3,500 years BP: The last survival of the mammal megafauna in the Americas

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ABSTRACT

The last ages of appearance of mammalian megafauna in Brazil are associated with the Pleistocene/Holocene transition, establishing a consensus of extinction of this magnificent fauna during this period of time. In recent decades, direct dating of skeletal remains of this extinct fauna in Argentina, the Caribbean and Alaska, demonstrates that extinctions mammalian megafauna until the middle Holocene. Here, eight fragments of megafauna teeth from the Brazilian Intertropical Region were dated, in the locations of Itapipoca (Ceará State) and the Rio Miranda valley (Mato Grosso do Sul State), with the respective ages: Itapipoca – *Eremotherium laurillardi* (PDR-01: age = 6,161 ± 364 RC years BP; PDR-02: age = 7,415 ± 167 RC years BP), *Smilodon populator* (PDR-03: age = 7,803 ± 179 RC years BP), *Toxodon platensis* (PDR-05: age = 7,804 ± 226 RC years BP), *Xenorhinotherium bahiense* (PDR-06: age = 3,587 ± 112 RC years BP), *Notiomastodon platensis* (PDR-07: age = 7,940 ± 502 RC years BP) and *Palaeolama major* (PDR-09: age = 3,492 ± 165 RC years BP); Miranda river - *Eremotherium laurillardi* (PDR-11: age = 5,942 ± 294 RC years BP). The ages obtained demonstrate that the latest ages of megafauna appearance in Brazil are associated with the middle and late Holocene. In South America, the extinction of megafauna has been attributed to many causes, climate/environmental changes or even the synergy between these hypotheses. The ages obtained in this analysis, together with archaeological evidence, demonstrate that the Overkill and Blitzkieg theories are not plausible explantions for the extinction of South American megafauna. We believe that the extinction of megafauna in South America is the result of the synergy between environmental/climatic changes between the Last Glacial Maximum and the Holocene Climatic Optimum, with selective hunting of females and young individuals, autoecological factors of megafauna as supporting agents.

1. Introduction

The temporal distribution of Quaternary megafauna in South America is a subject of constant debate, with geochronological studies of this fauna being few in relation to the various paleontological sites recorded. The vast majority of published works present taxonomic data (e.g.: Ficarelli et al., 1995; Dudley, 1996; Cartelle, 1999; Lucas, 2009; Porpino et al., 2009, 2014; Cozzuol et al., 2012; Fernicola and Porpino, 2012 Mothé et al., 2012), demonstrating how diverse this fauna was in South America. Many previous geochronological studies have failed to obtain ages beyond the early Holocene, with the youngest ages relating to the Pleistocene/Holocene transition (e.g; McNeish et al., 1970, Borrero, 1997; Peyre et al., 1998; Auler et al., 2006; Oliveira et al., 2010; Dantas et al., 2013; Hubbe et al., 2013; França et al., 2014), supporting the proposal for the extinction of megafauna mammals in this period. However, some studies have obtained early and middle Holocene ages (Collantes et al., 1993; Neves and Piló, 2003; Guthrie, 2004; Johnson et al., 2012; Prado et al., 2015), demonstrating that this interpretation is currently questionable.

There are several paleontological sites containing fossils of late

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Quaternary megafauna in the American continent, from Alaska to Patagonia. In South America, three zoogeographical regions stand out in the quantity and diversity of species of this mammal fauna, which are: Brazilian Intertropical Region (BIR; Fig. 1; Pansani et al., 2016), Pampeam and Chaco (Cione et al., 2009). In recent decades, there has been an effort by the Brazilian scientific community to acquire geochronological data for the Quaternary megafauna of the Brazilian Intertropical Region (BIR), most of which are from the Pleistocene/Holocene (e.g. Auler et al., 2006; Hubbe et al., 2007; Ribeiro et al., 2013; Dantas et al., 2013; França et al., 2014; Scherer et al., 2017; Faria et al., 2020a).

The Pampean region in Argentina presents distinct localities with paleontological and archaeological sites with the presence of Quaternary megafauna with Early and Middle Holocene ages (Collantes et al., 1993; Borrero, 1997; Politis and Gutiérrez, 1998; Suárez, 2003; Politis et al., 2004; Prado et al., 2005, 2015; Hubbe et al., 2007; Steele and Politis, 2009; Johnson et al., 2012). Middle and Late Holocene ages have also been recorded in Alaska (Guthrie, 2004), Cuba (MacPhee et al., 1999), and Haiti (Iturralde-Vinent et al., 2000; Steadman et al., 2005). Despite the growing number of geochronological studies in Brazil, paleontological sites of South American megafauna have received little attention, making it difficult to establish their temporal distribution with greater precision. Therefore, it is difficult to clarify the probable causes of megafauna extinction in South America, being the continent with the most significant loss of megafauna genera and species. (Barnosky and Lindsey, 2010).

Many studies have proposed different hypotheses for the extinction of South American mammal megafauna. Cartelle (1999) points out that the extinction of Brazilian megafauna occurred at the end of the Pleistocene, due to the cold and dry environmental conditions of the last glacial period. Ficcarelli et al. (2003), based on data from Ecuador, suggest that increased aridity followed by high humidity and specific geographic factors during the Pleistocene-Holocene transition were the main conditions for this extinction event. Vivo and Carmignotto (2004) proposed that the increase in forest areas in response to increased humidity in the Mid-Holocene caused the extinction of megafauna adapted to open environments.

Steadman et al. (2005), through dating and compilation of geochronological data from the Americas, concluded that this event was asynchronous between islands and continents, favored by the activity of human hunters. Cione et al. (2003, 2009) proposed that the extinction of mammalian megafauna in South America is a synergistic phenomenon between environmental and climatic fluctuations, autoecological factors and, also, the strong impact of anthropogenic activities (Broken Zig Zag hypothesis). Barnosky and Lindsey (2010) also pointed out to the synergy between anthropogenic activities and environmental/climatic changes, indicating that anthropogenic impacts combined with rapid climate changes during the Pleistocene/Holocene transition were the driving force for this extinction event.

This profusion of hypotheses used to explain the extinction of mammalian megafauna in the late Quaternary of South America, combined with the geochronological data available in the literature regarding the large number of paleontological sites with megafauna remains, clearly indicates the lack of consensus on the causes of the extinction event. The aim of this study is to present eight new ages for the Holocene megafauna of the BIR: from material collected at Jirau tank deposit Itapipoca, Ceará State, Brazil; and fluvial deposits from the Miranda valley (Miranda, Mato Grosso do Sul State, Brazil). As a corollary, we evaluate some proposed models of megafauna extinction in the continent.

2. Material and methods

2.1. Material

The eight dated samples are from paleontological sites in peripheral locations in the Brazilian Intertropical Region (BIR; Fig. 1). Seven samples of fossil teeth (two *Eremotherium laurillardi*, dentine; one of *Smilodon populator*, enamel and dentine; one of *Notiomastodon platensis*,
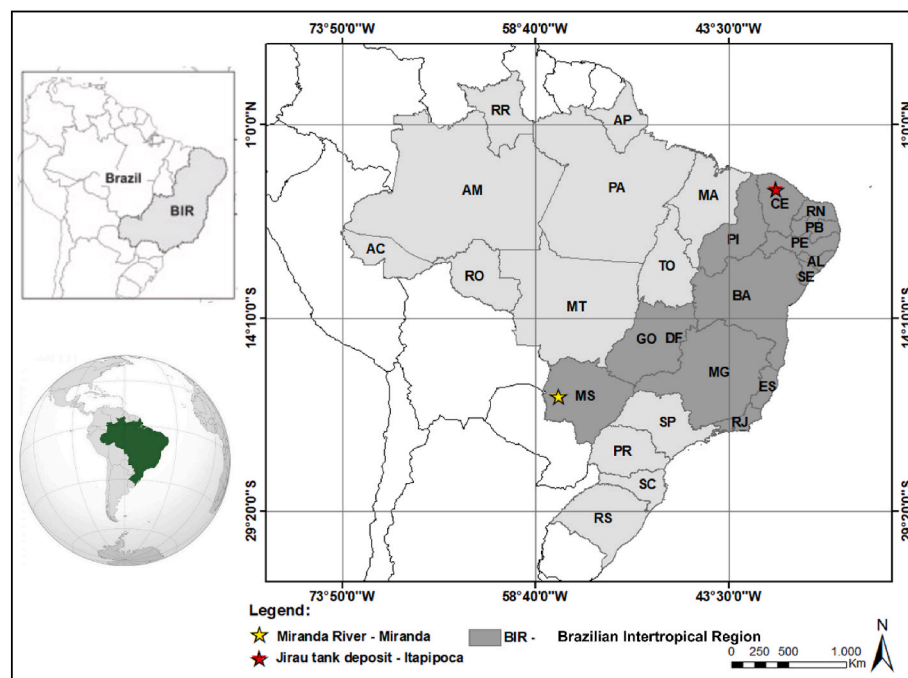

Fig. 1. Location map of the Brazilian Intertropical Region in South America, showing the location of Itapipoca (Ceará State) and Miranda River (Mato Grosso do Sul State). Adapted from Pansani et al. (2019). The acronyms: BIR – Brazilian Intertropical Region; PI – Piauí State; CE – Ceará State; PB – Paraíba State; PE – Pernambuco State; RN – Rio Grande do Norte State; AL – Alagoas State; SE –Sergipe State; BA – Bahia State; GO – Goiás State; MT – Mato Grosso State; MS – Mato Grosso do Sul State; MG – Minas Gerais State; ES – Espírito Santo State; RJ – Rio de Janeiro State; SP – São Paulo State; PR – Paraná State; MA – Maranhão State; MT – Mato Grosso State; AM – Amazonas State; TO – Tocantins State; RO – Rodônia State; PA – Pará State; AP – Amapá State; RR – Roraima State; RS – Rio Grande do Sul State; AC – Acre State.

enamel and dentine; one of Toxodontidae indet., enamel and dentine; one of *Xenorhinotherium bahiense*, enamel and dentine; and one of *Palaeolama major*, enamel and dentine) come from the Jirau Paleontological Site (03°21′23.1″ S 39°42′20.2″ W; Itapipoca, Ceará State). This presents a complex taphonomic history, revealing attritional accumulation under environmental conditions with strong seasonal climate control (for more information see Araújo-Júnior et al., 2013, 2017; Faria et al., 2020b). These fossils were provided by the Itapipoca Prehistory Museum (MUPHI), corresponding to small uncatalogued fragments from the technical reserve. A tooth fragmente (dentine) taken from a mandibular branch of *Eremotherium laurillardi* (ZUFMSFOS00097) belonging to the Zoology collection of the Biology Department of the Federal University of Mato Grosso do Sul, was also dated, originating from fluvial sediments of the Miranda River (20°14′27.30″S; 56°23′59.30″W; Miranda, Mato Grosso do Sul State). These samples were selected to carry out geochronological analyzes (AMS^{14}C) at the Radiocarbon Analysis Laboratory of the Fluminense Federal University (LAC-UFF), Brazil.

2.2. Analytical methods

2.2.1. Collagen extraction

The dentine used for dating was separated from the enamel fraction at LAC-UFF (Radiocarbon Analysis Laboratory of the Fluminense Federal University) were manually separated and observed under the microscope to identify diagenetic changes. This procedure was performed on fragments of teeth from the species *Notiomastodon platensis*, Toxodontidae, *Smilodon populator*, *Palaeolama major* and *Xenorhinotherium bahiense*, because the teeth of these taxa are composed of enamel and dentine, and dentine tissue that has collagen in its composition is used for collagen extraction. The eight samples of teeth were observed under a microscope to identify diagenetic changes and, subsequently, subsampled for chemical treatment. This was carried out in two stages, involving acid/base/acid treatment. The first, decalcification, was the addition of 3 mL of hydrochloric acid (0.5 M HCl) for 36 h, followed by treatment with sodium hydroxide (0.1 M NaOH, 30 min) to remove humic acids from the burial environment (Brock et al., 2010). In the second step, hydrochloric acid (0.5 N HCl, 15 min) was added again. These steps were performed at room temperature. After that, gelatinization was performed by adding 0.01 M HCL (pH 3 solution) at 65 °C for 24 h (Oliveira et al., 2021). After gelatinization, the samples proceeded to the ultrafiltration step.

2.2.2. Ultrafiltration

Collagen extraction was performed using two filters: a Milex 0.45 μm, to remove insoluble contaminants. Then, the samples were transferred to VIVASPIN 30KD ultrafilter, and centrifuged at 3,000 rpm in 10-min cycles until 0.5–1.0 mL of the remaining solution (Oliveira et al., 2021). The solution was stored with the same amount of ultrapure water in the freezer for 48 h before yarnization (Brock et al., 2010).

2.2.3. Graphitization and measurement

In order to transform the carbon into CO_2, the material was burned at 900 °C during 3 h in vacuum ampoules containing cupric oxide and silver. The sample was purified in a vacuum system and transferred to a graphitization tube. The conversion of carbon dioxide into graphite takes place in vacuum-sealed ampoules containing titanium hydride, zinc and, iron in a muffle furnace at 550 °C (Macario et al., 2017). The graphite was analyzed in an accelerator with a single acceleration stage, a 250 kV SSAMS from NEC, at the Instituto de Física da Universidade Federal Fluminense (Brazil), and the carbon isotope ratios were determined. Results were normalized to National Bureau of Standards oxalic acid (SEM 4990c). To verify the quality of the collagen used in the dating, analyzes of the atomic C/N ratio were carried out in the Radioecology and Environmental Change Laboratory at the Fluminense Federal University (LARA-UFF).

3. Results

The dates obtained by AMS ^{14}C for the eight samples of megafauna fossil teeth are shown in Table 1. All ages obtained are distributed between the Middle and Late Holocene, with the youngest going well beyond the Pleistocene-Holocene boundary. Fig. 2 presents the conventional radiocarbon age calibration graphs for statistical refinement, using the High Probability Density (HPD) band method for the eight dated samples. All samples were calibrated at a 95.4% confidence interval that is represented by gray areas in the graphs. Table 1 shows the respective radiometric ages and also the atomic C/N ratio of the analyzed samples.

4. Discussion

4.1. Collagen quality

To ensure that the collagen analyzed was not altered or degraded by diagenetic processes, we performed analyses of the C/N ratio, values between 2.9 and 3.6 are indicators of collagen preservation (DeNiro, 1985; Ambrose, 1990; Bocherens et al., 2016), corroborating the results obtained.

4.2. Geochronology

The time scale for the Quaternary of South America was established in the Pampean region (Argentina), with four South American Land Mammal Ages (SALMAs): Ensenadan, Bonaerian, Lujanian and Platan (Cione and Tonni, 1999). The megafauna of BIR and Pampas are generally associated with the Bonaerian and Lujanian stages, with temporal distribution between 400,000 and 10,000 years BP (Dantas and Cozzuol, 2016). Geochronological data acquired through different methods (ESR-Electron Spin Resonance, AMS^{14}C, ^{14}C and U-series), indicated the presence of megafauna in the BIR between 400,000 and 9, 000 years BP (Fig. 3A; Neves and Piló, 2003; Auler et al., 2006; Ribeiro et al., 2013, 2021; Dantas et al., 2013, 2017; França et al., 2014; Scherer et al., 2017; Pansani et al., 2019; Faria et al., 2020a), thus ranging from the Bonaerian to early Platan. This temporal distribution is very similar to that of the Pampean region and extends of 450,000 to 6,000 years BP (Fig. 3B; Collantes et al., 1993; Suárez, 2003; Cione and Tonni, 2005;

Table 1

Radiometric ages (AMS^{14}C) for the megafauna of Jirau and Miranda River. The acronyms: BP – before present; cal. – calibrated; (d) dentine; SD – standard deviation; CI – confidence interval; C/N – cabon nitrogen atomic ratio. Samples PDR-01, PDR-02, PDR-03, PDR-05, PDR-06, PDR-07 and PDR-09 are samples of uncatalogued tooth fragments from the MUPHI collection of Itapipoca, Ceara State. Sample PDR-11, from the Miranda River basin, Mato Grosso do Sul State, registry number ZUFMSFOS00097 of the UFMS Zoology Collection.

| Sample	Taxon	Radiocarbon date, RC yr ± 1 SD)	Calibrated age range (cal. BP; 95.4% C.I.)	C/N
PDR-01$^{(d)}$	*Eremotherium laurillardi*	6,161 ± 364	6,208–7,714	2.9
PDR-02$^{(d)}$	*Eremotherium laurillardi*	7,415 ± 167	7,867–8,536	3.1
PDR-03$^{(d)}$	*Smilodon populator*	7,803 ± 179	8,189–9,079	3
PDR-05$^{(d)}$	Toxodontidae indet.	7,804 ± 226	8,049–9,270	3
PDR-06$^{(d)}$	*Xenorhinotherium bahiense*	3,587 ± 112	3,493–4,217	3.4
PDR-07$^{(d)}$	*Notiomastodon platensis*	7,940 ± 502	7,836–10,159	2.9
PDR-09$^{(d)}$	*Palaeolama major*	3,492 ± 165	3,353–4,231	3
PDR-11$^{(d)}$	*Eremotherium laurillardi*	5,942 ± 294	6,120–7,427	3.2
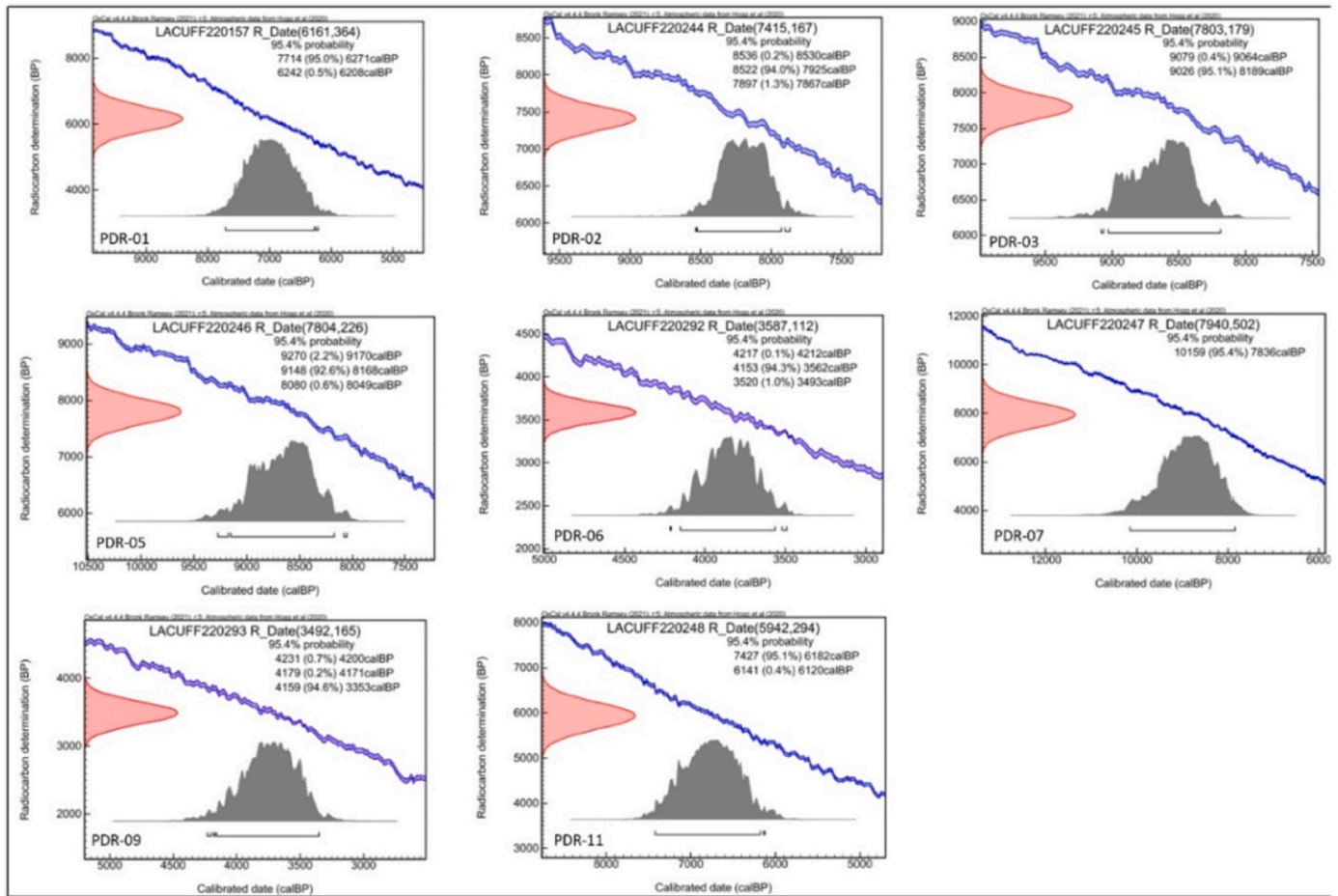
Fig. 2. OxCal Calibration graphs for eight samples, obtained using the high probability density band method (HDP - High Probability Density).
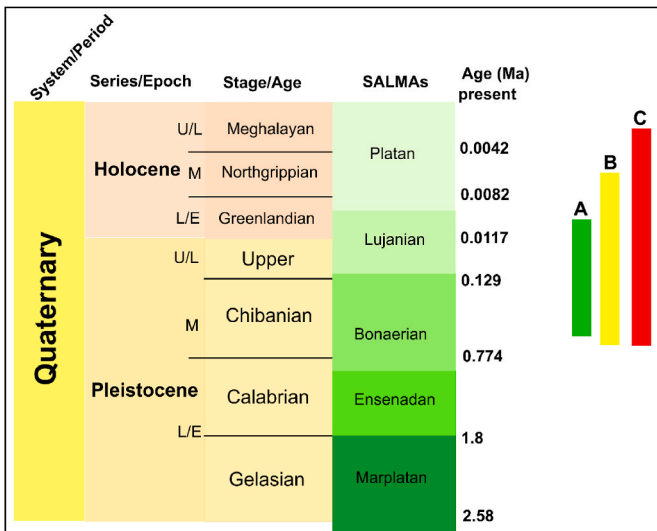

Fig. 3. Quaternary time scale with the South American Land Mammal Ages (SALMAs); A - Temporal distribution of megafauna in BIR, as inferred solely from previously published data; B - temporal distribution of megafauna in South America; C - temporal distribution of megafauna in BIR, incorporating both previously published data and data from the present work.

Politis et al., 2004; Messineo and Politis, 2009; Johnson et al., 2012; Hubbe et al., 2012; Rafuse, 2013; Prado et al., 2015). Our data indicate the presence of megafauna in South America until 3,500 years RC BP,

which corresponds to the late Platan (Fig. 3C).

Table 2 presents geochronological data on megafauna from different locations in the Americas, demonstrating the survival of this mammalian fauna until the beginning of the late Holocene. This indicates that the extinction of megafauna did not occur in the Pleistocene-Holocene, as already indicated by Faure et al. (1999) and Vivo and Carmignotto (2004). The data in Table 2 demonstrate that the ages obtained in this analysis are the youngest obtained for BIR, with the age obtained for *Eremotherium laurillardi* (5,948 ± 294 RC years BP) in the Miranda River valley being the youngest age obtained for this taxon in South America. The ages obtained for *Xenorhintherium bahiense* (3,587 ± 112 RC years BP) and *Palaeolama major* (3,492 ± 165 RC years BP) from Itapipoca are the youngest obtained for the Americas. In Itapipoca, the dating of the taxa *P. major* and *X. bahiense* were isolated from the other taxa, for an interval of approximately 2,500 years BP. We interpret this temporal distance as that these species were actually the last representatives of megafauna to frequent this region, long after the extinction of the other species.

4.3. Hypothesis of BIR as a refuge for megafauna

The ages obtained in this analysis (Table 1) led us to postulate the hypothesis that the BIR had some areas functioning as environmental refuges during the early, middle and early Holocene of the late Holocene. As demonstrated in the literature, all extinct megafauna taxa are associated with open environments (MacFadden and Shockey, 1997; Cartelle, 1999; Higgins and MacFadden, 2004), such as: savanna, woodland, grassland and steppe. Therefore, the survival of megafauna is related to the presence of open vegetation formations within the

Table 2

Holocene geochronological data from different locality in the Americas, obtained through different dating methods. The acronyms represent Brazilian states of CE (Ceará State); MS (Mato Grosso do Sul State); MG (Minas Gerais State); BA (Bahia State); SE (Sergipe State); AL (Alagoas State).

Taxon	Locality	Date (RC years BP)	Calibrated age (cal. BP)	Author/Method
Eremotherium laurillardi	Jirau – CE	6,161 ± 364	6,208–7,714	Present study
Eremotherium laurillardi	Jirau – CE	7,415 ± 167	7,867–8,536	Present study
Smilodon populator	Jirau – CE	7,803 ± 179	8,189–9,079	Present study
Toxodontidae indet.	Jirau – CE	7,804 ± 226	8,049–9,270	Present study
Xenorhinotherium bahiense	Jirau – CE	3,587 ± 112	3,493–4,217	Present study
Notiomastodon platensis	Jirau – CE	7,940 ± 502	7,836–10,159	Present study
Palaeolama major	Jirau – CE	3,492 ± 165	3,353–4,231	Present study
Eremotherium laurillardi	Miranda River – MS	5,942 ± 294	6,120–7,427	Present study
Smilodon populator	Lagoa Santa – MG	9,260 ± 150	10,260–10,480	Piló and Neves (2003); AMS[14]C
Catonyx cuvieri	Lagoa Santa – MG	9,940 ± 40	11,320–11,600	Piló and Neves, 2003; AMS[14]C
Toxodon platensis	Toca dos Ossos – BA		10,664–10,790	Pansani et al., 2019; AMS[14]C
Toxodon platensis	Miranda River – MS		9,562–10,073	Pansani et al. (2019); AMS[14]C
Eremotherium laurillardi	Miranda River - MS		10,059–10,583	Pansani et al. (2019); AMS[14]C
Toxodon platensis	Baixa Grande – BA	9,000 ± 2,000		Ribeiro et al., 2013; ESR
Toxodontidae indet.	João Dourado - BA	9,600 ± 1,000		Faria et al. (2020a,b); ESR
Toxodontidae indet.	João Dourado – BA	9,100 ± 1,000		Faria et al. (2020a,b); ESR
Eremotherium laurillardi	Poço Redondo – SE	9,720 ± 30	11,084–11,233	França et al. (2014); [14]C
Eremotherium laurillardi	Poço Redondo – SE	9,730 ± 30	11,089–11,273	França et al. (2014); [14]C
Notiomastodon platensis	Maravilha – AL	10,000 ± 500		Oliveira et al. (2010); ESR
Notiomastodon platensis	Poço Redondo – SE	10,044 ± 30		França et al. (2014); [14]C
Eremotherium laurillardi	Poço Redondo – SE	10,990 ± 30		França et al. (2014); [14]C
Eremotherium laurillardi	Poço Redondo – SE	11,010 ± 30		França et al. (2014); [14]C
Cuvieronius humboldti	Monte Verde – Chile	11,900 ± 200		Borrero (1997); [14]C
Scelidodon chiliensis	Pampa de los Físiles - Peru	8,910 ± 200	9,780–10,150	Marshall et al. (1984); [14]C
Mylondontidae indet.	Santa Cruz – Argentine	8,639 ± 450		Borrero (1997); [14]C
Equus *neogeus*	Arroyo Seco – Argentina	8,890 ± 90	9,740–10,150	Borrero et al. (1998); AMS
Mylondontidae indet.	Tucumã - Argentina	8,600 ± 150		Collantes et al. (1993); [14]C

Table 2 (*continued*)

Taxon	Locality	Date (RC years BP)	Calibrated age (cal. BP)	Author/Method
Megatherium americanum	Arroyo Seco 2 – Argentina	8,390 ± 240		Borrero et al. (1998); AMS[14]C
Megatherium americanum	Arroyo Seco 2 – Argentina	7,320 ± 50		Borrero et al. (1998); AMS[14]C
Hippidion saldiasi	Pali Aike – Argentina	8,639 ± 450		Bird, 1988; [14]C
Doedicurus clavicaudatus	La Moderna – Argentina	7,510 ± 370		Politis et al. (2004); AMS[14]C
Doedicurus clavicaudatus	La Moderna - Argentiina	7,460 ± 80		Politis et al. (2004); AMS[14]C
Doedicurus clavicaudatus	La Moderna – Argentina	7,010 ± 100		Politis and Gutiérrez, 1998; AMS[14]C
Doedicurus clavicaudatus	La Moderna – Argentina	6,555 ± 160		Politis and Gutiérrez, 1998; AMS[14]C
Megatherium americanum	Arroyo Seco 2 – Argentina	10,500 ± 90		Politis et al. (1995); AMS[14]C
Equus neogeus	Arroyo Seco 2 – Argentina	11,000 ± 100		Politis et al. (1995); AMS[14]C
Equus neogeus	Arroyo Seco 2 – Argentina	8,890 ± 90		Politis et al. (1995); AMS[14]C
Equus sp.	Arroyo Seco 2 – Argentina	8,390 ± 240		Politis et al. (1995); AMS[14]C
Eutatus seguini	Arroyo Seco 2 – Argentina	7,388 ± 74		Prado et al. (2015); [14]C
Megatherium americanum	Passo Otero – Argentina	9,560 ± 50		Johnson et al., 2012; AMS[14]C
Palaeolama sp.	Arroyo Seco 2 – Argentina	9,775 ± 45		Prado et al. (2015); AMS[14]C
Magalocnus rodens	Cueva Beruvides – Cuba	6,250 ± 50		MacPhee et al. (1999); AMS14C
Parocnus brownii	Las Breas de San Felipe – Cuba	4,960 ± 280	4,950–6,350	MacPhee et al. (1999); AMS14C
Parocnus brownii	Las Breas de San Felipe – Cuba	10,250 ± 440	11,050–13,450	MacPhee et al. (1999); AMS14C
Parocnus brownii	Las Breas de San Felipe – Cuba	11,880 ± 420		MacPhee et al. (1999); AMS14C
Parocnus brownii	San Felipe – Cuba	4,690 ± 280		Iturralde-Vinent et al. (2000); AMS[14]C
Neocnus come	Trouing Ismays – Haiti	4,391 ± 42		Steadman et al. (2005); AMS[14]C
Neocnus come	Trouing Deron 1 – Haiti	4,486 ± 39		Steadman et al. (2005); AMS[14]C
Neocnus come	Trouing Attie – Haiti	6,161 ± 45		Steadman et al. (2005); AMS[14]C
Neocnus come	Trouing Jeremy 5 – Haiti	6,875 ± 47		Steadman et al. (2005); AMS[14]C

Table 2 (*continued*)

Taxon	Locality	Date (RC years BP)	Calibrated age (cal. BP)	Author/Method
Neocnus come	Trouing Jeremy 5 – Haiti	7,411 ± 51		Steadman et al. (2005); AMS[14]C
Neocnus come	Trouing Jeremy 5 – Haiti	8,326 ± 57		Steadman et al. (2005); AMS[14]C
Neocnus dousman	Trouing Marassa – Haiti	9,897 ± 65		Steadman et al. (2005); AMS[14]C
Mammuthus primigenius	St' Paul Island – Alaska	7,908 ± 100		Guthrie (2004); AMS[14]C
Nothrotheriops shastenses	Rampart, Arizona –USA	11,000 ± 140		Long et al. (1974); AMS
Nothrotheriops shastenses	Rampart, Arizona –USA	10,780 ± 200		Long et al. (1974); AMS
Nothrotheriops shastenses	Rampart, Arizona –USA	11,020 ± 200		Long et al. (1974); AMS
Nothrotheriops shastenses	Rampart, Arizona –USA	10,400 ± 275		Long et al. (1974); AMS
Nothrotheriops shastenses	Rampart, Arizona –USA	10,035 ± 250		Long et al. (1974); AMS
Nothrotheriops shastenses	Rampart, Arizona –USA	11,370 ± 300		Long et al. (1974); AMS
Nothrotheriops shastenses	Rampart, Arizona –USA	11,480 ± 200		Long et al. (1974); AMS
Nothrotheriops shastenses	Muav Caves, Arizona – USA	11,140 ± 160		Martin and Klein (1984); AMS
Nothrotheriops shastenses	Muav Caves, Arizona – USA	11,290 ± 170		Martin and Klein (1984); AMS
Nothrotheriops shastenses	Shelter Cave, New Mexico – USA	11,330 ± 370		Thompson et al. (1980); AMS

Caatinga and Cerrado biomes in the BIR, since plant species from these biomes were identified in the pollen record of Northeastern Brazil, from the last 40,000 BP years (Behling et al., 2000).

Itapipoca and Miranda are currently located in the Caatinga and "Cerradão", respectively, known generically as Seasonally Dry Tropical Forests (STDFs; Fig. 4), through paleodistribution maps, according to Werneck et al. (2011). STDFs are characterized by the seasonality of the climate regime, with several months of intense drought characterized by a vegetational mosaic (Mooney et al., 1995): forests (deciduous and semi-deciduous), shrubs, cactus, woodland and grassland. "Cerradão" are deciduous and semi-deciduous forests, within the cerrado biome (savannah), being generically classified as STDFs (Werneck et al., 2011). These vegetation formations present a degree of particularities that differentiate them (xeromorphism and rainfall), with the Caatinga presenting hyper-xerophytic vegetation in arid locations.

Werneck et al. (2011) identified areas of STDF stability in South America, from the Last Glacial Maximum (LGM – late Pleistocene) to the mid-Holocene, in Northeast Brazil and also in the state of Mato Grosso do Sul (Fig. 4). STDFs underwent fragmentation during the anomalous periods of humidity of the LGM in Northeast Brazil, detected through pollen records, at 40,000 years BP, 33,000 years BP, 24,000 years BP and between 15,500 and 11,800 years BP (De Oliveira et al., 1999;

Behling et al., 2000). These periods were identified as the wettest for the region, with the expansion of Atlantic and Amazonian forests over areas of Caatinga (Behling et al., 2000; Furley and Metcalfe, 2007). These conditions possibly favored the isolation of megafauna populations in Northeast Brazil during the late Pleistocene, due to the expansion of forests.

From 10,540 years BP to 6,790 years BP, a gradual increase in aridity was observed in the Northeast region of Brazil (Cruz et al., 2009), generating conditions for the expansion of open environments and, consequently, greater availability of habitats for megafauna. This expansion of open environments was observed through pollen records, with the expansion of cerrado (savanna) over areas of arboreal caatinga in Northeast Brazil (De Oliveira et al., 1999). An increase in temperature and humidity is detected with the Holocene Climatic Optimum (HCO), with the establishment of modern caatinga vegetation in 4,535 years BP, with a predominance of tree and shrub species with low proportions of grasses and herbaceous (De Oliveira et al., 1999). HCO was a global event, between 6,500 and 4,000 years BP marked by high levels of humidity in relation to the LGM, causing the replacement of vast areas of open vegetation formations in forests or closed vegetation landscapes in tropical regions (30° latitude belt; Figura 4) from South America (Vivo and Carmignotto, 2004).

This described scenario indicates the expansion of closed environments with a drastic reduction in open environments, generating less favorable conditions for the survival of megafauna in the Northeast region of Brazil. The ages obtained in Itapipoca (Table 1) demonstrate the survival of megafauna species from the early Holocene to the beginning of the late Holocene. This, together with palynological and paleoclimatic data, demonstrate that after the Pleistocene/Holocene transition, the Northeast region presented environmental conditions favorable to the survival of megafauna until the beginning of the late Holocene. The environmental and climatic changes described above for the Brazilian Northeast indicate the presence of an environment favorable to the survival of mammalian megafauna in Itapipoca during the Holocene (Figura 4). Therefore, corroborating the hypothesis of Northeast Brazil as a refuge and, consequently, the Itapipoca region for megafauna until the beginning of the late Holocene.

Lagoa Negra (lake), located 200 km from the Miranda River Basin, has the only pollen record for the region (De Oliveira et al., 1999). Between 10,200 years BP and 8,770 years BP the pollen spectrum is dominated by aquatic plants (macrophytes) from shallow waters, grasses and herbaceous, indicating drier conditions than today and also large areas of grassland. From 8,870 years BP to 7,840 years BP the situation is reversed, with the pollen spectrum dominated by the presence of trees deciduous and semi-deciduous and gallery forest, while grasses are from aquatic environments. This indicates an expansion of forest environments over grassland, due to wetter conditions in the region. From 7,840 years BP, a reduction in tree and aquatic plant pollens was observed, indicating a reduction in precipitation, with an increase in grass and herbaceous, suggesting the expansion of grassland over forest areas. From 5,190 years BP to the present, a significant increase in arboreal and algal elements and small amounts of grass and herbaceous pollens was observed, indicating the expansion of forest areas with possibly small areas of grassland. The scenario described from palynological data obtained by De Oliveira et al. (1999), together with the age obtained for the Miranda River basin, indicates favorable conditions for the survival of megafauna until the middle Holocene (Fig. 4).

The environmental changes described for both BIR locations indicate that these experienced diverse climatic and environmental conditions during the Holocene. The expansion and contraction of open environments, favorable to the survival of megafauna, during this period of time possibly generated the fragmentation and isolation of populations of megafauna species in the BIR. This cyclicality of fragmentation and expansion of open environments from the late Pleistocene to the beginning of the late Holocene may have generated favorable conditions for the extinction of megafauna, in which the locations of Itapipoca and
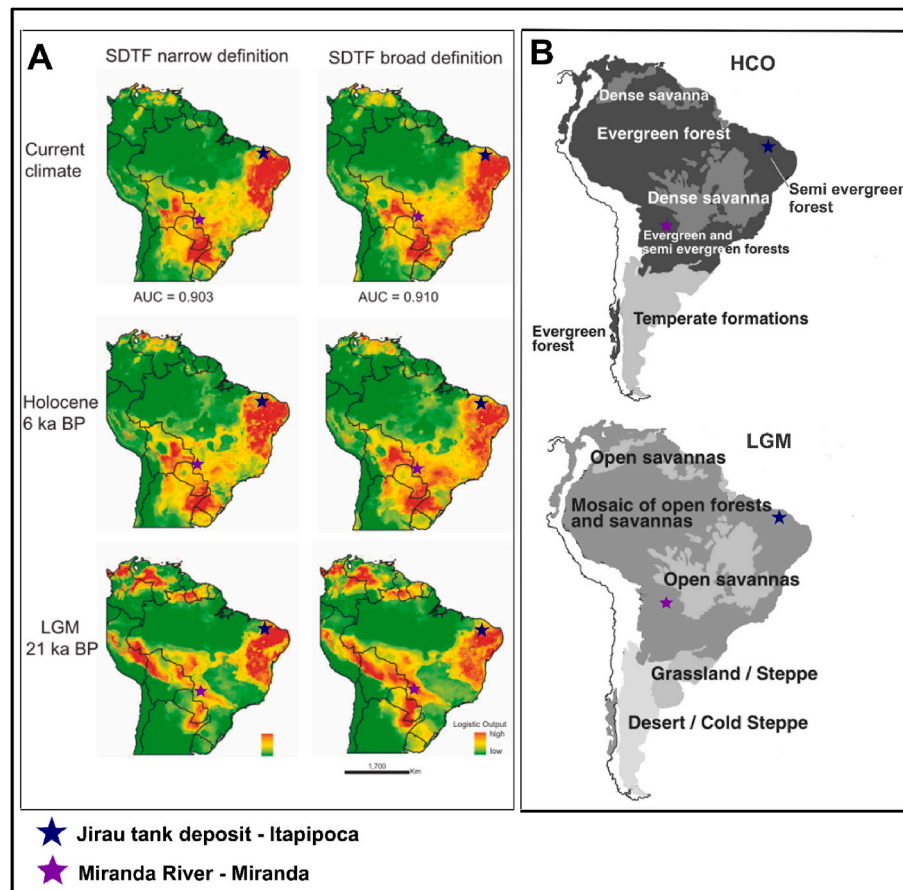
Fig. 4. Paleodistribution maps of the main vegetation formations of South America. A – STDFs on narrow and broad definition for the LGM, middle Holocene and present (Werneck et al., 2011), the warmer colors correspond to regions with STDFs in South America; B – map of vegetation distribution during the HCO and LGM in South America (modified from Vivo and Carmignotto, 2004). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

the Miranda River valley may have sheltered the last populations of megafauna in South America.

4.4. Debating megafauna extinction theories

During the late Quaternary, the large and medium-sized mammal fauna of South America suffered the most significant extinction event among the continents, with around 80% of large mammals and 100% of megamammals being lost. To explain this important geobiological phenomenon, many hypotheses have been proposed, such as: climate changes during the Pleistocene/Holocene (Cartelle, 1999), overkill and blitzkrieg (Martin, 1984), expansion of forest environments during the HCO (Vivo and Carmignotto, 2004), asymmetry between continent and islands (Steadman et al., 2005), and "Broken Zig-Zag" (Cione et al., 2009).

Cartelle (1999) proposes that the extinction of megafauna in South America is associated with late Pleistocene climate change, due to the cold climate and dry conditions of the LGM. This theory do not explain how tropical vegetation types functioned in different climatic regimes and their consequences on large and megamammal fauna. Therefore, the different ages recorded from the early Holocene to the late Holocene, even if punctual in different locations in the Americas (Table 2), indicate that the extinction of megafauna did not occur in the Pleistocene-Holocene transition, but rather throughout the middle and late Holocene.

Another proposed theory is the asynchronous extinction of insular and continental megafauna, due to the ages obtained in Cuba and Saint Paul Island (Alaska; Table 2), being younger than the continental ages

by thousands of years (Steadman et al., 2005). This hypothesis is supported by two lines of evidence: (1) radiocarbon ages of the last appearance of these animals that coincide with the arrival of humans in Cuba and Haiti; (2) if megafauna extinction were due to climate fluctuations, a concomitant extinction event between islands and mainland would result. The data presented by Steadman et al. (2005) were incomplete, as their compilation of geochronological data excludes data from paleontological and archaeological sites with megafaunal skeletal remains of Early and Middle Holocene ages in Argentina (Table 2). The data presented in Table 2 corroborate argument 2, demonstrating that extinction on both islands and continents are associated with climatic and environmental changes, due to its synchronism with continental ages.

We do not consider the Overkill and Blitzkrieg theories (Mosimann and Martin, 1975; Whittington and Dyke, 1984) as the most plausible to explain the extinction of megafauna in South America, due to the long time of interaction between humans and megafauna, since the accepted age for the arrival of humans in the Americas is between 29,000 and 14,000 years BP (Guidon et al., 2000; Fariña and Castilla, 2007; Peyre et al., 2009; Lahaye et al., 2015; Dillehay et al., 2015; Boëda et al., 2016; Vialou et al., 2017). The ages presented in Table 2 and the arrival time of humans indicate a long time of interaction with megafauna, ruling out human activities as a driving force for the extinction of megafauna in South America.

The small number of studies addressing chronological data and interspecific relationships between humans and mammalian megafauna in the Americas as a whole does not corroborate the overkill and Blitzkrieg hypothesis. There are few archaeological sites with direct evidence

of hunting of megafauna species in South America (Prous and Fogaça, 1999). In North America a similar situation was also observed, with only five species of megafauna known to be hunted by humans during the Clovis period (Grayson and Meltzer, 2003; Waters et al., 2014). This observation is also accepted by defenders of the Overkill hypothesis, such as Fiedel and Haynes (2004), due to the absence of strong archaeological evidence of interaction between megafauna and humans in the Americas. Archaeological evidence indicates that hunting was mainly focused on guanacos and deer, animals that survived the extinction (Cione et al., 2009). The scenario of preferential hunting by mega-mammals (Blitzkrieg) can be replaced by the modern view of hunting practices, where moderate and occasional hunting of the females, newborns and juveniles is necessary to generate extinction in thousands of years (Cione et al., 2009).

The autoecological factors may have contributed significantly to the extinction of South American megafauna, in a scenario of environmental stress due to environmental and climate changes during the late Pleistocene to the early late Holocene. The sexual maturity of almost all female mega-mammals is greater than ten years (Nowak, 1999). Pregnant females are more susceptible to hunters and predators, due to their reduced ability to perform evasive actions. The length of the lactation period is also another important factor to be considered, with a period exceeding 500 days being very common for large and mega-mammals (Hayssen and van Tienhoven, 1993). These autoecological factors over thousands of years in an environment of abrupt changes such as the late Quaternary, can have a negative impact on the number of megafauna individuals, generating increasingly smaller populations over time.

The theory of "Broken Zig-Zag", proposed by Cione et al. (2003), emphasizes that the extinction of the fauna of large and mega-mammals was caused by human hunters and gatherers. Favored by autoecological factors of the megafauna, abrupt environmental, climatic and distribution of open environments caused by the periodic oscillations that characterize the Late Quaternary, causing a considerable reduction of this fauna in response to cyclical environmental changes (Zig-Zag). The scarcity of archaeological records of interaction between humans and megafauna, as demonstrated above, does not support the theory that humans caused the extinction of megafauna. This leads us to believe that human activities played a supporting role in this event. Certainly, humans did not exterminate all large and mega-mammals, but they did kill many of them, causing changes that caused their remnants to disappear (Kay, 2002).

Vivo and Carmignotto (2004) propose that the extinction of megafauna in South America is related to environmental changes that occurred during the mid-Holocene, more precisely during the HCO. The loss of megamammal lineages was attributed, by the authors, to the drastic reduction in the area of open vegetation (savannas, savanna woodland, grassland), directly affecting the availability of habitats and ecological niches that supported megafauna. This expansion of forest environments in South America during the HCO may have caused the population isolation of megafauna species and, consequently, a reduction in gene flow, generating conditions favorable to the extinction of megafauna. The ages obtained in this analysis (Table 1) corroborate the hypothesis raised by Vivo and Carmignotto (2004) of megafauna extinction during the middle Holocene. Therefore, the regions of Vale do Rio Miranda and Itapipoca during the HCO indicate the presence of environmental refuges for megafauna in these locations. Therefore, the theory proposed by Vivo and Carmignotto (2004) is the best options to explain the extinction process of large and megamammal fauna during the Holocene.

5. Conclusions

The ages obtained in this study are the most recent for the BIR. The ages of *Palaeolama major* (3,492 ± 161 RC years BP) and *Xenorhinotherium bahiense* (3,587 ± 112 RC years BP) are the youngest obtained so far for extinct megafauna in the Americas. The

geochronological data obtained in this study and from other researchers demonstrate the presence of megafauna far beyond the Pleistocene/Holocene boundary, with a temporal distribution between 450,000 and 3,000 years BP in BIR. Geochronological, paleoclimatic and paleodistribution data of STDFs in South America corroborate the hypothesis that the Itapipoca and Miranda River valley locations were one of the last refuges of megafauna in South America. We believe that selective hunting of females and juveniles, autoecological factors of megafauna, are contributing attributes to the extinction of megafauna, with the driving force of this geobiological event being environmental/climatic changes during the LGM and the beginning of the late Holocene. It is likely that in the interglacials this fauna that was adapted to open environments did not die of starvation, but their populations may have been reduced under environmental stress. This caused isolation and reduced genetic flow between megafauna populations, due to the expansion of forest areas in South America, from the HCO to the present, creating conditions that promoted the extinction of the magnificent megafauna.

CRediT authorship contribution statement

Fábio Henrique Cortes Faria: Writing – review & editing, Writing – original draft, Validation, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Ismar de Souza Carvalho:** Writing – review & editing, Writing – original draft, Funding acquisition, Formal analysis. **Hermínio Ismael de Araújo-Júnior:** Writing – review & editing, Writing – original draft, Validation, Formal analysis, Conceptualization. **Celso Lira Ximenes:** Writing – review & editing, Writing – original draft, Formal analysis. **Edna Maria Facincani:** Writing – review & editing, Writing – original draft, Formal analysis.

Declaration of competing interest

The authors declare to the *Journal of South American Earth Sciences* that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All data used are available in the manuscript.

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