted earlier extinction times than that observed for *Megatherium*. Moreover, the high human population growth required to simulate overkill scenarios was attained only recently after the industrial revolution, specifically

---

Correspondence: M.S. Lima-Ribeiro, PaleoMACRO-ecology Lab, Instituto de Biociências, Regional Jataí, Universidade Federal de Goiás, Jataí, GO, Brazil. email: limaribeiro@ufg.br

in the mid-1900s, and it is therefore not applicable for Pleistocene hunter-gatherers. Conversely, although less frequent across simulations, models that correctly predicted the observed extinction time (16%) revealed plausible and empirically acceptable demographic parameters, encompassing low growth rates ($r_h < 0.70\%$) and mortality for the human population ($mo < 0.60\%$), combined with moderate values of individual meat consumption ($CI > 70$ g) and geographical range collapse in *Megatherium*, which is produced by climate change.

Conclusions: These findings, based on POM reasoning, highlight that unique mechanisms such as the overkill explanation for LQE, although feasible from model simulations, only occur with implausible parameter combinations and predict unrealistic extinction dynamics.

Keywords: ecological niche model, Late Quaternary extinctions, *Megatherium*,
overkill hypothesis, population modelling, predator–prey dynamics, South America.

INTRODUCTION

Extinction events are recurrent in Earth's evolutionary history and have an important role in shaping the evolution of life (Flessa *et al.*, 1986; Jablonski, 2001). The Late Quaternary extinction (LQE) is the last of these events, occurring recently in the geological time scale, and has important implications for understanding the current biodiversity conservation debate (Grayson, 1984). The majority of large-bodied animals on all continents and many island systems vanished over the last 50,000 years, when both humans spread out of Eurasia and there was abrupt climate change (Koch and Barnosky, 2006). Although the LQE has long been debated in the scientific literature (Grayson, 1984), its causes and implications are still to be resolved [see, for example, the conflicting ideas in Grayson and Meltzer (2003, 2004) and Fiedel and Haynes (2004)]. With few recent exceptions (see debate in Lima-Ribeiro and Diniz-Filho, 2013a, 2013b), the LQE debate has traditionally been framed by a narrative approach that is used in favour of either climatic or human impacts on the extinct megafauna. More recently, a new idea was proposed unifying the two impacts in a synergistic context (Nogués-Bravo *et al.*, 2008; Pushkina and Raia, 2008), which has been corroborated by studies using ecological and statistical models to disentangle the magnitude of each stressor rather than excluding possible causes (e.g. Prescott *et al.*, 2012; Sandom *et al.*, 2014; Araújo *et al.*, 2015; Varela *et al.*, 2015).

Here, we propose a macroecological approach to access the ecological mechanisms involved in the extinction of megafauna by integrating ecological niche modelling (ENM) and demographic modelling to simulate the impacts of both climate and humans on extinct species. Niche modelling is a powerful tool to model the geographical range of species and has recently been applied in a palaeobiological context to predict the magnitude of geographic range shifts (reduction, expansion) as a consequence of climate changes through time (Nogués-Bravo, 2009; Svenning *et al.*, 2011; Varela *et al.*, 2011). Additionally, demographic models, roughly based on Lotka-Volterra predator–prey dynamics, can be implemented using simulation strategies that permit evaluation of human hunting scenarios where the megafauna (prey) is an important food source for early human populations (predator) (Diniz-Filho, 2004; Lima-Ribeiro and Diniz-Filho, 2013c).

Our goal here is to couple ENM and demographic models to shed light on the LQE debate. We used predator–prey dynamics to determine the time-to-extinction under human pressure (i.e. time-to-extinction), while accounting for species distributional dynamics as a consequence of climate [i.e. from the Last Glacial Maximum (LGM), about 21,000 years ago, to the Pleistocene/Holocene transition, about 11,000 years ago]. We used environmental suitability from ENMs to estimate the carrying capacity (i.e. initial population size) for megafaunal species at the time of human arrival, which allows a direct integration between the two types of model (Lima-Ribeiro and Diniz-Filho 2013c). We suggest that the combination of distributional and demographic parameters (among multiple models) predicting the observed extinction patterns could be assumed to closely represent the processes and conditions that occurred from the end of the Pleistocene into the early Holocene, when the megafauna perished. Such a procedure, known to biologists as pattern-oriented modelling [POM (Grimm *et al.*, 2005; Grimm and Railsback, 2012)], allows one to establish which combination of parameters from complex models gives the best match between simulated scenarios and observed patterns, in a multivariate sense (see examples in Grimm *et al.*, 1996; Rangel *et al.*, 2007; Diniz-Filho *et al.*, 2014). To reach POM outputs, it is also important to explore uncertainties across different modelling components, such as ENM methods, palaeoclimatic simulations (Dorman *et al.*, 2008; Diniz-Filho *et al.*, 2009), and demographic parameters (Alroy, 2001; Diniz-Filho, 2004). In the context of LQE, considering uncertainties through the modelling components is essential to better explore different putative scenarios of nature and chronology of extinctions, and to establish the reliability of climate and human impacts determining the observed extinction patterns (e.g. time-to-extinction).

By integrating ENM and demographic models along a POM approach in the context of LQE, we are theoretically able to access (or at least to infer) the ecological mechanisms behind the climate and human effects and simulate the most plausible scenario increasing extinction risk of megafauna through time. As an example, we illustrate the usefulness of our framework using data from the extinct South American ground sloth *Megatherium.* Besides advancing the LQE debate, our framework also exemplifies a way by which palaeobiology may serve conservation biology. Knowing the mechanisms that raise species extinction risk in a climatically and anthropogenically impacted world, such as during an LQE event, is important for making conservation decisions more realistic, conservation planning more efficient, and improving conservation efforts in today's world.

MATERIALS AND METHODS

South American LQE and the model taxon

As a continent, South America experienced the highest loss of megafaunal diversity during the Late Quaternary. The Pleistocene of South America presented a rich megafaunal community composed of some 52 now-extinct genera (Koch and Barnosky, 2006). Some extinct South American taxa have current equivalents in other continents (such as equids in Africa and Eurasia). Yet, many taxa were definitively lost at the global level. The giant ground sloths (Megatheriidae and Mylodontidae) are an example of extinct megafauna without a living equivalent. In South America, the megatheriid ground sloths had existed since the Pliocene and were mainly represented by two genera during the Pleistocene, *Eremotherium* and *Megatherium*, until their extinction at the end of the Pleistocene and early Holocene. It is possible that both genera were represented over the Pleistocene of South America by a single species, *Eremotherium laurillardi* and *Megatherium americanum* respectively. However, because a great deal of ambiguity exists regarding taxonomic identity and affinity of species-level taxa in the fossil record, as well as the expansion, contraction, and replacement of extinct species nomenclature (see, for example, De Iuliis *et al.*, 2009), we considered only genus-level taxa in this study. Besides being conceptually recommended, this decision is also operationally necessary because the fossil record used to build ENMs was identified to the genus level (see ‘Ecological niche modelling’ below).

The megatheriid ground sloths weighed more than 3 tons (Cartelle and De Iuliis, 2006) and were distributed across the whole of South America. *Eremotherium* lived in tropical to sub-tropical forests mainly across the Amazonian and Atlantic forests, whereas *Megatherium* inhabited temperate arid to semi-arid environments across the Andes and Patagonia (Bargo *et al.*, 2006; Nascimento, 2008). Because of their large body size, the megafauna as a whole (including megatheriids) possessed a suite of ecological traits (e.g. slow reproductive rates) that made them more prone to extinction under intense climate change (Johnson, 2002; Lyons *et al.*, 2010). Furthermore, some studies have suggested that early Americans were big-game specialists that preferred to hunt large-bodied animals for subsistence (Surovell and Waguespack, 2009; but see Cannon and Meltzer, 2004 for a contradictory view). Indeed, there is clear evidence of anthropogenic marks on remains of megatheriid ground sloths, indicating hunting by humans at the end of the Pleistocene (Dantas *et al.*, 2012). However, the chronology of *Eremotherium* extinction and the timing of *Eremotherium*–human co-existence has not been resolved (Dantas *et al.*, 2012). In contrast, *Megatherium* presents a large amount of fossil remains aged to the Holocene, attesting to its long co-existence with humans (see dates and references in Table 1). Thus, *Megatherium* is a convenient model taxon to illustrate the usefulness of our macroecological

Table 1. Radiocarbon dates for age of last appearance of *Megatherium* in South America

Site name	Lab number	^{14}C age	Cal BP (1-sigma)	Cal BP (2-sigma)	Reference
Campo de Arce Río Quequén Chico	LP-174	13070 ± 120	16235–15260	16495–15160	1
Arroyo Seco 2	CAMS-58182	12200 ± 170	14505–13820	14955–13735	2, 3
Arroyo Seco 2	OXA-15871	12170 ± 55	14140–13980	14211–13839	4
Arroyo Seco 2	OXA-10387	12155 ± 70	14095–13895	14210–13795	5
Arroyo Seco 2	AA-62513	11770 ± 120	13740–13475	13860–13360	5
Arroyo Seco 2	CAMS-16389	11750 ± 70	13705–13475	13740–13450	3
Río Salado	GrA-49130	11590 ± 60	13475–13350	13550–13300	6
Arroyo Seco 2	AA-9049	10500 ± 90	12585–12190	12660–12100	3
Paso Otero 5	AA-39363	10440 ± 100	12525–12145	12595–12030	7, 8
Campo Laborde	AA-71665	9730 ± 290	11605–10660	12060–10270	5, 7
Paso Otero 5	GX-29795	9560 ± 60	11075–10755	11135–10700	7, 8
Arroyo Seco 2	LP-53	8390 ± 240	9595–9015	10120–8645	2, 3, 7, 9
Campo Laborde	AA-55118	8080 ± 200	9255–8660	9475–8485	2, 3, 5, 7
Campo Laborde	AA-55117	7750 ± 250	8980–8360	9250–8040	2, 3, 5, 7
Campo Laborde	AA-71666	7630 ± 460*	9010–8000	9520–7610	5, 7
Arroyo Seco 2	TO-1506	7320 ± 50*$^{+}$	8180–8050	8295–8010	2, 3, 9
Campo Laborde	AA-71667	6740 ± 480*	8155–7155	8540–6545	5, 7

Note: All dates are from sites located in the Argentine Pampas and were reliably determined on bone or tooth remains. *^{14}C-dates considered problematic by author and not used here for analyses ($^{+}$same as CAMS-58182).
References: 1, Tonni *et al.* (2003); 2, Hubbe *et al.* (2007); 3, Borrero (2009); 4, Steele and Politis (2009); 5, Politis and Messineo (2008); 6, Prado *et al.* (2015); 7, Gutiérrez and Martínez (2008); 8, Martínez (2001); 9, Borrero *et al.* (1998)

framework for accessing the ecological mechanisms behind both climate and human impacts in the context of megafaunal extinctions.

Ecological niche modelling

We used ecological niche modelling (ENM) techniques to estimate habitat change for *Megatherium* and the consequent shift in its geographical range through the last glacial. ENMs estimate the association between environmental aspects (most often climate) and known occurrences of species to characterize the range of conditions under which populations of species are viable (i.e. their 'niche') (Franklin, 2009; Peterson *et al.*, 2011). This suite of methods has been applied for diverse research purposes, including palaeobiology and palaeobiogeography (Svenning *et al.*, 2011; Varela *et al.*, 2011), and is able to predict the species distributions and habitat conditions when humans arrived in South America (Lima-Ribeiro *et al.*, 2012).

The occurrence records for *Megatherium* were obtained from dated fossil remains available in the literature. A total of 34 fossil records from glacial times (ranging from 45,000 to 15,000 years ago) was used as 'training' data to calibrate the ENMs, whereas 10 fossil records aged around the Pleistocene–Holocene boundary (~11,000 years BP) were used as 'independent test' data to validate the ENM projections at the interglacial period and test niche stability through time (see conceptual details in Peterson *et al.*, 2011). Past climatic conditions were compiled from the ecoClimate database [www.ecoclimate.org (see details in Lima-Ribeiro *et al.*, 2015)] for both the LGM (21,000 years BP) and mid-Holocene (6000 years BP) periods, and five coupled atmosphere–ocean general circulation models (AOGCMs): CCSM4, CNRM-CM5, MIROC-ESM, MPI-ESM-P, MRI-CGCM3. The mid-Holocene is a key period for which current interglacial climates are simulated and was considered here representative of climatic conditions around the Pleistocene–Holocene boundary, ~11,000 years BP (for supportive evidence, see Lima-Ribeiro and Diniz-Filho, 2013c, p. 74), the period considered to be when humans entered South America and began hunting megafauna (see 'Population modelling' below). Five climatic layers (annual mean temperature, temperature annual range, precipitation of wettest and driest month, and precipitation of warmest quarter) were selected among the full set of 19 bioclimatic variables from a factor analysis with varimax rotation (Kaiser, 1958), and used here as non-collinear predictors to build the ENMs. We considered the climate layers that are contemporary to the training fossil records (i.e. LGM) for variable selection.

The ENMs were built on the climatic scenario of LGM and then projected onto mid-Holocene conditions to obtain species distributions for the glacial and interglacial periods, respectively. We used the BioEnsembles platform (see Diniz-Filho *et al.*, 2009) to implement six presence-only algorithms: Bioclim, Ecological Niche Factor Analysis (ENFA), Euclidean distance, Gower distance, Mahalanobis distance, and Genetic Algorithm for Rule set Production (GARP; indeed, GARP is a presence-background algorithm). We assessed their predictive performance using true skill statistics (TSS) based on 50 repetitions of two-fold cross-validation (75% training and 25% test). Next, we tested the stability of climatic conditions occupied by species through the last glacial cycle, which is an important assumption when the ENMs are projected onto different climatic scenarios through time (Nogués-Bravo, 2009). We specifically computed how many fossil records aged at interglacial periods (~11,000 years BP) were forecast by the potential distribution predicted for mid-Holocene climatic conditions. Besides testing the assumption of niche stability, this procedure also represents an adequate ENM validation from independent test data (Nogués-Bravo, 2009). Finally, consensus maps were built by averaging the 30 ENMs (6 ENM methods × 5 AOGCMs) for both the LGM and mid-Holocene, weighted by TSS values.

A detailed description of the BioEnsembles platform, algorithm selection, AOGCMs, model building, fossil sampling, the quality of the fossil record and its implications for the ENMs is available at: www.evolutionary-ecology.com/data/3014Appendix.pdf (Fig. S1 and Tables S1, S2).

Population modelling

Human impact was assessed from demographic models based on Lotka-Volterra predator–prey dynamics (Gotelli, 2008). We used a couple of density-dependent difference equations (see Box 1) for simulating populations of humans and *Megatherium* interacting throughout the last 11,000 years [i.e. the time of human colonization of South America (Rothhammer and Dillehay, 2009)] and estimating the time under hunting pressure when the prey goes extinct, called here the ‘time-to-extinction’ (see also Alroy, 2001; Diniz-Filho, 2004; Lima-Ribeiro and Diniz-Filho, 2013c; Flores, 2014).

In this context, we assumed that the megafauna represents a food source for the earliest South American hunter-gatherers, thus we established the mutual feedback between predator and prey populations by exploiting the meat consumption parameter. This parameter indicates the amount of meat consumed by a human population (Box 1, equation 1.1), which is converted to the number of prey killed in a given period (Box 1, equation 1.2). For example, a growing human population requires increased food, elevating meat consumption. The higher meat consumption causes an over-exploitation of the prey population, which becomes scarce, thereby decreasing meat supply. The decreased availability of meat (prey scarcity) negatively affects human population size. A lowered human population results in a decreased meat requirement, which then leads to lower hunting pressure and positive prey growth rates. The increasing prey population permits the human population to increase again in number and so on. The mortality parameter (*mo*) regulates the scale in which prey scarcity negatively affects human growth due to nutritional deficit (Box 1, equations 2.1–2.3). Low mortality rates, pertaining to rich ecosystems where humans could switch to alternative prey, determine a positive growth rate for humans even under focal prey scarcity. High mortality rates, on the other hand, increase the dependence of humans on prey availability and establish stronger feedbacks between both populations, which vary cyclically through time (Stenseth, 1995). However, prey scarcity also regulates the number of prey killed. In a scenario of no prey preference, the probability of a hunter meeting its prey naturally decreases with decreasing prey population, so that the number of prey killed is density-dependent for prey population (Box 1, equation 1.2).

The values of basic human demographic parameters, such as growth rate (r_h), carrying capacity (K_h), and food requirements (CI), were selected from estimates accepted by human ecologists and archaeologists (Hassan, 1980; Kelly, 1995; Hern, 1999), by considering palaeolithic hunters to be equivalent to living hunter-gatherers (Frisch, 1978). The basic demographic parameters for *Megatherium* were estimated from macroecological relationships based on body size [$M = 3700$ kg (Fariña *et al.*, 1998; Bargo, 2001; Brassey and Gardiner, 2015)]. Actually, allometric equations represent a unique way to infer population parameters for extinct species. The allometric equations of Silva and Downing (1995) and Brown (1995) were used here to estimate population density (Dn) and intrinsic rate of population increase (r_p) of *Megatherium*, respectively (Box 1, equations 4 and 5).

Box 1. Parameters (with sampling distribution) and equations used to simulate the extinction dynamic of *Megatherium* in South America under human hunting pressure

Parameter		**Sampling distribution**	**Source**
N	population size for prey (individuals)	n/a	eq. (1) and eq. (2)
H	population size for humans (individuals)	n/a	eq. (1) and eq. (2)
K_p	carrying capacity for prey (individuals)	n/a	Random ensembles *vs. Dn*
K_h	carrying capacity for humans (individuals)	Uniform (1×10^6, 4×10^6)	Cohen (1995), Hern (1999)
r_p	intrinsic rate of population increase for prey (%)	Uniform (0.001, 0.01)	eq. (3) (Brown, 1995)
r_h	intrinsic rate of population increase for humans (%)	Uniform (0.002, 0.02)	Hassan (1980), Hern (1999)
Dn	population density (individuals/km^2)	Normal (mean = 0.27, SD = 0.005)	eq. (4) (Silva and Downing, 1995)
mo	mortality rate for human population due to the scarcity of prey (%)	Uniform (0.001, 0.01)	n/a
CI	meat consumption by each human (g)	Uniform (5, 250)	Kelly (1995), Gnecco (2003)
M	body mass of prey (kg)	Uniform (3700, 6000)	Fariña *et al.* (1998), Smith *et al.* (2003)
A	proportion of the prey's biomass used for human feedings (%)	Uniform (0.3, 1)	n/a

Population equations

eq. (1)	$N_{(t+1)} = [N_{(t)} + r_p N_{(t)} * (1 - N_{(t)}/K_p)] - NR$	Logistic equation for population growth of prey, in discrete time
eq. (1.1)	$C = (CI/1000) * H * 365$	Amount of meat consumed by the human population H per year (g)
eq. (1.2)	$NR = [C/(M * A)] * (N_{(t)}/K_p)$	Actual number of hunted prey per year, taking into account the effect of prey rarity
eq. (2)	$H_{(t+1)} = [H_{(t)} + r_h H_{(t)} (1 - H_{(t)}/K_h)] - HR$	Logistic equation for population growth of humans, in discrete time
eq. (2.1)	$NP = C/(M * A)$	Potential number of hunted prey per year determined by total meat supply
eq. (2.2)	$DF = (NP - NR) * M * A$	Deficit in prey, in kilograms of meat per year
eq. (2.3)	$HR = mo * (DF/CI)$	Human mortality by nutritional deficit (prey rarity)

Allometric equations

eq. (3)	$r = \exp\,[1.4967 - 0.37 * \ln(M)]$	Allometric relationship for population rate of increase (r)
eq. (4)	$\text{Log10}\,(Dn) = 1.33 + [-0.71 * \log_{10}(M)] + \{0.05 * [\log_{10}(M)2]\}$	Allometric relationship for density (Dn)

We assumed that *Megatherium* attained its maximum population density (*Dn*) in the most suitable regions at the LGM, which was modelled to decrease following a Gaussian curve with respect to climatic conditions during the mid-Holocene. Suitability values were obtained by randomly combining the 30 ENMs (6 ENM methods × 5 AOGCMs) in an ensemble approach across 4000 repetitions (Diniz-Filho *et al.*, 2015), from which carrying capacity was computed as the sum of densities from all grid cells calibrated across the Gaussian curve.

We simulated how long a modest initial population of hunter-gatherers with 100 individuals (similar to Alroy, 2001), arriving in South America about 11,000 years ago (Rothhammer and Dillehay, 2009) and growing henceforth, would take to drive *Megatherium* to extinction. Because of uncertainties in demographic parameters, all population modelling was based on random sampling from a plausible range of parameters as established in the literature (see Box 1). For each of 4000 random ensembles, 100 population models were built with randomly sampled demographic parameters, which resulted in a total of 400,000 simulations, thus covering a wide part of the parameter space. The values of all selected demographic (r_h, K_h, etc.) and distributional parameters (geographic range size and range shift), together with the respective predicted time-to-extinction, were stored for each simulation for further analysis. The time-to-extinction was estimated from two extinction scenarios: (1) 'numeric extinction', in which *Megatherium* was considered extinct just when the last individual disappeared ($N < 1$); and (2) 'ecological extinction', which considers the species extinct when there is less than 10 individuals left ($N < 10$). This threshold for ecological extinction is arbitrary and does not mean that *Megatherium*'s population should be viable with at least 10 individuals and able to survive in the long term [see the current debate between conservation biologists Jamieson and Allendorf (2012, 2013) and Frankham *et al.* (2013)]. Instead, it expresses an attempt to deal with the temporal bias on the extinction time produced along a sequence of ^{14}C-dates and might be most closely comparable with the observed extinction pattern. In addition to operationally configuring a case for sensitivity analyses subsequently (see 'Data analysis' subsection below), considering the temporal bias on extinction time is conceptually important in the context of extinctions assessed from ^{14}C-dated fossil records.

Some authors have argued that the age of last appearance (youngest ^{14}C-dates) does not express the actual time a species became numerically extinct, but the time its populations reached a critical size below which fossilization is unlikely (Barnosky and Lindsey, 2010; Bradshaw *et al.*, 2012; Johnson *et al.*, 2013; Saltré *et al.*, 2015). In contrast, Lima-Ribeiro and Diniz-Filho (2013a, 2013b) have advocated that age of last appearance expresses the time at which species do not perform their ecological role in the ecosystems anymore because they have reached the point at which their population is below the minimum viable size, even although they still are numerically non-extinct [i.e. species became ecologically extinct (*sensu* Estes *et al.*, 1989)]. Thus, the arbitrary threshold of 10 individuals expresses the timing of ecological extinction for *Megatherium* and keeps both observed and predicted extinction patterns conceptually comparable under the ecologically extinct scenario, or at least counteracts the numerically extinct scenario also considered here.

A script in R for population modelling is available online at GitHub (https:github.com/limaribeiro/MegatheriumSimulation).

Data analysis

We used a pattern-oriented modelling (POM) approach (Grimm *et al.*, 2005; Grimm and Railsback, 2012) to find the combination of demographic parameters and niche models that correctly predicts the observed extinction time that is known (or assumed known) for *Megatherium*. The observed extinction time was primarily established as the youngest calibrated age (age of last appearance) from a time-series (Table 1) of reliable ^{14}C-dates on *Megatherium* remains using the Mead and Meltzer scale (Mead and Meltzer, 1984). Radiocarbon dates were calibrated to calendar years using the IntCal13 calibration curve (Reimer *et al.*, 2013) implemented in the Calib 7.1 software (http://calib.qub.ac.uk/calib/). To avoid uncertainties regarding the chronology of extinction from the youngest calibrated age, we statistically estimated the timing of extinction from six different methods for sensitivity analyses: GRIWM (Bradshaw *et al.*, 2012), S&S (Strauss and Sadler, 1989), SOL (Solow, 1993), MCY (McInerny *et al.*, 2006), SR (Solow and Roberts, 2003), and RS (Roberts and Solow, 2003). We also tested the overkill hypothesis by finding the combination of parameters needed to generate the extreme 'Blitzkrieg' scenario, in which the prey would become extinct within 1000 years after humans arrived in South America (Martin, 1967, 1973).

We used classification trees to investigate the parameter space under both the numerical and ecological extinction scenarios, from which the actual and overkill extinction patterns were established (a categorical response variable indicating if *Megatherium* was extinct under each scenario or not). The classification trees were fitted using the specific R-package 'tree' (Ripley, 2015) with categorical response variable (extinct or not) and distributional (geographic range size and range shift) and demographic parameters (r_h, K_h, etc.) as predictors. The relative role of each parameter in establishing the time-to-extinction was assessed from a logistic regression (link logit) fitted with the function *glm* from the basic R-package 'stats' (R Development Core Team, 2015). Finally, we assessed the 'co-occurrence' pattern among the 30 ENMs (5 ENM methods × 6 AOGCMs) across the random ensembles that correctly estimated the actual extinction pattern of *Megatherium*, using the R-packages 'cooccur' (Griffith *et al.*, 2014) and 'network' (Butts, 2008, 2015). The 'cooccur' fits a probabilistic model of ENM co-occurrence among the set of repetitions, whereas 'network' encodes a complex relational structure among selected ENMs across repetitions.

RESULTS

Ecological niche models and the palaeodistribution of *Megatherium*

The consensus maps from 30 ENMs predicted that *Megatherium* was potentially distributed over a large and continuous geographical range across the mid-latitudes of South America during the LGM (Fig. 1A), as expected by its preference for tropical-temperate climates (see Bargo *et al.*, 2006 and references therein). However, its potential geographical range was reduced considerably during the Holocene. On average, the suitable area for *Megatherium* was reduced by some 30% from the LGM to the Holocene, but as much as 50% under the most extreme predictions (Fig. 1B). Moreover, *Megatherium*'s geographical range fragmented into two suitable areas across the Andes and Atlantic coastal region, disconnected by the Gran Chaco and Cerrado (Fig. 1B), matching the pattern of generalized tracks found by Gallo *et al.* (2013). The predictive ability of all ENMs was generally better than random classifications, with TSS values usually higher than 0.2. Yet, the interglacial projections

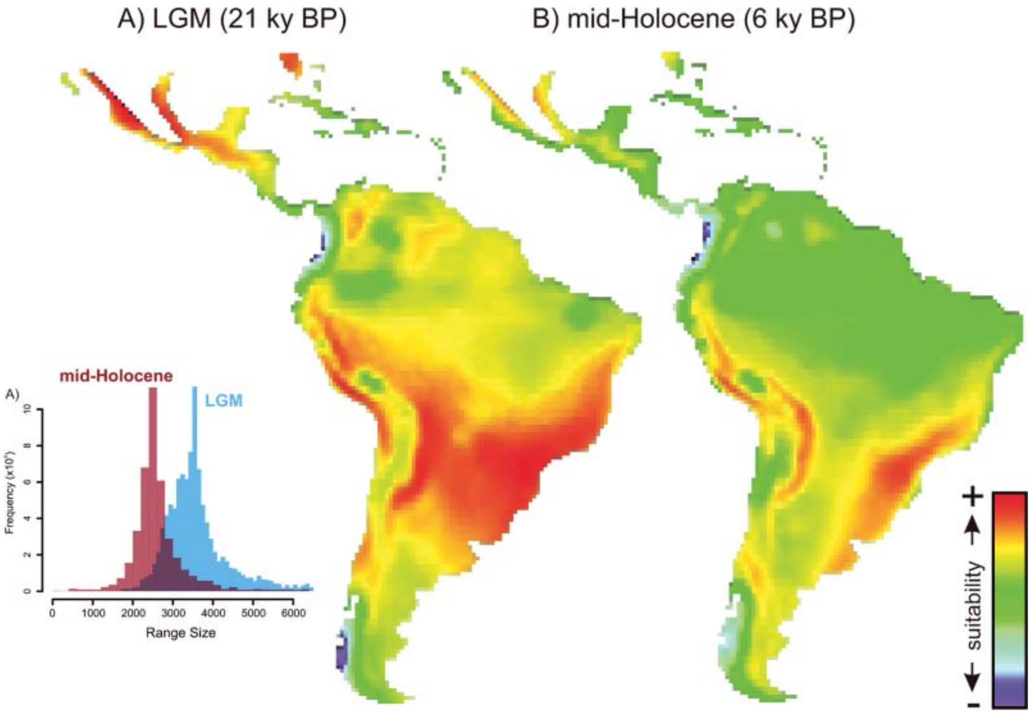


Fig. 1. Consensus maps showing the potential distribution of *Megatherium* at (A) the LGM (21,000 years BP) and (B) the mid-Holocene (6000 years BP) in South America. Inset: The histograms show the frequency distributions of the range sizes predicted by 4000 random ensembles.

predicted at least one-half of the independent test data (dated fossil record around 11,000 years BP) and were then used to build random ensembles for demographic modelling.

Random ensembles estimated a negatively normally distributed range shift, indicating that most models predicted a range reduction from the LGM to the Holocene, largely corroborating the distributional pattern seen in the consensus maps. All ENM methods and AOGCMs were equally combined in the random ensembles, which were built by selecting from one to all 30 models uniformly distributed. More details are provided in Figs. S2, S3 and Tables S3, S4 (3014Appendix).

Population models

Demographic models simulating human hunting predicted extinction of *Megatherium* in 75% of cases for both ecological and numerical extinction scenarios, with a median time-to-extinction of around 1800 years, with a right-skewed distribution (Fig. 2A,B). The time-to-extinction varied considerably within the explored space of demographic parameters, and differed slightly between ecological and numerical extinction scenarios (median difference in time-to-extinction from both scenarios was 69 years, also right-skewed; Fig. 2C).

Regression analyses showed that variance in demographic parameters (e.g. population growth, carrying capacity) was generally better at estimating the time-to-extinction than distributional features (e.g. range size) (Fig. 3). In addition, time-to-extinction is primarily

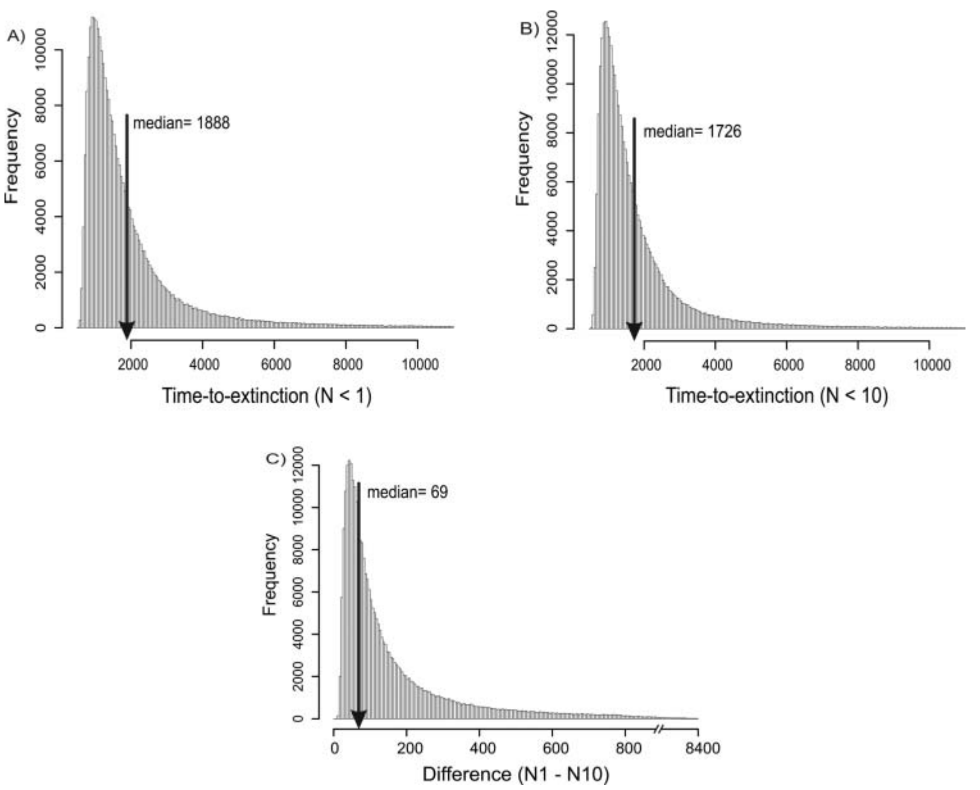


Fig. 2. Distribution of time-to-extinction predicted for numerical (A) and ecological (B) extinction scenarios, and the difference between them (C) for the 400,000 demographic models.

defined by variance in demographic parameters linked to human populations (r_h, CI, K_h, A, mo) rather than to prey populations (r_p, K_p, M, Dn) (Fig. 3). In general, high values for human population parameters such as growth rate (r_h), individual meat consumption (CI), carrying capacity (K_h), and a large range reduction from the LGM to the Holocene accelerate the extinction of *Megatherium*, whereas high human mortality (mo) and large geographical ranges at the LGM delay *Megatherium* extinction considerably (Table 2). More details are provided in Figs. S4–S7 and Tables S5, S6.

Extinction dynamics of *Megatherium*

Observed extinction time

The time-series of reliable radiocarbon determinations representing the last appearance dates for *Megatherium* in South America indicates that this species went extinct in the Argentine Pampas some 9250 to 8040 years ago (2-sigma calibrated age from the youngest reliable ^{14}C-date; Table 1). Additionally, different statistical methods predicted a younger unbiased extinction time spanning from 7910 to 3890 years ago. However, the POM results did not differ significantly from most analyses of these different observed extinction patterns. Thus, to synthesize descriptions, we report below only the POM results predicting

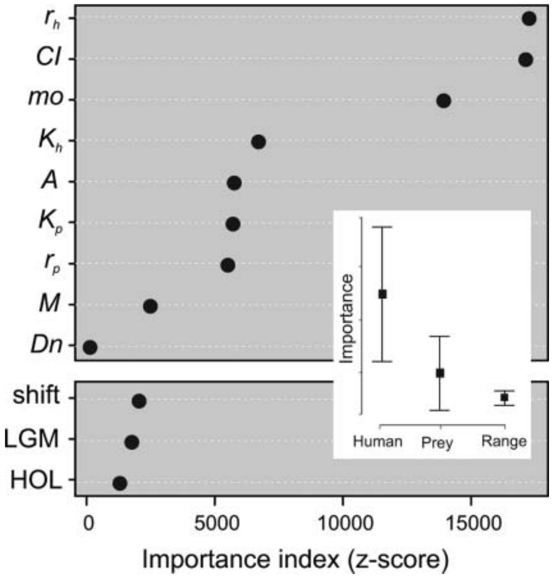


Fig. 3. Importance of demographic parameters (upper panel) and distributional features (lower panel) in defining the time-to-extinction for *Megatherium* under the ecological extinction scenario. The inset shows the mean and confidence interval of importance for human and prey demographic parameters and distributional features. The index of variable importance reflects the absolute magnitude of z-scores from a generalized linear model fitted using the loglink and the Poisson family. Shift: the shift in range size between the LGM and mid-Holocene; LGM: geographic range size at LGM (21,000 years BP); HOL: range size at mid-Holocene (6000 years BP). See specifications for demographic parameters in Box 1.

Table 2. Coefficients (slope-b and standard error) from generalized linear models fitted using the loglink and the Poisson family among demographic/distributional parameters and time-to-extinction

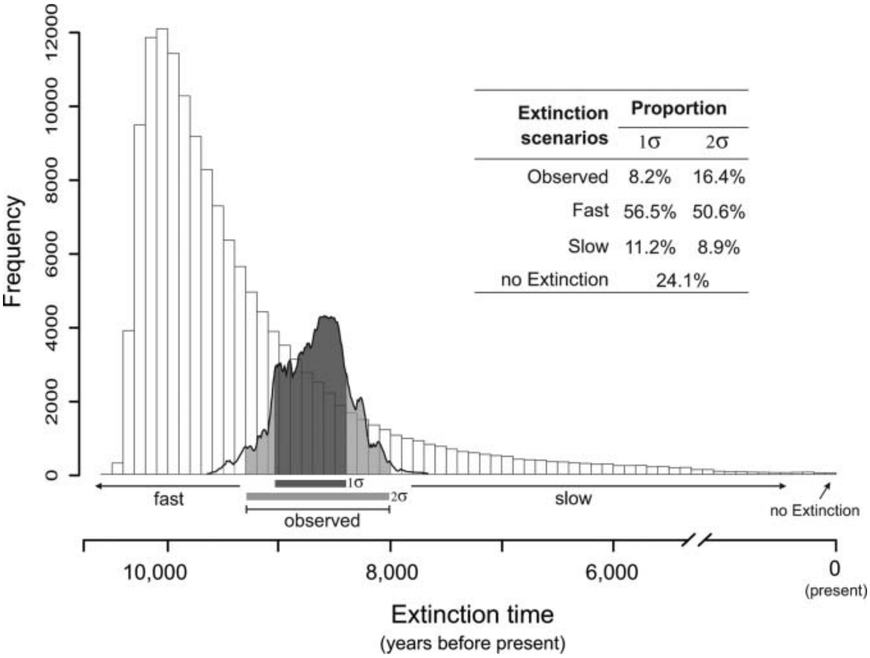
Parameter	Slope	SD
r_h	-1.06×10^{2}	6.12×10^{-3}
r_p	5.31×10^{1}	9.64×10^{-3}
K_h	-1.95×10^{-7}	2.91×10^{-11}
K_p	3.59×10^{-7}	6.28×10^{-11}
mo	1.39×10^{2}	9.99×10^{-3}
CI	-6.41×10^{-3}	3.74×10^{-7}
A	7.16×10^{-1}	1.24×10^{-4}
Range LGM	1.49×10^{-4}	6.44×10^{-8}
Range HOL	-1.51×10^{-4}	7.18×10^{-8}
Range shift	-1.50×10^{-4}	6.41×10^{-8}

Note: Range LGM: geographic range size at LGM (21,000 years BP); Range HOL: range size at mid-Holocene (6000 years BP); Range shift: the shift in range size between the LGM and mid-Holocene. See specifications for demographic parameters in Box 1.

the observed extinction pattern delimited around the 2-sigma youngest calibrated age under the ecological extinction scenario. The ecological extinction scenario conceptually represents more adequate ecological and evolutionary dynamics in the context of LQE, although the results also did not differ systematically from the numerical extinction scenario. Nevertheless, we present the complete results in 3014Appendix.

The observed extinction time delimited around 2-sigma calibrated age from the youngest reliable ^{14}C-date for *Megatherium* in South America was predicted by 16% of the demographic models (Fig. 4). Most models estimated fast extinctions (51%; i.e. predicted *Megatherium* was extinct before its observed time of extinction), whereas a few models estimated a long time to extinction (8%; i.e. predicted extinction time was younger than observed extinction time) (Fig. 4). Almost one-quarter of the models failed to predict extinction.

Following the POM reasoning and the classification tree in Fig. 5, the 'correct' timing of *Megatherium*'s extinction (2-sigma youngest calibrated age) was obtained only in a narrow window in the parameter space, encompassing specifically the lowest growth ($r_h < 0.70\%$) and mortality rates for humans ($mo < 0.60\%$) combined with moderate values of individual



Extinction scenarios	Proportion	
	1σ	2σ
Observed	8.2%	16.4%
Fast	56.5%	50.6%
Slow	11.2%	8.9%
no Extinction	24.1%	

Fig. 4. Distribution of predicted extinction times throughout the demographic simulations (bars) and the observed extinction time delimited by the calibrated age from the youngest reliable ^{14}C-date for *Megatherium* in South America (dark grey line: 1-sigma; light grey line: 2-sigma). 'Fast' and 'slow' extinction times represent models predicting extinctions earlier (older) and later (younger) than the observed extinction time, respectively. Table shows the proportion of models predicting the extinction scenarios as delimited from 1-sigma (8980–8360 years ago) and 2-sigma (9250–8040 years ago) ranges from calibrated age. The proportion of models predicting no extinction is constant, regardless of comparisons with observed extinction time. See the complete time-series of ^{14}C-dates and calibrated ages in Table 1.

meat consumption ($CI > 70$ g). If such low rates of human population growth (r_h) were combined with high human mortality ($mo > 0.60\%$) and low individual meat consumption ($CI < 30$ g), *Megatherium* would survive longer through the Holocene or would not go extinct from human exploitation either (Fig. 5). In contrast, fast extinctions were predicted over a wider region in the parameter space, mainly indicating a vigorous human population (i.e. highest rates of human population growth: $r_h > 1\%$) over-exploiting the prey *Megatherium* (individual meat consumption: $CI > 70$ g), and with human survivorship slightly dependent on a shortage of meat (i.e. low human mortality: $mo < 0.60\%$ in response to prey extinction). More details are provided in Figs. S7 and S8.

The 'correct' estimates of *Megatherium*'s extinction time were attained from distributional dynamics predicted from all 4000 random ENM ensembles when combined with different values of demographic parameters in the predator–prey simulations. No pattern of shared selection (or co-occurrence) among the 30 ENMs (6 methods × 5 AOGCMs) was observed across all random ensembles that correctly predicted the extinction time of *Megatherium* (Fig. 6A); that is, no specific combination of ENM methods and palaeoclimatic simulations (AOGCMs) was fundamental to ensuring that the demographic models correctly estimated the timing of extinction. However, some combinations of ENM methods and AOGCMs (MRI-Maha and MRI-GARP) were more frequently present in the random ensembles from which demographic models correctly predicted the extinction time of *Megatherium*. Such ENM–AOGCM combinations occupy central nodes in the network

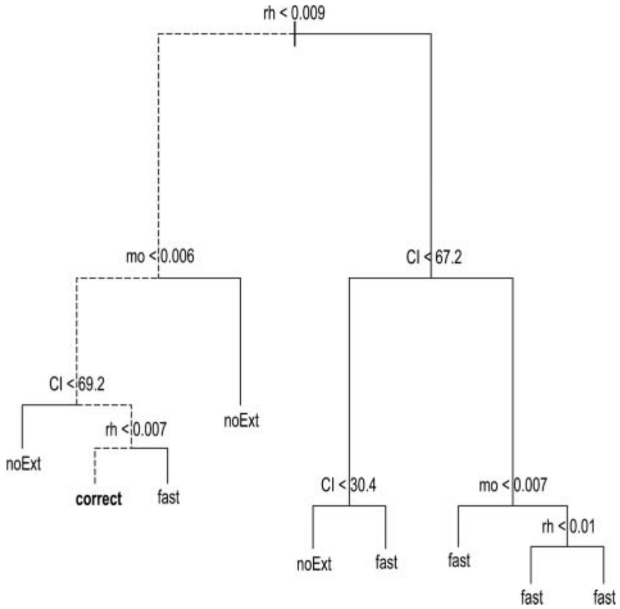


Fig. 5. Classification tree showing the predictions for extinction scenarios by combining the multiple demographic parameters across predator–prey simulations. The dashed line shows the space of demographic parameters needed to 'correctly' predict the observed timing of *Megatherium*'s ecological extinction (2-sigma calibrated age: 9250–8040 years ago). 'Fast' and 'slow' indicate the combination of parameters predicts an earlier (older than 9250 years ago) and later (younger than 8040 years ago) extinction time, respectively. 'NoExt' indicates that demographic models were not able to predict *Megatherium*'s extinction when built from that specific parameter space.

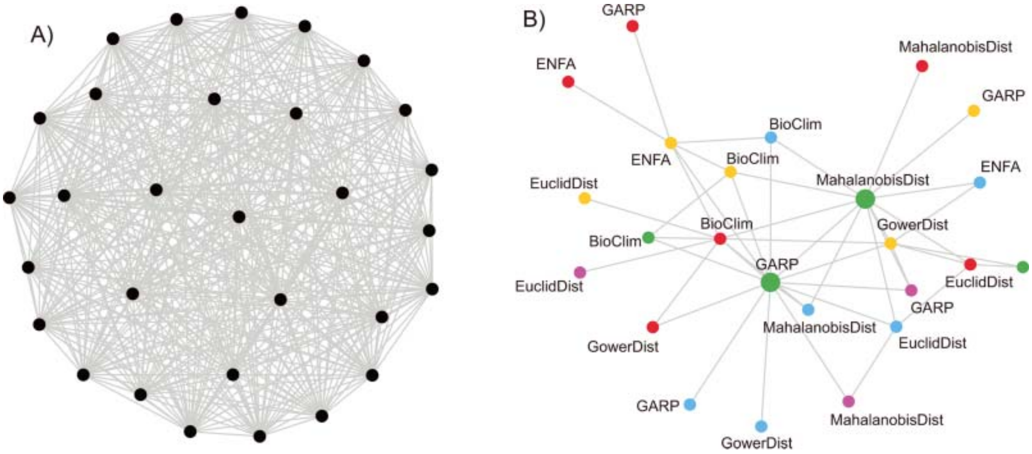


Fig. 6. Networks showing the relationships among ENM methods and AOGCMs across the random ensembles correctly predicting *Megatherium*'s extinction time. (A) Overall combinations. (B) Most frequent combinations. The nodes represent the 30 ENM–AOGCM combinations linked to each other if they were selected in a specific ensemble. In general, all ENM–AOGCM combinations were present in demographic models correctly predicting extinction time (all nodes are equally linked in A), but some combinations were more frequently selected among such random ensembles (MRI-Maha and MRI-GARP represent central nodes in B with more links than any other combinations). Colours in (B) indicate different AOGCMs: yellow, CCSM; purple, CRNM; blue, MIROC; red, MPI; green, MRI.

and represent hubbies with multiple links. On the other hand, the nodes with single or short links (e.g. MIROC-Gower, MIROC-GARP, CCSM-GARP) represent ENM–AOGCM combinations that were less frequent among those random ensembles that correctly predicted *Megatherium*'s time of extinction (Fig. 6B). More details are provided in Figs. S8, S9 and Tables S7, S8.

Testing the overkill hypothesis

The demographic models predicting the overkill scenario represent a group of models that estimate a fast extinction time for *Megatherium* in South America. From these extreme demographic models, ~38% (or 20% of all models) yielded a time-to-extinction less than 1000 years (i.e. matched the predictions of the overkill hypothesis). Such a massive overkill would only be possible under unrealistically high human population growth parameters (r_h ~ 1.7%; $t = 1723.9$, $P < 0.001$) and extreme exploitation of *Megatherium* (high meat consumption: CI ~ 175 g), combined with a small prey population (~16% of maximum K_p) and large carrying capacity for humans (~70% of maximum K_h) (Table 3).

Following the POM reasoning, the overkill scenario would be the most likely, by combining the highest values of human population growth rates ($r_h > 1.3\%$), individual meat consumption ($CI > 100$ g), and human carrying capacity ($K_h > 2.1 \times 10^6$ individuals) with the lowest values of carcass utilization (A) and human mortality (mo) in a similar simulation (Fig. 7). In contrast, if demographic models are permissive and less extreme values of these parameters are considered, simulations yield longer than 1000 years for time-to-extinction, hence failing to match the prediction of the overkill hypothesis. More details are provided in Fig. S10.

Table 3. Mean of main demographic parameters estimating extreme extinction scenarios

Parameter	Overestimates	Overkill
r_h	0.0137	0.0169
r_p	0.0053	0.0053
K_h	2,606,164	2,782,588
K_p	734,323	693,895
mo	0.0049	0.0047
CI	149.9	175.8
A	0.63	0.58

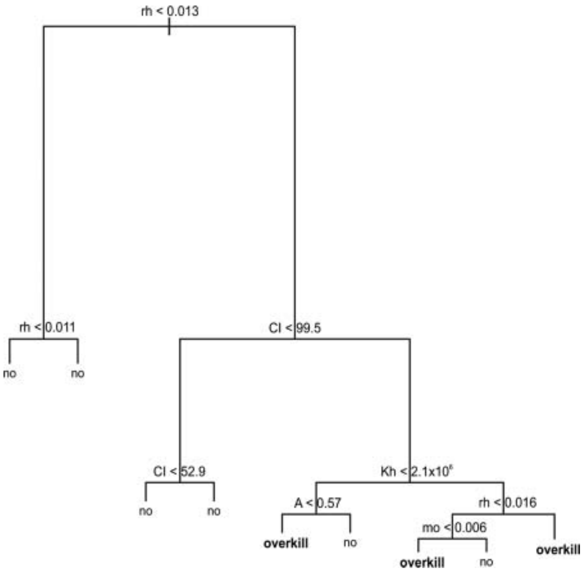


Fig. 7. Classification tree showing likely combinations of parameter space across demographic models needed to predict extreme extinction scenarios matching the overkill hypothesis (time-to-extinction <1000 years).

DISCUSSION

Determinants of *Megatherium*'s extinction dynamics in South America

Demographic-based determinants

Population models coupled with ecological niche modelling and palaeoclimatic simulations were able to establish the extinction dynamics of *Megatherium* through the latest Pleistocene and early Holocene in South America in response to the effects of human hunting and climate change. The POM approach revealed realistic (or at least acceptable) values for demographic and distributional parameters for the prey and for human populations across simulations, predicting an accurate extinction time for *Megatherium*.

Palaeodemographic estimates, for example, indicate that human populations living through the Neolithic (~12,000 to 4000 years ago) grew at relatively slow rates [around 0.1–0.4% per year (Hassan, 1980; Hern, 1999)], as shown in our simulations ($r_h < 0.7\%$; Fig. 5). The hunter-gathering lifestyle provides little potential for economic growth and a limited capability to extract and use resources, and thereby is considered the main determinant of slow human population growth in prehistoric times (Hassan, 1980).

Besides slow human growth, our modelling also complies with a somewhat high meat consumption rate ($CI > 70$ g) like that expected for hunter-gatherers. Taking into account that each person consumes a maximum 1780 g of meat per day from multiple sources (small and large animal species) in modern hunting and gathering societies (Kelly, 1995) and that the extinct megafauna represented around a quarter of consumed meat by tropical hunter-gatherers (Gnecco, 2003; Rowcliffe *et al.*, 2003), a meat consumption rate of 70 g per day from a single megafauna species (*Megatherium*) is empirically acceptable for early South Americans. A meat consumption rate of 70 g per day represents around 4% of the maximum daily meat requirement, or 15% of megafauna consumption, and seems conceptually realistic for the tropical-temperate ecosystems where *Megatherium* lived in South America. During the end of the Pleistocene and the early Holocene, this region was occupied by a rich biodiversity, including some 52 other now-extinct megafaunal genera (Koch and Barnosky, 2006; Borrero, 2009), which would easily complement the human meat supply [see also the simulations for consumption of minifauna in Bulte *et al.* (2006) and Abramson *et al.* (2015)]. The rich biodiversity available as food in tropical-temperate ecosystems should make human survival independent of a single prey (Gnecco, 2003); that is, the scarcity or extinction of a unique prey species is not expected to affect significantly human mortality rates (Smith, 1975), as was also shown across our simulations that correctly predicted *Megatherium*'s extinction time ($mo < 0.6\%$).

In contrast, rapid human population growth, usually higher than 1% a year, was only attained after the industrial revolution (Hern, 1999). Such rates were due to changes in the structure of socioeconomic resources with positive feedbacks on carrying capacity (Cohen, 1995; Stutz, 2014). Even higher growth rates for human populations, like those needed to predict the overkill scenario ($r_h > 1.3\%$), were only reached around the mid-1900s, when the human population grew exponentially and doubled over a period of 30–40 years (DeLong and Burger, 2015). It seems conceptually and empirically evident that the earliest South American hunter-gatherers were unable to achieve such fast growth rates (Frisch, 1978) [but see also the effects from evolutionary changes in life-history traits in Milot *et al.* (2011)]. Thus, although feasible from model simulations (as defended in Mosimann and Martin, 1975), our findings do not support the overkill hypothesis as a realistic scenario for explaining the extinction of *Megatherium* in South America.

Geographic range-based determinants

Similar to the demographic dynamics, the distributional features related to geographic range size and shift as predicted by ENMs also affect the ability of models to predict the actual extinction pattern of *Megatherium* in South America. In line with other studies that examined the effect of global climate change on extinct megafauna (Nogués-Bravo *et al.*, 2010), our findings clearly show that a drastic reduction in geographic range size and climatic suitability from the LGM to the Holocene favoured the extinction scenarios; that is, smaller geographical ranges would have increased extinction risk and rapidly driven species to extinction (see similar results in Pushkina and Raia, 2008).

However, distributional features had less influence than demographic parameters in determining the time-to-extinction. The fact that all ENM–AOGCM combinations successfully produced the actual extinction time indicates that uncertainties among ENM predictions generate a weaker impact on the demographic models than uncertainties across the space of the demographic parameters. Based on our findings, further studies should attempt to improve demographic models by better delineating the space of feasible demographic parameters instead of exhaustively exploring the uncertainties from ENM predictions.

POM approach and the LQE debate

The POM approach has increasingly been applied to ecological and evolutionary questions (Grimm *et al.*, 1996; Rangel *et al.*, 2007; Diniz-Filho *et al.*, 2014), and was shown here to be a promising and helpful tool for decoding the complex puzzle of the LQE. Population models have been used for a long time to simulate the dynamics of megafaunal extinction (Mosimann and Martin, 1975; Whittington and Dyke, 1984; Alroy, 2001; Brook and Bowman, 2004; Flores, 2014; Abramson *et al.*, 2015). Unfortunately, uncertainty regarding basic parameters inferred from fossil data and the complex nature of the synergetic interaction between human and climatic impacts have hampered the identification of general principles underlining the LQE or supported feasible, but contrasting and somewhat unrealistic extinction scenarios (for a critical review, see Yule *et al.*, 2009). A general characteristic of these simulations is fitting a model to a particular dataset by adding numerous unconstrained, often uncertain, parameters, achieving a best match to theoretical expectations instead of exploring the feasible parameter space to determine what combinations explain best the observed patterns underlining the LQE.

Mosimann and Martin (1975), for example, used demographic modelling in the LQE context with human population growth around 4% a year to support the overkill scenario in North America (see also Whittington and Dyke, 1984). Recent estimates indicate a maximum growth rate of 1.8% per year in modern societies, making these modelling outcomes hard to support (Frisch, 1978). More recently, Alroy (2001) built a complex and spatially explicit simulation model based on more realistic human parameters, and showed that the overkill scenario may take place under slower human growth rates ($r > 1.4\%$ per year). However, our findings indicate that even Alroy's (2001) slower human growth rates are unrealistic to predict the observed extinction pattern of *Megatherium* and exceed almost three times the actual growth rates for Neolithic hunter-gatherer societies [0.1–0.4% (Hassan, 1980; Hern, 1999)]. Because rapid extinction was the most frequent scenario throughout the parameter space we explored, it is natural that previous simulations not addressing the POM reasoning have most often spuriously supported extreme scenarios [as predicted by Martin's overkill hypothesis (Martin 1967, 1973)] than the observed extinction patterns. In other words, the POM approach was crucial to establish that overkill is feasible from population model simulations, as revealed by previous simulations (Mosimann and Martin, 1975; Whittington and Dyke, 1984; Alroy, 2001), but only under unrealistic human population parameters (Hassan, 1980; Hern, 1999).

Moreover, most previous simulations supporting the overkill assumed the only impact on megafauna was the arrival of big-game hunters in North America [but see also the global model for prehistoric overkill in Martin (1984)]. That is, these simulations ignored the stressful impacts of climate change on megafauna through the last glacial cycle (Nogués-Bravo *et al.*, 2010). In fact, simplistic dynamics depicting single causes have been the rule in narrative reviews trying to explain the LQE (see details in Lima-Ribeiro and Diniz-Filho, 2013a, 2013b). Of course, simplistic dynamics are likely to lack the underlying process needed to produce the intended pattern, thus they cannot satisfactorily explain reality. The principle of POM is based on the reasoning that patterns contain coded information on the internal organization of a system, thus the best combination of parameters will reveal the likely underlying processes yielding such observed pattern (Grimm *et al.*, 2005). Therefore, the POM approach is far more robust and comprehensive than standard and isolated simulations or narrative reviews for decoding complex ecological and evolutionary dynamics not feasible from observational data (e.g. fossil observations) or extinct species, as has been the case of many LQE simulations. To improve the POM approach in the context of the LQE, we recommend future studies explore multiple observed patterns to orient the parameterization of models decoding extinction dynamics for multiple species at different spatial and temporal scales.

Perspectives for conservation biology from palaeobiology: a POM approach based on the LQE context

The current new challenge to conservation biologists is preserving not just individual species, but also the function of the natural ecosystems to which they belong (Svenning *et al.*, 2016), under the increasing effects of multiple forces altering the Earth's systems and its biota throughout the Anthropocene (Dirzo *et al.*, 2014). In a broad sense, the longer threatened species survive in functioning ecosystems, the more efficient and desirable conservation efforts are. To reach such efficiency, it is necessary to establish reference conditions within which species may survive – that is, determine how species respond to multiple stressors, and evaluate whether species can persist naturally under different magnitudes of changing environment. However, conservation biologists have rarely established complete ecological baselines (i.e. the reference conditions) based on neontological data restricted to the near-time (e.g. spanning a past few decades), or have simply ignored such features by assuming that species were stable through deep-time (Liow, 2012). In an attempt to solve such flaws, palaeobiologists have recently proposed applying fossil data linking multiple scales of time and space to establish more reliable and complete baselines, document a wider range of ecological variability, and assist in developing more effective conservation strategies (Rick and Lockwood, 2013). A basic idea is to classify species' extinction risk by considering their response to the similar pressures that occurred in deep-time (Dietl *et al.*, 2015). For example, species with stable features in the past (e.g. stable geographical range), but widely varying in the present and/or in the future, should occupy the highest ranks of extinction risk (i.e. species that never experienced the magnitude of variation that ecosystems are currently facing or will experience in the future). On the other hand, species for which current pressures were 'normal' during their evolutionary history are not too much of a concern because they already experienced a similar range of variation in the past and have already survived naturally through these pressures (Hadly and Barnosky, 2009).

We now live in an anthropogenically driven world characterized by global warming, rapid human population growth, and by habitat loss resembling the end of the Pleistocene when the megafauna vanished from Earth. Our framework, then, illustrates a promising tool to directly apply palaeobiology to help us better understand modern conservation problems and identify priorities for effective conservation strategies. The niche and population models properly coupled in an interactive way are able to establish the 'normal' climate and human effects that extant species experienced throughout the Late Quaternary. Thus, by exploring our POM-based approach in the context of the LQE, we may establish the range of feasible demographic parameters attained by species and humans in an interacting prehistoric world and compare these with the magnitude of current climatic and anthropogenic conditions in which conservation plans are formulated. Although our framework was applied here in the context of a single prey (humans hunting *Megatherium* only), it is scalable to multi-prey systems by considering interactions and human hunting preferences for multiple species (see Lima-Ribeiro and Diniz-Filho, 2013c), which will make it widely applicable to one of the most challenging scenarios for modern conservation biology. Viewed against this audacious conservation background, we believe our framework coupling ENMs and population models in a POM approach is useful not only to superficially compare palaeobiological and neontological data, but directly infer ecological mechanisms behind additive effects from climate change and human impacts on living species compared with their own Pleistocene experiences or from their now-extinct relatives.

CONCLUDING REMARKS

Our findings suggest that *Megatherium* went extinct in South America by virtue of a synergistic effect that included both climatic and human impacts, and do not support single stressors as the cause of its extinction. Populations of *Megatherium* were narrowly distributed on fragmented ranges across southern South America in response to climate depreciation when humans arrived and potentially determined its timing of extinction. The POM approach delineated empirically acceptable values for human demographic parameters needed to correctly estimate *Megatherium*'s extinction dynamics, particularly slow growth rates, negligible dependence of human population on a meat supply from a single species, and acceptable individualistic meat consumption rate for tropical-temperate ecosystems. In addition, the specific space of demographic parameters needed to achieve the extreme extinction scenario matching the overkill hypothesis is not empirically supported for prehistoric hunter-gatherers. Although possible based on our models, the parameter values are unrealistic to attain an overkill scenario in the case of *Megatherium*.

POM reveals a powerful and helpful approach to solve the puzzle of the LQE and improve the debate about its causes and implications. Besides advancing the LQE debate, our framework also exemplifies a promising way by which palaeobiology may serve conservation biology. Although the operational details need to be adjusted, knowing which mechanisms raise species extinction risk in a climatically and anthropogenically impacted world, just like during the LQE event, is potentially useful in making more informed conservation decisions, making conservation planning more efficient, and improving conservation actions in the modern world.

ACKNOWLEDGEMENTS

We acknowledge the World Climate Research Programme's Working Group on Coupled Modeling by the CMIP5 and PMIP3, and we thank the climate modelling groups (Table S2) for producing and making available model outputs. We appreciate financial support from CNPq (productivity grants to J.A.F.D-F. and 447426/2014-1 to M.S.L-R.) and FAPEG (2012/1026.700.1086) for our research programme on macroecology and palaeobiology. We are grateful to Pasquale Raia and Mikael Fortelius for inviting us to participate in this special issue of EER on 'Evolutionary Macroecology' and two anonymous reviewers for valuable comments that improved previous versions of our manuscript.

REFERENCES

Abramson, G., Laguna, M.F., Kuperman, M.N., Monjeau, A. and Lanata, J.L. 2015. On the roles of hunting and habitat size on the extinction of megafauna. *Quat. Int.*, in press [DOI: 10.1016/j.quaint.2015.08.043].

Alroy, J. 2001. A multispecies overkill simulation of the end-Pleistocene megafaunal mass extinction. *Science*, **292**: 1893–1896.

Araujo, B.B.A., Oliveira-Santos, L.G.R., Lima-Ribeiro, M.S., Diniz-Filho, J.A.F.D. and Fernandez, F.A.S. 2015. Bigger kill than chill: the uneven roles of humans and climate on late Quaternary megafaunal extinctions. *Quat. Int.*, in press [DOI: 10.1016/j.quaint.2015.10.045].

Bargo, M.S. 2001. The ground sloth *Megatherium americanum*: skull shape, bite forces, and diet. *Acta Palaeontol. Polon.*, **46**: 173–192.

Bargo, M., Iuliis, G. and Vizcaíno, S.F. 2006. Hypsodonty in Pleistocene ground sloths. *Acta Palaeontol. Polon.*, **51**: 53–61.

Barnosky, A.D. and Lindsey, E.L. 2010. Timing of Quaternary megafaunal extintion in South America in relation to human arrival and climate change. *Quat. Int.*, **217**: 10–29.

Borrero, L.A. 2009. The elusive evidence: the archeological record of the South American extinct megafauna. In *American Megafaunal Extinctions at the End of the Pleistocene* (G. Haynes, ed.), pp. 145–168. New York: Springer.

Borrero, L.A., Zarate, M., Miotti, L. and Massone, M. 1998. The Pleistocene–Holocene transition and human occupations in the southern cone of South America. *Quat. Int.*, **49/50**: 191–199.

Bradshaw, C.J.A., Cooper, A., Turney, C.S.M. and Brook, B.W. 2012. Robust estimates of extinction time in the geological record. *Quat. Sci. Rev.*, **33**: 14–19.

Brassey, C.A. and Gardiner, J.D. 2015. An advanced shape-fitting algorithm applied to quadrupedal mammals: improving volumetric mass estimates. *R. Soc. Open Sci.*, **2**: 150302.

Brook, B.W. and Bowman, D.M.J.S. 2004. The uncertain blitzkrieg of Pleistocene megafauna. *J. Biogeogr.*, **31**: 517–523.

Brown, J.H. 1995. *Macroecology*. Chicago, IL: University of Chicago Press.

Bulte, E., Horan, R.D. and Shogren, J.F. 2006. Megafauna extinction: a paleoeconomic theory of human overkill in the Pleistocene. *J. Econ. Behav. Org.*, **59**: 297–323.

Butts, C. 2008. network: a package for managing relational data in R. *J. Stat. Soft.*, **24**: i02.

Butts, C. 2015. *network: classes for relational data*. The Statnet Project [http://www.statnet.org]. R package v. 1.12.0 [http://CRAN.R-project.org/package = network].

Cannon, M.D. and Meltzer, D.J., 2004. Early Paleoindian foraging: examining the faunal evidence for large mammal specialization and regional variability in prey choice. *Quat. Sci. Rev.*, **23**: 1955e1987.

Cartelle, C. and De Iuliis, G. 2006. *Eremotherium laurillardi* (Lund) (Xenarthra, Megatheriidae), the Panamerican giant ground sloth: taxonomic aspects of the ontogeny of skull and dentition. *J. Syst. Palaeontol.*, **4**: 199–209.

Cohen, J.E. 1995. Population growth and earth's human carrying capacity. *Science*, **269**: 341–346.

Dantas, M.A.T., Queiroz, A.N., Santos, F.V. and Cozzuol, M.A. 2012. An anthropogenic modification in an *Eremotherium* tooth from northeastern Brazil. *Quat. Int.*, **253**: 107–109.

De Iuliis, G., Pujos, F.O. and Tito, G. 2009. Systematic and taxonomic revision of the Pleistocene ground sloth *Megatherium* (*Pseudomegatherium*) *tarijense* (Xenarthra: Megatheriidae). *J. Vert. Paleontol.*, **29**, 1244.

DeLong, J.P. and Burger, O. 2015. Socio-economic instability and the scaling of energy use with population size. *PLoS One*, **10**: e0130547.

Dietl, G.P., Kidwell, S.M., Brenner, M., Burney, D.A., Flessa, K.W., Jackson, S.T. *et al.* 2015. Conservation paleobiology: leveraging knowledge of the past to inform conservation and restoration. *Annu. Rev. Earth Planet. Sci.*, **43**: 79–103.

Diniz-Filho, J.A.F. 2004. Macroecological analyses support an overkill scenario for Late Pleistocene extinctions. *Braz. J. Biol.*, **64**: 407–414.

Diniz-Filho, J.A.F., Bini, L.M., Rangel, T.F., Loyola, R.D., Hof, C., Nogués-Bravo, D. *et al.* 2009. Partitioning and mapping uncertainties in ensembles of forecasts of species turnover under climate change. *Ecography*, **32**: 897–906.

Diniz-Filho, J.A.F., Soares, T.N. and Telles, M.P.C. 2014. Pattern-oriented modeling of population genetic structure. *Biol. J. Linn. Soc.*, **113**: 1152–1161.

Diniz-Filho, J.A.F., Rodrigues, H., Telles, M.P.C., Oliveira, G., Terribile, L.C., Soares, T.N. *et al.* 2015. Correlation between genetic diversity and environmental suitability: taking uncertainty from ecological niche models into account. *Mol. Ecol. Res.*, **15**: 1059–1066.

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B. and Collen, B. 2014. Defaunation in the Anthropocene. *Science*, **345**: 401–406.

Dorman, C.F., Purschke, O., Márquez, J.R.G., Lautenbach, S. and Schröder, B. 2008. Components of uncertainty in species distribution analysis: a case study of the great grey shrike. *Ecology*, **89**: 3371–3386.

Estes, J.A., Duggins, D.O. and Rathbun, G.B. 1989. The ecology of extinctions in kelp forest communities. *Conserv. Biol.*, **3**: 251–264.

Fariña, R.A., Vizcaíno, S.F. and Bargo, M.S. 1998. Body mass estimations in Lujanian (late Pleistocene-early Holocene of South America) mammal megafauna. *Mastozool. Neotrop.*, **5**: 87–108.

Fiedel, S. and Haynes, G. 2004. A premature burial: comments on Grayson and Meltzer's 'Requiem for overkill'. *J. Archaeol. Sci.*, **31**: 121–131.

Flessa, K.W., Erben, H.K., Hallam, A., Hsü, K.J., Hüssner, H.M., Jablonski, D. *et al.* 1986. Causes and consequences of extinction. In *Patterns and Processes in the History of Life* (D.M. Raup and D. Jablonski, eds.), pp. 234–257. Berlin: Springer.

Flores, J.C. 2014. Modelling Late Pleistocene megafaunal extinction and critical cases: a simple prey–predator perspective. *Ecol. Model.*, **291**: 218–223.

Frankham, R., Brook, B.W., Bradshaw, J.A., Trail, L.W. and Spielman, D. 2013. 50/500 rule and minimum viable populations: response to Jamieson and Allendorf. *Trends Ecol. Evol.*, **28**: 187–188.

Franklin, J. 2009. *Mapping Species Distributions: Spatial Inference and Predictions*. Cambridge: Cambridge University Press.

Frisch, R.E. 1978. Population, food intake, and fertility. *Science*, **199**: 22–30.

Gallo, V., Avilla, L.S., Pereira, R.C.L. and Absolon, B.A. 2013. Distributional patterns of herbivore megamammals during the Late Pleistocene of South America. *Ann. Acad. Bras. Ciênc.*, **85**: 533–546.

Gnecco, C. 2003. Against ecological reductionism: Late Pleistocene hunter-gatherers in the tropical forests of northern South America. *Quat. Int.*, **109/110**: 13–21.

Gotelli, N.J. 2008. *A Primer of Ecology*. Sunderland, MA: Sinauer Associates.

Grayson, D.K. 1984. Nineteenth-century explanations of Pleistocene extinctions: a review and analysis. In *Quaternary Extinctions: A Prehistoric Revolution* (P.S. Martin and R.G. Klein, eds.), pp. 5–39. Tucson, AZ: University of Arizona Press.

Grayson, D.K. and Meltzer, D.J. 2003. A requiem for North American overkill. *J. Archaeol. Sci.*, **30**: 585–593.

Grayson, D.K. and Meltzer, D.J. 2004. North American overkill continued? *J. Archaeol. Sci.*, **31**: 133–136.

Griffith, D., Veech, J. and Marsh, C. 2014. *cooccur: probabilistic species co-occurrence analysis in R*. R package v. 1.2 [http://CRAN.R-project.org/package = co-occur].

Grimm, V. and Railsback, S.F. 2012. Pattern-oriented modelling: a 'multi-scope' for predictive systems ecology. *Phil. Trans. R. Soc. Lond. B: Biol. Sci.*, **367**: 298–310.

Grimm, V., Franka, K., Jeltsch, F., Brandla, R., Uchmariskib, J. and Wissela, C. 1996. Pattern-oriented modelling in population ecology. *Sci. Total Environ.*, **183**: 151–166.

Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W.M., Railsback, S.F. *et al.* 2005. Pattern-oriented modeling of agent-based complex systems: lessons from ecology. *Science*, **310**: 987–991.

Gutiérrez, M.A. and Martínez, G.A. 2008. Trends in the faunal human exploitation during the Late Pleistocene and Early Holocene in the Pampean region (Argentina). *Quat. Int.*, **191**: 53–68.

Hadly, E.A. and Barnosky, A.D. 2009. Vertebrate fossils and the future of conservation biology. In *Conservation Paleobiology: Using the Past to Manage for the Future* (G.P. Dietl and K.W. Flessa, eds.), pp. 39–59. Lubbock, TX: The Paleontological Society.

Hassan, F. 1980. The growth and regulation of human population in prehistoric times. In *Biosocial Mechanisms of Population Regulation* (N.N. Cohen, R.S. Malpass and H.G. Klein, eds.), pp. 305–319. New Haven, CT: Yale University Press.

Hern, W. 1999. How many times has the human population doubled? Comparisons with cancer. *Popul. Environ.*, **21**: 59–80.

Hubbe, A., Hubbe, M. and Neves, W. 2007. Early Holocene survival of megafauna in South America. *J. Biogeogr.*, **34**: 1642–1646.

Jablonski, D. 2001. Lessons from the past: evolutionary impacts of mass extinctions. *Proc. Natl. Acad. Sci. USA*, **98**: 5393–5398.

Jamieson, I.G. and Allendorf, F.W. 2012. How does the 50/500 rule apply to MVPs? *Trends Ecol. Evol.*, **27**: 578–584.

Jamieson, I.G. and Allendorf, F.W. 2013. A school of red herring: reply to Frankham et al. *Trends Ecol. Evol.*, **28**: 188-189.

Johnson, C.N. 2002. Determinants of loss of mammal species during the Late Quaternary 'megafauna' extinctions: life history and ecology, but not body size. *Proc. R. Soc. Lond. B: Biol. Sci.*, **269**: 2221–2227.

Johnson, C.N., Bradshaw, C.J.A., Cooper, A., Gillespie, R. and Brook, B.W. 2013. Rapid megafaunal extinction following human arrival throughout the New World. *Quat. Int.*, **308/309**: 273–277.

Kaiser, H.F. 1958. The varimax criterion for analytic rotation in factor analysis. *Psychometrika*, **23**: 187–200.

Kelly, R.L. 1995. *The Foraging Spectrum: Diversity in Hunter-gatherer Lifeways*. Washington, DC: Smithsonian Institution Press.

Koch, P.L. and Barnosky, A.D. 2006. Late Quaternary extinctions: state of the debate. *Annu. Rev. Ecol. Evol. Syst.*, **37**: 215–250.

Lima-Ribeiro, M.S. and Diniz-Filho, J.A.F. 2013a. American megafaunal extinctions and human arrival: an improved evaluation using a meta-analytical approach. *Quat. Int.*, **299**: 38–52.

Lima-Ribeiro, M.S. and Diniz-Filho, J.A.F. 2013b. Insistence on narrative reviews or preference for overkill hypothesis? Re-analyses show no evidence against Lima-Ribeiro & Diniz-Filho's conclusions. *Quat. Int.*, **308/309**: 278–281.

Lima-Ribeiro, M.S. and Diniz-Filho, J.A.F. 2013c. *Modelos ecológicos e a extinção da megafauna: clima e homem na América do Sul*. São Carlos: CUBO.

Lima-Ribeiro, M.S., Varela, S., Nogués-Bravo, D. and Diniz-Filho, J.A.F. 2012. Potential suitable areas of giant ground sloths dropped before its extinction in South America: the evidences from bioclimatic envelope modeling. *Nature Conserv.*, **10**: 145–151.

Lima-Ribeiro, M.S., Varela, S., González-Hernández, J., Oliveira, G., Diniz-Filho, J.A.F. and Terribile, L.C. 2015. ecoClimate: a database of climate data from multiple models for past, present, and future for macroecologists and biogeographers. *Biodivers. Inform.*, **10**: 1–21.

Liow, L.H. 2012. Why paleobiological insights matter for conservation biologists. *Raffles Bull. Zool.*, **25**: 25–28.

Lyons, S.K., Wagner, P.J. and Dzikiewicz, K. 2010. Ecological correlates of range shifts of Late Pleistocene mammals. *Phil. Trans. R. Soc. Lond. B: Biol. Sci*, **365**: 3681–3693.

Martin, P.S. 1967. Prehistoric overkill. In *Pleistocene Extinction: The Search for a Cause* (P.S. Martin and H.E. Wright, Jr., eds.), pp. 75–120. New Haven, CT: Yale University Press.

Martin, P.S. 1973. The discovery of America: the first Americans may have swept the Western Hemisphere and decimated its fauna within 1000 years. *Science*, **179**: 969–974.

Martin, P.S. 1984. Prehistoric overkill: the global model. In *Quaternary Extinctions: A Prehistoric Revolution* (P.S. Martin and R.G. Klein, eds.), pp. 354–403. Tucson, AZ: University of Arizona Press.

Martínez, G. 2001. 'Fish-Tail' projectile points and megamammals: new evidence from Paso Otero 5 (Argentina). *Antiquity*, **75**: 523–528.

McInerny, G.J., Roberts, D.L., Davy, A.J. and Cribb, P.J. 2006. Significance of sighting rate in inferring extinction and threat. *Conserv. Biol.*, **20**: 562–567.

Mead, J.I. and Meltzer, D.J. 1984. North American Late Quaternary extinctions and the radiocarbon record. In *Quaternary Extinctions: A Prehistoric Revolution* (P.S. Martin and R.G. Klein, eds.), pp. 440–450. Tucson, AZ: University of Arizona Press.

Milot, E., Mayer, F.M., Nussey, D.H., Boisvert, M., Pelletier, F. and Réale, D. 2011. Evidence for evolution in response to natural selection in a contemporary human population. *Proc. Natl. Acad. Sci. USA*, **108**: 17040–17045.

Mosimann, J.E. and Martin, P.S. 1975. Simulating overkill by Paleoindians. *Am. Sci.*, **63**: 304–313.

Nascimento, E.R. 2008. Os Xenarthra Pilosa (Megatheriidae), Notoungulata (Toxodontidae) e Proboscidea (Gomphotheriidae) da formação Rio Madeira, Pleistoceno Superior, estado de Rondônia, Brasil. PhD thesis, Universidade Federal do Rio Grande do Sul, Porto Alegre.

Nogués-Bravo, D. 2009. Predicting the past distribution of species climatic niches. *Glob. Ecol. Biogeogr.*, **18**: 521–531.

Nogués-Bravo, D., Rodríguez, J., Hortal, J., Batra, P. and Araújo, M.B. 2008. Climate change, humans, and the extinction of the woolly mammoth. *PLoS Biol.*, **6**: 685–692.

Nogués-Bravo, D., Ohlemüller, R., Batra, P. and Araújo, M.B. 2010. Climate predictors of late Quaternary extinctions. *Evolution*, **64**: 2442–2449.

Peterson, A.T., Soberón, J., Pearson, R.G., Anderson, R.P., Martínez-Meyer, E., Nakamura, M. *et al.* 2011. *Ecological Niches and Geographic Distributions*. Princeton, NJ: Princeton University Press.

Politis, G. and Messineo, P. 2008. The Campo Laborde site: new evidence for the Holocene survival of Pleistocene megafauna in the Argentine Pampas. *Quat. Int.*, **191**: 98–114.

Prado, J.L., Martinez-Maza, C. and Alberdi, M.T. 2015. Megafauna extinction in South America: a new chronology for the Argentine Pampas. *Palaeogeogr. Palaeoclim. Palaeoecol.*, **425**: 41–49.

Prescott, G.W., Williams, D.R., Balmford, A., Green, R.E. and Manica, A. 2012. Quantitative global analysis of the role of climate and people in explaining late Quaternary megafaunal extinctions. *Proc. Natl. Acad. Sci. USA*, **109**: 4527–4531.

Pushkina, D. and Raia, P. 2008. Human influence on distribution and extinctions of the late Pleistocene Eurasian megafauna. *J. Human Evol.*, **54**: 769–782.

R Development Core Team 2015. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.

Rangel, T.F.L.V.B., Diniz-Filho, J.A.F. and Colwell, R.K. 2007. Species richness and evolutionary niche dynamics: a spatial pattern–oriented simulation experiment. *Am. Nat.*, **170**: 602–616.

Reimer, P.R., Bard, E., Bayliss, A., Beck, W., Blackwell, P.G., Ramsey, C.B. *et al.* 2013. IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. *Radiocarbon*, **55**: 1869–1887.

Rick, T.C. and Lockwood, R. 2013. Integrating paleobiology, archeology, and history to inform biological conservation. *Conserv. Biol.*, **27**: 45–54.

Ripley, B. 2015. *tree: classification and regression trees*. R package v. 1.0-36 [http://CRAN.R-project.org/package = tree].

Roberts, D.L. and Solow, A.R. 2003. Flightless birds: when did the dodo become extinct? *Nature*, **426**: 245.

Rothhammer, F. and Dillehay, T.D. 2009. The Late Pleistocene colonization of South America: an interdisciplinary perspective. *Ann. Human Genet.*, **73**: 540–549.

Rowcliffe, J.M., Cowlishaw, G. and Long, J. 2003. A model of human hunting impacts in multi-prey communities. *J. Appl. Ecol.*, **40**: 872–889.

Saltré, F., Brook, B.W., Rodrígues-Rey, M., Cooper, A., Johnson, C.N., Turney, C.S.M. *et al.* 2015. Uncertainties in dating constrain model choice for inferring extinction time from fossil records. *Quat. Sci. Rev.*, **112**: 128–137.

Sandom, C., Faurby, S., Sandel, B. and Svenning, J.-C. 2014. Global late Quaternary megafauna extinctions linked to humans, not climate change. *Proc. R. Soc. Lond. B: Biol. Sci.*, **281**: 20133254.

Silva, M. and Downing, J.A. 1995. The allometric scaling of density and body mass: a nonlinear relationship for terrestrial mammals. *Am. Nat.*, **145**: 704–727.

Smith, F.A., Lyons, S.K., Ernest, S.K.M., Jones, K.E., Kaufman, D.M., Dayan, T. *et al.* 2003. Body mass of Late Quaternary mammals. *Ecology*, **84**: 3403.

Smith, V.L. 1975. The primitive hunter culture, Pleistocene extinction and the rise of agriculture. *J. Polit. Econ.*, **83**: 717–755.

Solow, A.R. 1993. Inferring extinction from sighting data. *Ecology*, **74**: 962–964.

Solow, A.R. and Roberts, D.L. 2003. A nonparametric test for extinction based on a sighting record. *Ecology*, **84**: 1329–1332.

Steele, J. and Politis, G. 2009. AMS ^{14}C dating of early human occupation of southern South America. *J. Archaeol. Sci.*, **36**: 419–429.

Stenseth, N.C. 1995. Snowshoe hare populations: squeezed from below and above. *Science*, **269**: 1061.

Strauss, D. and Sadler, P.M. 1989. Classical confidence intervals and Bayesian probability estimates for ends of local taxon ranges. *Math. Geol.*, **21**: 411–421.

Stutz, A.J. 2014. Modeling the pre-industrial roots of modern super-exponential population growth. *PLoS One*, **9**: e105291.

Surovell, T.A. and Waguespack, N., 2009. Human prey choice in the Late Pleistocene and its relation to megafaunal extinctions. In *American Megafaunal Extinction at the End of the Pleistocene* (G. Haynes, ed.), pp. 77–105. New York: Springer Science.

Svenning, J.-C., Flojgaard, C., Marske, K.A., Nogués-Bravo, D. and Normand, S. 2011. Applications of species distribution modeling to paleobiology. *Quat. Sci. Rev.*, **30**: 2930–2947.

Svenning, J.-C., Pedersen, P.B.M., Donlan, C.J., Ejrnæs, R., Faurby, S., Galetti, M. *et al.* 2016. Science for a wilder Anthropocene: synthesis and future directions for trophic rewilding research. *Proc. Nat. Acad. Sci. USA*, **113**: 898–906.

Tonni, E.P., Huarte, R.A., Carbonari, J.E. and Figini, A.J. 2003. New radiocarbon chronology for the Guerrero Member of the Luján Formation (Buenos Aires, Argentina): palaeoclimatic significance. *Quat. Int.*, **109/110**: 45–48.

Varela, S., Lobo, J.M. and Hortal, J. 2011. Using species distribution models in paleobiogeography: a matter of data, predictors and concepts. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, **310**: 451–463.

Varela, S., Lima-Ribeiro, M.S., Diniz-Filho, J.A.F. and Storch, D. 2015. Differential effects of temperature change and human impact on European Late Quaternary mammalian extinctions. *Global Change Biol.*, **21**: 1475–1481.

Whittington, S.L. and Dyke, B. 1984. Simulating overkill: experiments with the Mosimann and Martin model. In *Quaternary Extinctions: A Prehistoric Revolution* (P.S. Martin and R.G. Klein, eds.), pp. 451–465. Tucson, AZ: University of Arizona Press.

Yule, J.V., Jensen, C.X.J., Joseph, A. and Goode, J. 2009. The puzzle of North America's Late Pleistocene megafaunal extinction patterns: test of new explanation yields unexpected results. *Ecol. Model.*, **220**: 533–544.