A review of the time scale and potential geographic distribution of *Notiomastodon platensis* (Ameghino, 1888) in the late Pleistocene of South America

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ABSTRACT

The objectives of the present study were to (1) provide new dates of *Notiomastodon platensis* (Ameghino, 1888) fossils from the Brazilian Intertropical Region, derived from Electron Spin Resonance (ESR); (2) propose a timeline for the occurrence of *N. platensis* in South America based on published data (ESR, ^{14}C, [230]Th/[234]U) and, finally, (3) propose a geographic distribution for the species over the period between 21 ka (Last Glacial Maximum) and 120 ka (Interglacial period). The new dates presented here, together with the available estimates, indicate that the species occurred in South America between at least 530 ka and 6 ka (middle Pleistocene–early Holocene). The Paleo-Species Distribution Models created for the 21 ka and 120 ka periods overlapped with the distribution of dry forest habitats during the Last Glacial Maximum, which clearly indicates that the species was associated with this type of vegetation.

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1. Introduction

Notiomastodon platensis (Ameghino, 1888) is an extinct South American species of proboscidean. Analyses of isotopes, dental characteristics and enamel wear indicate that, depending on the habitat and latitude occupied by the species, its diet composition may have varied from exclusively grass-based (C_3 or C_4) to include only C_3 plant material, such as leaves and fruits (*e.g.* Asevedo et al., 2012; Dantas et al., 2013).

The species is generally attributed to the period between the middle Pleistocene (?) and early Holocene (Alberdi et al., 2008), based on the estimated age of the sediments where fossils have been found. This has resulted in a lack of any reliable definition of the temporal range of the species, and thus of its geographic distribution. Given this situation, the present study aimed to (1) present a new dates of the *N. platensis* fossils collected in the Brazilian Intertropical region based on the Electron Spin Resonance (ESR) technique, (2) propose a timeline for the occurrence of *N. platensis* in South America based on a review of the published data (ESR, ^{14}C, [230]Th/[234]U), and finally, (3) propose a geographic distribution for the species over the period between 120 ka (Interglacial period) and 21 ka (Last Glacial Maximum – LGM).

2. Material and methods

2.1. Electron Spin Resonance dates

Teeth of *N. platensis* were collected from three sites in the Brazilian Northeast – Fazenda São José (Poço Redondo, Sergipe, Brazil; 09°55′37″S, 37°45′13″W), Lajedo II (Jaguarari, Bahia, Brazil; 10°21′17″S, 40°16′19″W) and Tanque Grande (Matina, Bahia, Brazil; 13°54′21″S. 42°55′18″W). The soil attached to the specimens was

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also preserved for analysis. These specimens were analyzed in the Universidade de São Paulo Physics Department and the Institute for Nuclear and Energy Research, both in São Paulo, Brazil.

Prior to analysis, the soil was removed from the teeth and stored. The teeth were cleaned and then treated thermally to detach the enamel from the dentine by freezing and defrosting with liquid nitrogen. The remaining dentine was drilled off. The enamel was treated chemically with a 1:10 HCl solution in an ultrasound bath, which eliminated a layer of approximately 100 μm. The thickness of the enamel was determined before and after this acid etching. The enamel was pulverized manually to <0.5 mm in an agate mortar and pestle. This powder was divided into aliquots of approximately 50 mg and irradiated with different doses of gamma rays to construct a dose–response curve. Irradiation was conducted at IPEN using a Gammacell Cobalt-60 irradiator in the open air at room temperature with a dose rate of 2.49 kGy/h, with a 0.4 g/mm^2 thick Lucite build-up cap being placed over the samples.

The ESR spectra of the samples were recorded using a Jeol FA200 X Band (ν ~9 GHz) spectrometer with the following acquisition parameters: modulation amplitude of 0.1 mT, scan range of 10 mT, scan time of 1 min, and 2 mW incident microwave power. The peak to peak amplitude at $g_\perp$ was used to construct the dose–response curve and equivalent dose (D_e) determination. The experimental data points were fitted using Ikeya's (1993) equation:

$$I = I_0 \left\{ 1 - e^{ -\left[\frac{(D + D_e)}{D_0} \right] } \right\} \quad (1)$$

where I = ESR signal intensity, I_0 = signal intensity at saturation, D = additive dose, D_0 = dose at saturation, and D_e = the Equivalent Dose.

The concentrations of ^{238}U, ^{232}Th, and K present in the soil and fossil samples (enamel and dentine) were estimated by Neutron Activation Analysis (NAA). These data were used to calculate the internal and external dose rates, converting D_e into ages, using the DATA software (Grün, 2009). The correction of the cosmic ray dose rate took into account the geographical coordinates of the finds and the depth at which the fossils were found (Prescott and Hutton, 1994).

2.2. Data review

In order to interpret the temporal distribution of *N. platensis* in South America, data from 20 previous studies (Table 1) were analyzed in conjunction with the ESR dates estimates from the present study. These studies provide estimates based on ESR, radiocarbon (^{14}C), and Uranium series dates approaches (^{230}Th/^{234}U, U-series).

Table 1
Datings and diet of *Notiomastodon platensis* in South America.

Localities (reference)	Coordinates	Age (ka)	Method	Diet
BRAZIL, ~460 ka[4]				
Continental shelf/RS (Lopes et al., 2010)	33°35′26.39″S, 53°20′22.11″W	464 ± 65	ESR	–
BRAZIL, ~120 ka[3]				
Jaguarari/BA (our data)	10°21′17″S, 40°16′19″W	114 ± 20	ESR	–
Matina/BA (our data)	13°54′21″S, 42°55′18″W	100 ± 20	ESR	–
Continental shelf/RS (Lopes et al., 2010)	33°35′26.39″S, 53°20′22.11″W	165 ± 28	ESR	–
BRAZIL, ~60 ka[2]				
B. Madre Deus/PE (Kinoshita et al., 2008)	08°10′48″S, 36°09′36″W	60 ± 9	ESR	–
B. Madre Deus/PE (Kinoshita et al., 2008)*	–	63 ± 8	ESR	–
Águas de Araxá/MG (Avilla et al., 2013)	19°35′38.40″S, 46°56′27.47″W	64 ± 5	ESR	–
BRAZIL, ~50 ka[2]				
Gararu/SE (Dantas et al., 2011)	10°00′39″S, 37°05′33″W	50	ESR	–
Baixa Grande/BA (Ribeiro et al., 2013)	11°32′07″S, 40°07′11″W	50 ± 10	ESR	–
BRAZIL, ~40 ka[2]				
Puxinamã/PB (Kinoshita et al., 2005)*	07°11′53.17″S, 35°55′34.71″W	39 ± 7	ESR	–
Maravilha/AL (Oliveira et al., 2010)	09°22′11″S, 37°24′54″W	39.8 ± 1	ESR	–
Poço Redondo/SE (Dantas et al., 2011)*	09°55′37″S, 37°45′13″W	42	ESR	–
Continental shelf/RS (Lopes et al., 2010)*	–	38 ± 2	ESR	–
BRAZIL, ~21 ka[1]				
Itaituba/PA (Rossetti et al., 2004)	04°15′1.7″S, 56°00′50″W	18,730–17,860	^{14}C	δ^{13}C = −26.90‰
Barcelona/RN (Dantas et al., 2013)	05°57′03.84″S, 35°55′14.31″W	18,930–19,450	^{14}C	δ^{13}C = 0.44‰
Puxinamã/PB (Kinoshita et al., 2005)*	–	30 ± 5	ESR	–
Poço Redondo/SE (our data)*	09°55′37″S, 37°45′13″W	28 ± 3	ESR	–
Canhoba/SE (Dantas et al., 2013)	10°05′06″S, 37°01′14″W	21,180–21,550	^{14}C	δ^{13}C = −1.86‰
Cel. João Sá/BA (Dantas et al., 2013)	10°17′27″S, 37°59′20″W	16,800–17,380	^{14}C	δ^{13}C = −1.04‰ and −0.49‰
Continental shelf/RS (Lopes et al., 2010)	33°35′26.39″S, 53°20′22.11″W	18 ± 3	ESR	–
Uruguaiana/RS (Kerber et al., 2011)*	29°39′56″S, 56°52′14″W	23 ± 5	ESR	–
Uruguaiana/RS (Kerber et al., 2011)*	–	28 ± 3	ESR	–
BRAZIL, ~10 ka[2]				
Maravilha/AL (Oliveira et al., 2010)*	–	10 ± 0.5	ESR	–
PERU, ~300 ka[4]				
La Huaca Piura (Falguères et al., 1994)	4°54′40.56″S, 80°57′29.13″W	304 ± 54	U-Series	–
PERU, ~21 ka[1]				
Ferreñafe (Falguères et al., 1994)	6°43′05.73″S, 79°46′13″W	26 ± 2	U-Series	–
PERU, ~15 ka[2]				
Pampa de lós fósiles (Falguères et al., 1994)	8°8′36.93″S, 78°28′30.70″W	15 ± 0.5	U-Series	–
La Cumbre (Ossa and Moseley, 1972)	7°56′41″S, 79°7′7″W	16,445–12,923	^{14}C	–
ECUADOR, ~21 ka[1]				
Carchi province (Coltorti et al., 1998)	0°39′45.19″N, 78°1′10.34″W	20,012–19,550	^{14}C	–
ARGENTINA, ~40 ka[2]				
Arenero Sposito (Domingo et al., 2012)	33°40′55.21″S, 59°39′54.59″W	41–37	^{14}C	δ^{13}C = −7.0 and −9.4‰

Table 1 (*continued*)

Localities (reference)	Coordinates	Age (ka)	Method	Diet
ARGENTINA, ~21 ka[1]				
Arroyo Tapalqué (Alberdi and Prado, 2008)	36°21′19.97″S, 60°1′25.16″W	24,136–27,597#	14C	–
Arroyo Tapalqué (Alberdi and Prado, 2008)	36°21′19.97″S, 60°1′25.16″W	21,029–22,520#	14C	–
Santiago del Estero (Alberdi et al., 2008)	27°47′3.91″S, 64°16′2.21″W	23,335–24,289#	14C	–
Sta Clara Del Mar (Alberdi and Prado, 2008)	37°50′53″S, 57°30′20″W	21,019–21,579#	14C	–
ARGENTINA, ~10 ka[2]				
Punta de Agua (Domingo et al., 2012)	28°36′00″S, 68°39′0.01″W	14–8	14C	$\delta^{13}C = -5.9‰$
URUGUAY, ~21 ka[1]				
Montevideo (Gutiérrez et al., 2005)	34°53′1″S, 56°10′55″W	20,483–21,422#	14C	$\delta^{13}C = -9.56‰$
CHILE, ~10 ka[2]				
Tagua–Tagua (Domingo et al., 2012)	34°26′16.69″S, 71°5′16.51″W	11–6	14C	–

[1]Datings used to make the potential distributions models at 21 ka and 120 ka; [2]Data used as independent test for the 21 ka distribution map model; [3],[4]Data used as independent test for the 120 ka distribution map model; *These points are the same that was used for modeling, thus was not used as test data. #Calculated with Calib 6.0 (http://calib.qub.ac.uk/calib/calib.html; last accessed 05 April 2013).

For the purposes of the present study, the classification of Mothé et al. (2012) was followed. In this case, the dates attributed to *Haplomastodon* (Ossa and Moseley, 1972; Falguères et al., 1994), *Haplomastodon chimborazi* (Proaño, 1922) (Coltorti et al., 1998), *Haplomastodon waringi* (Holland, 1920) (Rossetti et al., 2004; Kinoshita et al., 2005), *Stegomastodon waringi* (Holand, 1920) (Kinoshita et al., 2008; Oliveira et al., 2010; Lopes et al., 2010; Domingo et al., 2012; Ribeiro et al., 2013), *Stegomastodon platensis* (Ameghino, 1888) (Alberdi and Prado, 2008; Alberdi et al., 2008; Domingo et al., 2012) and the Gomphotheriidae (Kerber et al., 2011) were considered to be *N. platensis* (Ameghino, 1888).

2.3. Paleo-Species Distribution Models

Paleo-Species Distribution Models (PSDMs) were used to estimate the potential distribution of *N. platensis* in South America. These models have been used successfully in a number of recent studies of paleoecology and paleobiogeography (Nogués-Bravo, 2009).

Varela et al. (2011) concluded that the PSDM approach provides an effective tool for understand the determinants of species evolution and geographic distributions. This approach helped to evaluate fundamental questions such as the effectiveness of a species' response to environmental change, resulting from extreme climatic events or whether glacial refugia made a significant contribution to present-day distribution patterns.

The 14 localities (Table 1) where *N. platensis* fossils were found in South America at around 21 ka (dated directly from the fossils) were used to create the 21 ka and 120 ka PSDMs. The 21 ka model was validated using a single replication (Bootstrap), with dates of 10, 15, 40, 50, and 60 ka being used as independent tests (Table 1), while the 120 ka model was validated using five dates older than 120 ka (Table 1).

Climate reconstructions for 21 ka and 120 ka, with a spatial resolution of 10′ (20 km²) were acquired from the images database of the Worldclim version 1.4 project (Hijmans et al., 2005). The climatic variables used for analysis were the annual mean temperature, mean diurnal range, maximum temperature in the warmest month, minimum temperature in the coldest month, annual precipitation, precipitation in the wettest month and precipitation in the driest month.

Potential distributions maps of *N. platensis* were produced using the Maxent (Machine-Learning Maximum Entropy Model) program (Phillips et al., 2006). The interpretation of the predictive maps (PSDMs) was based on the minimum training presence threshold.

3. Results and discussion

3.1. Temporal distribution

The new Electron Spin Resonance (ESR) dates of *N. platensis* fossils from Poço Redondo (Sergipe, Brazil), Jaguarari and Matina (Bahia, Brazil) indicates ages of 28 ± 3 ka, 114 ± 20 ka, and 100 ± 20 ka, respectively (Tables 2 and 3, Fig. 1). Taken together with the available data (Table 1), these results (considering the minimum and maximum standard error limits) indicate that the species would have probably occurred in South America between 530 ka and 6 ka (middle Pleistocene to early Holocene).

Table 2
Uranium, thorium, potassium concentration obtained by neutron activation analysis.

Sample	U (mg kg⁻¹)	Th (mg kg⁻¹)	K (%)
Enamel			
Lajedo II	0.106 ± 0.002	<0.01	<0.075
Fazenda São José	0.116 ± 0.002	<0.01	<0.075
Matina	0.233 ± 0.005	<0.01	<0.075
Dentine			
Lajedo II	3.30 ± 0.01	<0.01	<0.075
Fazenda São José	0.445 ± 0.005	<0.01	<0.075
Matina	1.30 ± 0.02	0.45 ± 0.03	<0.075
Soil			
Lajedo II	2.3 ± 0.4	3.3 ± 0.2	0.5 ± 0.2
Fazenda São José	1.7 ± 0.1	7.4 ± 0.4	2.2 ± 0.3
Matina	3.9 ± 0.6	7.1 ± 0.9	0.16 ± 0.08

Table 3
Equivalent dose and age results according to the Uranium Uptake model: Early Uptake (EU) and Linear Uptake (LU).

Sample	Age (ka)	
	EU	LU
Lajedo II	108 ± 20	114 ± 20
Fazenda São José	27 ± 3	28 ± 3
Matina	100 ± 20	100 ± 20

Alberdi et al. (2008) have assigned the species to sediments with ages between the middle and late Pleistocene found in Brazil, Argentina, Paraguay, and Uruguay, and to the upper Pleistocence of Ecuador, Peru, Chile, Colombia, and Venezuela. However, the dates (all based on 14C – see Table 1) available from Argentina (Alberdi and Prado, 2008; Alberdi et al., 2008; Domingo et al., 2012), Uruguay (Gutiérrez et al., 2005), Chile (Domingo et al., 2012), and Ecuador (Coltorti et al., 1998) indicate that the species occurred in these regions only at the end of the Pleistocene. This may be due to the limitations of 14C (AMS) dates, restricted to younger than 58 ka (Bird et al., 2004), and the lack of alternative data (*e.g.* ESR) from these countries. New analyses based on ESR may provide more reliable dates for the fossils from Argentina, Uruguay, Chile, and
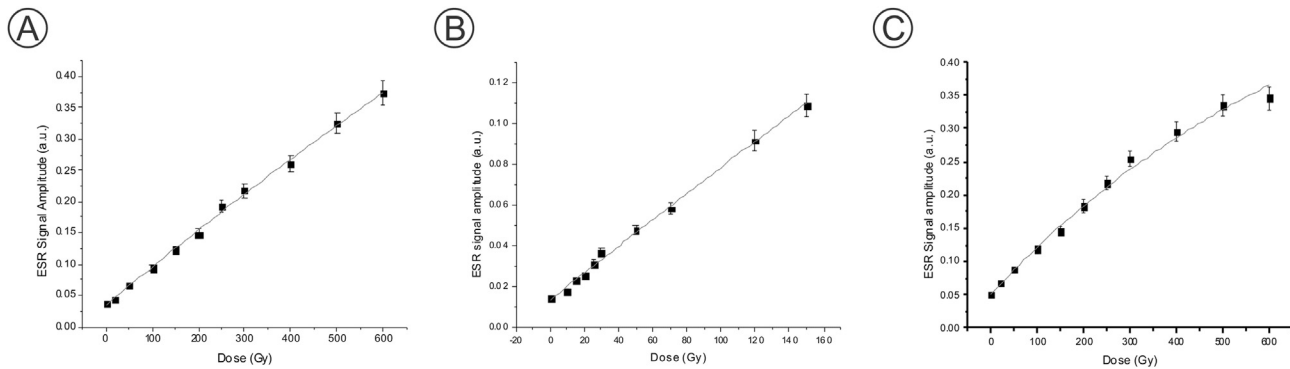
Fig. 1. Dose Response Curves from (A) Lajedo II, Jaguarari, Bahia (B) Fazenda São José, Poço Redondo, Sergipe and (C) Tanque Grande, Matina, Bahia.

Ecuador, amplifying the time range and confirming the current interpretation based on a relative dates approach.

This conclusion is reinforced by the $^{230}Th/^{234}U$ dates of fossils from Peru (Falguères et al., 1994), for example, which indicates that the species occurred in Peru between 358 ka and 15 ka. However, this contradicts the time scale proposed by Alberdi et al. (2008), and indicates that the species was present in this region at least since the middle Pleistocene, possibly throughout the whole South America.

A larger number of date estimates are available for Brazilian samples of N. platensis in comparison with other South American countries. These values have been derived primarily from the fossils found in two regions: the Brazilian Intertropical Region (BIR), as defined by Cartelle (1999), where the species has been recorded between 120 ka and 10 ka (Table 1); and Southern Brazil, with known dates of between 530 ka and 18 ka.

The dates recorded in the present study for the BIR have expanded considerably the known period of occurrence of the N. platensis in this region, even though the local fossils are still attributed to the late Pleistocene. It seems like even older fossils may eventually be found in the Brazilian Intertropical Region, given the dates (U-series) available for the fossils of associated species found in caves, which indicates a period of occurrence between 350 ka and 10 ka (Auler et al., 2006).

The oldest occurrence of a proboscidean in South America is a fossil found in the middle part of the Uquia formation (~2.5 million years) in Northern Argentina. However, this material had not diagnostic features which allowed the authors to attribute to N. platensis or Cuvieronius hyodon (Fischer, 1814) (López et al., 2001; Reguero et al., 2007). Thus, the only evidence for the occurrence of N. platensis in South America during earlier times − around the mid-late Pleistocene transition − is from southern Brazil, which reinforces the conclusion that new ESR dates for the fossils found in other South American localities may reveal much older dates than those available at the present time.

3.2. Paleo-Species Distribution Models

The Paleo-Species Distribution Models (PSDM) generated for the 21 and 120 ka periods are in Fig. 2. The model for the 120 ka period (AUC 0.815: Fig. 2), which is characterized by a predominantly humid climate (Auler and Smart, 2001; Wang et al., 2004), indicates that the distribution of N. platensis was smaller and more restricted to the Central, Northeastern and Southern of the continent, in comparison with 21 ka model (AUC 0.815: Fig. 2). The values for the AUC test indicate that the models are good predictors of the area used by this species.

The models indicate that N. platensis occurred on the Pacific coast of Peru, Ecuador, Colombia, and Chile, the Caribbean coast of

Colombia and Venezuela, the Amazon basin (only for the 21 ka model), BIR, the Chaco (Bolivia and Argentina), the Southern Pampas, and Patagonia and Tierra del Fuego. In most cases, the available evidence is restricted to Carbon isotope ratios, which have been used to identify the composition of the species paleodiet, and the types of habitat it occupied (e.g. Sánchez et al., 2004; Dantas et al., 2013).

3.2.1. Pacific coast of Peru, Ecuador and Colombia

The only data available for this region are $\delta^{13}C$ analyses from Peru and Ecuador, which attribute the fossils to late Pleistocene, although with no absolute dates (Sánchez et al., 2004; Domingo et al., 2012). The dietary value for Peru is $\delta^{13}C = -9.2‰$ (Domingo et al., 2012), while in Ecuador, values vary from $\delta^{13}C = -5.97‰$ to $-0.78‰$ (Sánchez et al., 2004). These data indicate that N. platensis inhabited a relatively closed environment, and has a mixed diet, with a predominance of C_3 plants. In Ecuador, more open habitats were occupied, with a mixed diet (C_3/C_4 plants) and higher consumption of C_4 plants.

3.2.2. Caribbean coast of Colombia and Venezuela

Although this species is recorded in this region (Villarroel and Clavijo, 2005; Chávez-Aponte et al., 2008), there are no data available, not even for $\delta^{13}C$, which precludes any inferences on the type of habitat occupied by N. platensis in the Caribbean coast of Colombia and Venezuela.

3.2.3. Amazon basin

Only one fossil date, $\delta^{13}C = -26.90‰$ (Rossetti et al., 2004, Table 1), is available for the whole Amazon basin. This estimate indicates a diet based exclusively on C_3 plants during the LGM, which is consistent with the interpretation of Guimarães et al. (2008), who concluded that this species was a primary disperser of the seeds of a number of different plant species typically found in both dry and humid forests.

Anhuf et al. (2006) concluded that, during the LGM, the area of the Amazon Forest was reduced by approximately 53% in comparison with its present-day distribution, with the rainforest being replaced by more extensive areas of dry forest. The fossil analyzed by Rossetti et al. (2004) was found within the contemporary range of the dry forests (Fig. 2), as defined by Anhuf et al. (2006).

Assuming that N. platensis is associated primarily with seasonal dry forest, it is interesting to note that the 120 ka model does not indicate the existence of a potential niche for the species within the Amazon basin (Fig. 2). The 120 ka period was more humid than 21 ka, resulting in an expansion of the rainforest and a reduction of the more seasonal dry forests. The adaptations of N. platensis for dry forest may account for its absence from potential areas of occurrence in the Amazon basin during the 120 ka period, although, as
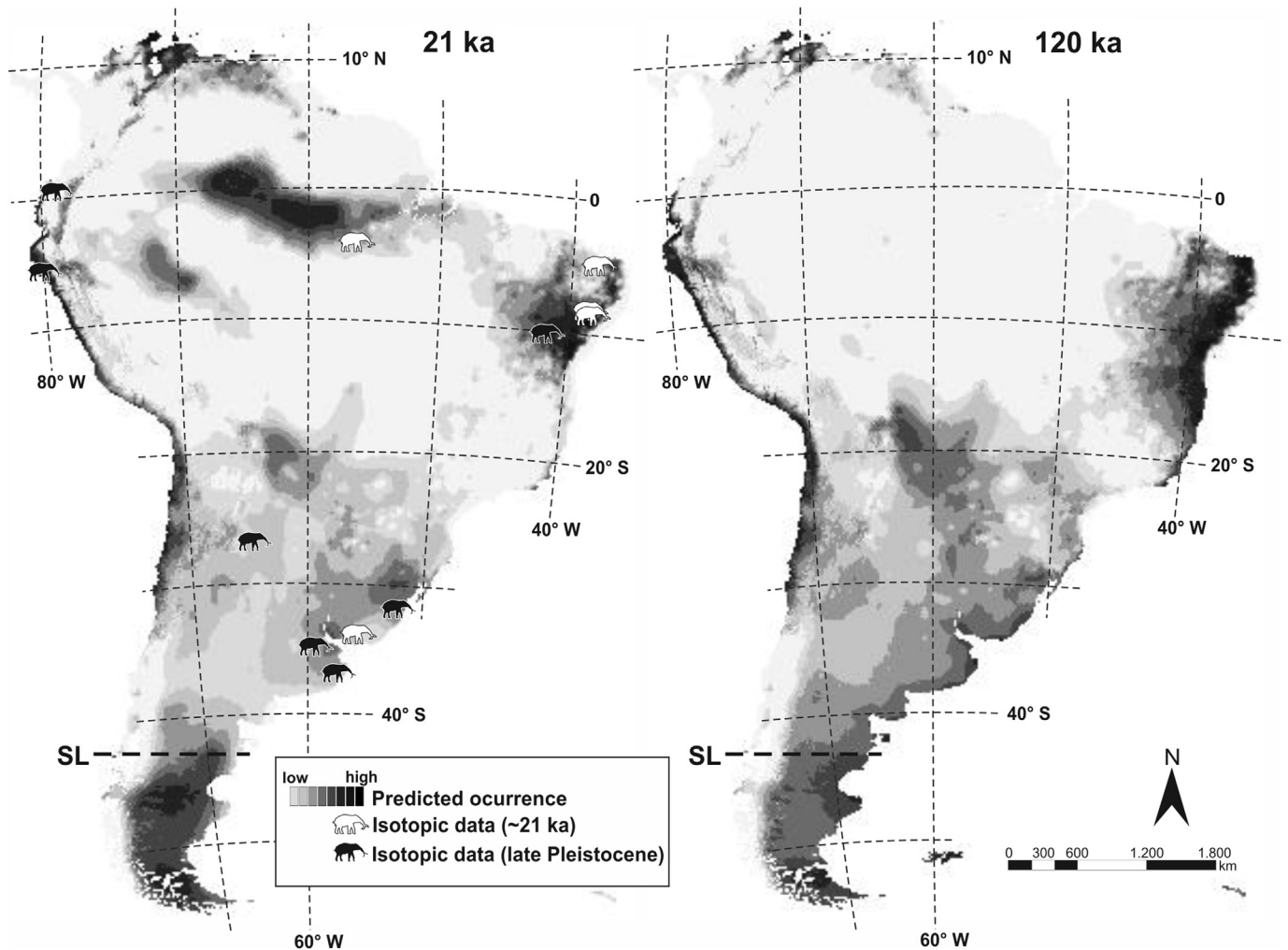
Fig. 2. Maps of the potential distribution of *Notiomastodon platensis* at 120 ka and 21 ka. SL = Southern Limit.

there are no data on diet (*e.g.* carbon isotopes data) for this period, this conclusion is somewhat speculative.

3.2.4. Brazilian Intertropical Region

Dantas et al. (2013) presented $\delta^{13}C$ data for *N. platensis* from the Brazilian Intertropical Region (BIR), obtained from fossils collected between 6° and 10° S, which suggests a grazing niche for the species at around 21 ka (Table 1). The same type of diet was recorded by Silva (2008; $\delta^{13}C = 1.47\permil$) and Viana et al. (2011; $\delta^{13}C = 0.00\permil$) for fossils of this species from the late Pleistocene found at 9°S. Sánchez et al. (2004) presented data indicate a mixed diet for the species at 11°S, which was interpreted by Dantas et al. (2013) as evidence of a denser habitat than found at lower latitudes. There are only a few palynological data for this region (De Oliveira et al., 1999; Behling et al., 2000), but a number of authors have concluded that a seasonal dry forest, similar to present-day Caatinga scrub, which that dominates the Brazilian Northeast, was already well established during the LGM (Pennington et al., 2000; Mayle, 2006).

3.2.5. The Chaco (Bolivia and Argentina)

The dietary diet available for the middle Pleistocene of Bolivia (*e.g.* MacFadden et al., 1994) are similar to those recorded for the late Pleistocene, which indicate that local habitats were relatively stable during this period. The only data available for the late

Pleistocene are those of Domingo et al. (2012), which suggest a mixed diet ($\delta^{13}C = -7.2\permil$ to $-5.9\permil$) of C_3/C_4 plants, typical of open habitats.

3.2.6. The Pampas

This region includes parts of Southern Bolivia and Brazil, and Northern Argentina, where *N. platensis* had a mixed diet of C_3 shrubs and C_4 grasses (Sánchez et al., 2004; Lopes et al., 2013), which indicates that the species inhabited a savanna-type environment.

3.2.7. The Pacific coast of Chile

In Northern Chile, at the Pleistocene to Holocene (14–6 kyr), *N. platensis* presented a diet of C_3 plants ($\delta^{13}C = -14.8\permil$ to $-4.00\permil$; Domingo et al., 2012), and probably inhabited forested environments. The opposite was found in Southern region, Pino et al. (2012) suggests that this species lived, 12,386–13,425 cal BP, in hills, floodplains and wetlands environments (Pilauco site, Osorno).

3.2.8. Patagonia and Tierra del Fuego

The 120 ka and 21 ka PSDMs indicate the presence of potential areas for the occurrence of *N. platensis* in Patagonia and Tierra del Fuego during both periods, although fossils are absent. It thus seems like that local topographic (relief) features created

geographic barriers to dispersal, resulting in a discontinuous distribution of appropriate habitats (Southern Limit − SL in Fig. 2).

4. Conclusions

Analyzed together with the data available in the literature, the results of the present study indicate that *N. platensis* was present in South America between at least 530 ka (middle Pleistocene) and 6 ka (early Holocene). The available dates allowed the development of models of the potential distribution of the species during two distinct periods (21 and 120 ka) and climates, although while the data derived from the Electron Spin Resonance (ESR) technique cover the whole Pleistocene, the ^{14}C data are limited to 58 ka, which reinforces the need for new analyses based on ESR.

Comparisons of these models with the proposed distribution of dry forests during the Last Glacial Maximum (Pennington et al., 2000; Mayle, 2006) indicated a considerable overlap in the data, which reinforces the conclusion that *N. platensis* was associated with this type of vegetation. More reliable dates of the fossil evidence will refine the understanding of the occurrence of *N. platensis* during the Pleistocene/Holocene, and will provide a better model of the spatial distribution of the species in the 21 ka and 120 ka periods, which may contribute to the development of more definitive zoogeographic models.

Acknowledgments

References

Alberdi, M.T., Cerdeño, E., Prado, J.L., 2008. *Stegomastodon platensis* (Proboscidea, Gomphotheriidae) en el Pleistoceno de Santiago del Estero, Argentina. Ameghiniana 45 (2), 257–271.

Alberdi, M.T., Prado, J.L., 2008. Presencia de Stegomastodon (Gomphotheriidae, Proboscidea) en el Pleistoceno Superior de la zona costera de Santa Clara del Mar (Argentina). Estudios Geologicos 64 (2), 175–185.

Anhuf, D., Ledru, M.P., Behling, H., Da Cruz Jr., F.W., Cordeiro, R.C., Van der Hammen, T., Karmann, I., Marengo, J.A., De Oliveira, P.E., Pessenda, L., Siffedine, A., Albuquerque, A.L., Da Silva Dias, P.L., 2006. Paleo-environmental change in Amazonian and African rainforest during the LGM. Palaeogeography, Palaeoclimatology, Palaeoecology 239, 510–527.

Asevedo, L., Winck, G.R., Mothé, D., Avilla, L.S., 2012. Ancient diet of the Pleistocene gomphothere *Notiomastodon platensis* (Mammalia, Proboscidea, Gomphotheriidae) from lowland mid-latitudes of South America: Stereomicrowear and tooth calculus analyses combined. Quaternary International 255, 42–52.

Auler, A.S., Piló, L.B., Smart, P.L., Wang, X., Hoffmann, D., Richards, D.A., Edwards, R.L., Neves, W.A., Cheng, H., 2006. U-series dates and taphonomy of Quaternary vertebrates from Brazilian Caves. Palaeogeography, Palaeoclimatology, Palaeoecology 240, 508–522.

Auler, A.S., Smart, P.L., 2001. Late quaternary paleoclimate in semiarid Northeastern Brazil from U-series dates of travertine and water-table speleothems. Quaternary Research 55, 159–167.

Avilla, L.S., Figueiredo, A.M.G., Kinoshita, A., Bertoni-Machado, C., Mothé, D., Asevedo, L., Baffa, O., Dominato, V.H., 2013. Extinction of a gomphothere population from Southeastern Brazil: taphonomic, paleoecological and chronological remarks. Quaternary International 305, 85–90. http://dx.doi.org/10.1016/j.quaint.2012.09.015.

Behling, H., Arz, H.W., Tzold, J.R.P., Wefer, G., 2000. Late Quaternary vegetational and climate dynamics in northeastern Brazil, inferences from marine core GeoB 3104-1. Quaternary Science Reviews 19, 981–994.

Bird, M.I., Fifield, L.K., Turney, C.S.M., Santos, G.M., 2004. Datações próximo ao limite da técnica radiocarbono. In: Anais, Encontro de Física e Arqueologia − descobertas e datações. Parque Nacional da Serra da Capivara, Piauí, Brasil, pp. 27–48.

Cartelle, C., 1999. Pleistocene mammals of the Cerrado and Caatinga of Brazil. In: Eisenberg, J.F., Redford, K.H. (Eds.), Mammals of the Neotropics. The University of Chicago Press, pp. 27–46.

Chávez-Aponte, E.O., Alfonzo-Hernández, I., Carrillo-Briceño, J.D., 2008. Morfología dentaria de los gonfoterios de la localidad de Muaco, estado Falcón, Venezuela. Interciencia 33 (10), 771–775.

Coltorti, M., Ficcarelli, G., Jahren, H., Moreno Espinosa, M., Rook, L., Torre, D., 1998. The last occurrence of Pleistocene megafauna in the Ecuadorian Andes. Journal of South American Earth Sciences 11 (6), 581–586.

Dantas, M.A.T., Dutra, R.P., Cherkinsky, A., Fortier, D.C., Kamino, L.H.Y., Cozzuol, M.A., Ribeiro, A.S., Vieira, F.S., 2013. Paleoecology and radiocarbon dates of the Pleistocene megafauna of the Brazilian Intertropical Region. Quaternary Research 79, 61–65.

Dantas, M.A.T., Porpino, K.O., Bauermann, S.G., Prata, A.P.N., Cozzuol, M.A., Kinoshita, A., Barbosa, J.H.O., Baffa, O., 2011. Megafauna do Pleistoceno superior de Sergipe, Brasil: registros taxonômicos e cronológicos. Revista Brasileira de Paleontologia 14 (3), 311–320.

De Oliveira, P.E., Barreto, A.M.F., Suguio, K., 1999. Late Pleistocene/Holocene climatic and vegetational history of the Brazilian Caatinga: the fossil dunes of the middle São Francisco river. Palaeogeography, Palaeoclimatology, Palaeoecology 152, 319–337.

Domingo, L., Prado, J.L., Alberdi, M.T., 2012. The effect of paleoecology and paleobiogeography on stable isotopes of Quaternary mammals from South America. Quaternary Sciences Reviews 55, 103–113.

Falguères, C., Fontugne, M., Chauchat, C., Guadelli, J.L., 1994. Datations radiométriques de l'extinction dês grandes faunes pléistocènes au Pérou. Comptes rendu Academie des Sciences Paris 319 (2), 261–266.

Grün, R., 2009. The DATA program for the calculation of ESR age estimates on tooth enamel. Quaternary Geochronology 4 (3), 231–232.

Guimarães Jr., P.R., Galetti, M., Jordano, P., 2008. Seed dispersal anachronisms: rethinking the fruits extinct megafauna ate. Plos One 3 (3), 1–13.

Gutiérrez, M., Alberdi, M.T., Prado, L., Perea, D., 2005. Late Pleistocene Stegomastodon (Mammalia, Proboscidea) from Uruguay. Neue Jahrbuch Geologie Palaontologie Mittel 2005 (11), 641–662.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25, 1965–1978.

Ikeya, M., 1993. New Applications of Electron Paramagnetic Resonance. Dates, Dosimetry and Microscopy. World Scientific, New Jersey, USA, p. 500.

Kerber, L., Kinoshita, A., José, F.A., Figueiredo, A.M.G., Oliveira, E.V., Baffa, O., 2011. Electron Spin Resonance dates of the southern Brazilian Pleistocene mammals from Touro Passo Formation, and remarks on the geochronology, fauna and palaeoenvironments. Quaternary International 245, 201–208.

Kinoshita, A., Barreto, A., Alves, R., Figueiredo, A.M., Sarkis, J.E.S., Dias, M.L., Baffa, O., 2008. ESR dates of teeth from northeastern Brazilian megafauna. Radiation Measurements 43, 809–812.

Kinoshita, A., Franca, A.M., Almeida, J.A.C., Figueiredo, A.M., Nicolucci, P., Graef, C.F.O., Baffa, O., 2005. ESR dates at K and X band of northeastern Brazilian megafauna. Applied Radiation and Isotopes 62, 225–229.

Lopes, R.P., Oliveira, L.C., Figueiredo, A.M.G., Kinoshita, A., Baffa, O., Buchmann, F.S., 2010. ESR dates of pleistocene mammal teeth and its implications for the biostratigraphy and geological evolution of the coastal plain, Rio Grande do Sul, southern Brazil. Quaternary International 212, 213–222.

Lopes, R.P., Ribeiro, A.M., Dillenburg, S.R., Schultz, C.L., 2013. Late middle to late Pleistocene paleoecology and paleoenvironments in the coastal plain of Rio Grande do Sul state, Southern Brazil, from stable isotopes in fossils of *Toxodon* and *Stegomastodon*. Palaeogeography, Palaeoclimatology, Palaeoecology 369, 385–394.

López, G., Reguero, M., Lizuain, A., 2001. El registro más antiguo de mastodontes (Plioceno tardío) de América del Sur. Ameghiniana 38 (Suplemento 4), 35R–36R.

MacFadden, B.J., Wang, Y., Cerling, T.E., Anaya, F., 1994. South American fóssil mammals and carbon isotopes: a 25 million-year sequence from the Bolivian Andes. Palaeogeography, Palaeoclimatology, Palaeoecology 107, 257–268.

Mayle, F.E., 2006. The Late Quaternary biogeographical history of South American seasonally dry tropical forests: insights from palaeo-ecological data. In: Pennington, R.T., Lewis, G.P., Ratter, J.A. (Eds.), Neotropical Savannas and Dry Forests: Plant Diversity, Biogeography and Conservation, Systematics Association Special vol. 69. CRV Press, Taylo and Francis, London, PP, pp. 395–416.

Mothé, D., Avilla, L.S., Cozzuol, M., Winck, G.R., 2012. Taxonomic revision of the Quaternary gomphotheres (Mammalia: Proboscidea: Gomphotheriidae) from the South American lowlands. Quaternary International 276–277, 2–7.

Nogués-Bravo, D., 2009. Predicting the past distribution of species climatic niches. Global Ecology and Biogeography 18, 521–531.

Oliveira, L.C., Kinoshita, A., Barreto, A.M.F., Figueiredo, A.M., Silva, J.L.L., Baffa, O., 2010. ESR dates of teeth from Brazilian megafauna. Journal of Physics. Conference Series 249:012062.

Ossa, P.P., Moseley, M.E., 1972. La Cumbre, a Preliminary Report on Research into thé Early Occupation of thé Moche Valley, Peru. Ñawpa-Pacha 9, 1–16.

Pennington, T.R., Prado, D.E., Pendry, C.A., 2000. Neotropical seasonally dry forests and Quaternary vegetation changes. Journal of Biogeography 27, 261–273.

Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling 190, 231–259.

Pino, M., Chávez-Hoffmeister, M., Navarro-Harris, X., Labarca, R., 2012. The late Pleistocene Pilauco site, Osorno, south-central Chile. Quaternary International 299, 3–12.

Prescott, J.R., Hutton, J.T., 1994. Cosmic ray contributions to dose rates for lumi-nescence and ESR dates: large depths and long-term time variations. Radiation Measurements 23 (2/3), 497–500.

Reguero, M.A., Candela, A.M., Alonso, R.N., 2007. Biochronology and biostratigraphy of the Uquía Formation (Pliocene–early Pleistocene, NW Argentina) and its significance in the Great American Biotic Interchange. Journal of South Amer-ican Earth Sciences 23, 1–16.

Ribeiro, R.C., Kinoshita, A., Figueiredo, A.M.G., Carvalho, I.S., Baffa, O., 2013. Electron spin resonance dates of the Late Quaternary megafauna fossils from Baixa Grande, Bahia, Brazil. Quaternary International 305, 91–96. http://dx.doi.org/10.1016/j.quaint.2012.07.017.

Rossetti, D.F., Toledo, P.M., Moraes-Santos, H.M., Araújo Santos Jr., A.E., 2004. Reconstructing habitats in central Amazonia using megafauna, sedimentology, radiocarbon, and isotope analyses. Quaternary Research 61, 289–300.

Sánchez, B., Prado, J.L., Alberdi, M.T., 2004. Feeding ecology, dispersal, and extinc-tion of South American Pleistocene gomphotheres (Gomphotheriidae, Probo-scidea). Paleobiology 30, 146–161.

Silva, J.L.L. da, 2008. Reconstituição paleoambiental baseada no estudo de mamí-feros pleistocênicos de Maravilha e Poço das Trincheiras, Alagoas, nordeste do Brasil. Curso de Pós Graduação em Geociências, Universidade Federal de Per-nambuco, Recife, p. 244. Tese de Doutorado.

Varela, S., Lobo, J.M., Hortal, J., 2011. Using species distribution models in paleo-biogeography: a matter of data, predictors and concepts. Palaeogeography, Palaeoclimatology, Palaeoecology 310, 451–463.

Viana, M.S.S., Silva, J.L.L. da, Oliveira, P.V. de, Julião, M.S. da S., 2011. Hábitos ali-mentares em herbívoros da megafauna pleistocênica do Nordeste do Brasil. Estudos Geológicos 21 (2), 89–95.

Villarroel, C., Clavijo, J., 2005. Los mamíferos fósiles y las edades de las sedimentitas continentales del Neógeno de la Costa Caribe Colombiana. Revista de la Academia Colombiana de Ciencias 29 (112), 345–356.

Wang, X., Auler, A.S., Edwards, R.L., Cheng, H., Cristalli, P.S., Smart, P.L., Richards, D.A., Shen, C.C., 2004. Wet periods in northeastern Brazil over the past 210 kyr linked to distant climate anomalies. Nature 432, 740–743.