Quaternary Science Reviews 221 (2019) 105864



Contents lists available at ScienceDirect

Quaternary Science Reviews

journal homepage: www.elsevier.com/locate/quascirev

Isotopic paleoecology (δ^{13} C, δ^{18} O) of Late Quaternary megafauna from Mato Grosso do Sul and Bahia States, Brazil



QUATERNARY



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ARTICLE INFO

Article history: Received 5 April 2019 Received in revised form 31 July 2019 Accepted 1 August 2019 Available online xxx

Keywords: Pleistocene Holocene Paleoclimatology South America Stable isotopes Brazilian Intertropical Region Niche width

ABSTRACT

In the present study, the paleoecology (diet and niche width) of Late Quaternary megamammals that inhabited the Brazilian Intertropical Region (BIR) was assessed at two sites in the states of Bahia and Mato Grosso do Sul. The δ^{13} C analyses suggest a generalist diet for Notiomastodon platensis, Palaeolama major, Holmesina paulacoutoi and Glyptotherium sp., while Equus neogeus was a grazer with a diet consisting exclusively of C_4 grasses, and *Eremotherium laurillard*, a predominant browser with a diet consisting predominantly of C₃ plants. A distinct diet pattern was inferred for one species: Toxodon platensis with a mixed-diet preferring C₄ grasses in Mato Grosso do Sul but predominantly the C₃ feeder in Bahia. These results show a high ecological plasticity of this species and may suggest distinct ecological pressures or different vegetation configurations in the two regions. Diet reconstitutions based on δ^{13} C analyses suggest that an open savanna-like landscape predominated in both areas. The δ^{18} O values reveal that Mato Grosso do Sul could have experienced wetter climatic conditions than Bahia during the Late Quaternary, suggesting a humid corridor in midwestern Brazil, or that there were different contents of δ^{18} O of water sources between these areas. Hence, we assume that the same faunistic composition in different geographical areas is not enough to delimit the ecosystems of the BIR, and we recommend that the definitions of BIR should be revised to include more refined paleoclimate data. Other studies around the world should consider the same for delimitations of zoogeographic regions.

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1. Introduction

In South America, Late Pleistocene megafauna consisted of several native taxa (*e.g. Toxodon, Glyptodon, Holmesina, Pampatherium, Glossotherium, Mylodon, Eremotherium*) together with some North American taxa (*e.g. Notiomastodon, Smilodon, Equus, Palaeolama*) which had dispersed into South America during the Great American Biotic Interchange (Webb, 1985, 2006; Prado and Alberdi, 2014; Bacon et al., 2016). American megafauna gradually disappeared during the Late Quaternary (Gill et al., 2009; Barnosky and Lindsey, 2010), and the loss of taxa in South America was more significant when compared to other continents (Barnosky et al., 2004; Koch and Barnosky, 2006; Barnosky and Lindsey, 2010).

In this paper, we focus on the Late Quaternary Brazilian Intertropical Region (BIR; Fig. 1), defined by Cartelle (1999) as a paleozoogeographic region inhabited by autochthonous and allochthonous megamammals species that coexisted sympatrically in dry seasonal forests and savanna-like environments. Recently, the BIR was expanded to include Mato Grosso do Sul State (Central-Western Brazil), because of the discovery of megamammals common to both regions (Pansani et al., 2016; Oliveira et al., 2017).

Mato Grosso do Sul State is an important region for the study of the evolution, paleoecology, paleoenvironment and extinction of mammals, but its Quaternary megafauna remains poorly studied (*e.g.* Salles et al., 2006; Perini et al., 2009; Oliveira et al., 2017) despite the high diversity (47 taxa) of medium and large bodied

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Fig. 1. Map of (A) Brazilian Intertropical Region (BIR) within South America, and (B), state map of Brazil showing the BIR, including Miranda River Mato Grosso do Sul State, and Tocas dos Ossos Cave, Bahia State, adapted from Dantas et al. (2017).

extant mammals (Tomas et al., 2017). Moreover, the extant vegetation reflects paleobiogeographic events conditioned by climate changes (semi-arid to humid tropical) that South America has experienced since the Late Pleistocene to Holocene (Barbosa, 2012), making it an interesting region to investigate paleoecological aspects of extinct megamammals.

The paleodiet and ecological dynamics, such as niche inferences, of the Pleistocene megafauna of the Brazilian Intertropical Region have recently been studied based on different methodologies, including the study of stable isotopes (e.g. Marcolino et al., 2012; França et al., 2014; Dantas et al., 2017). For more than a decade the use of mammalian tissues (bone and tooth) in stable isotopes analyses has shown that fossils of mammals retain important information (carbon and oxygen contents) that can reveal unknown aspects of ancient environments and ecology, and even patterns of global changes (e.g. MacFadden et al., 1999; Ben-David and Flaherty, 2012: Phillips, 2012; Bocherens and Drucke, 2013). This approach can help us to better understand and test assumptions on the evolution of megafauna and their ecological relation to the environment, often combining them with different methods, such as an analysis of functional morphology, ecomorphology, palynology and paleobotanic (e.g. Van deer Hammen, 1974; Ferraz-Vicentini and Salgado-Labouriau, 1996; Pennington et al., 2000; Moreno and León, 2003; Bargo et al., 2006; Bargo and Vizcaíno, 2008; Figueirido and Soibelzon, 2009; Soibelzon et al., 2014).

The main aims of this work are: 1) to investigate the diet and paleoecology of Late Quaternary megamammals recovered in the Miranda River in Mato Grosso do Sul and Toca dos Ossos Cave in Bahia based on δ^{13} C analyses; 2) to investigate palaeoclimatic aspects of these two areas within the Brazilian Intertropical Region based on δ^{18} O analyses; and 3) to compare the paleoecological scenarios and paleoenvironmental conditions of both areas.

2. Material and methods

2.1. Sample choice and aspects

Samples of four taxa (*Eremotherium laurillardi, Glyptotherium* sp., *Holmesina paulacoutoi*, and *Toxodon platensis*) from the Miranda River, Mato Grosso do Sul (20°14'27.30"S/56°23'59.30"W), and four species (*Palaeolama major, Notiomastodon platensis, T. platensis* and *E. laurillardi*) from the Toca dos Ossos Cave, Ourolândia, Bahia (10°55″52″S/41°03'24"W), both in Brazil, were analyzed for their isotopic content. In addition, published isotopic data for *Equus neogeus, Notiomastodon platensis* (*= Stegomastodon waringi; Mothé* et al., 2012) and *Toxodon platensis* from Toca dos Ossos, Bahia, were included in our analysis (MacFadden et al., 1999; Sánchez et al., 2004; MacFadden, 2005).

Material of *E. laurillardi* (CAP/1B-349), *Glyptotherium* sp. (CAP/ 1B-345), *H. paulacoutoi* (CAP/1B-340) and *T. platensis* (CAP/1B-355) from Mato Grosso do Sul are housed at the Laboratório de Estudos Paleobiológicos (LEPBio) in the Universidade Federal de São Carlos *campus* Sorocaba, Sorocaba, São Paulo, Brazil. Material of *E. laurillardi* (LEG 1636), *T. platensis* (T07) and *N. platensis* (T06) from Bahia and *P. major* (LPUFS 5219) are housed at the Laboratório de Ecologia e Geociências (LEG) of the Universidade Federal da Bahia (IMS/CAT, Vitória da Conquista, Bahia, Brazil) and the Laboratório de Paleontologia of Universidade Federal de Sergipe (LPUFS, São Cristovão, Sergipe, Brazil), respectively.

The fossils from Mato Grosso do Sul were found by local residents in dredged sediments from the Miranda River channel, in the region of Serra da Bodoquena, and donated to the authors in 2014. Out of the total there was one phalange attributed to *Eremotherium laurillardi*, four osteoderms of *Glyptotherium* sp., two osteoderms of *Holmesina paulacoutoi* and one tooth of *Toxodon platensis* (Pansani

et al., 2016).

Caves in the Serra da Bodoquena karst (Salles et al., 2006; Scheffler et al., 2010; Oliveira, 2013; Oliveira et al., 2017) and riverbank outcrops along the Miranda River (Scheffler et al., 2010) are known to preserve remains of Pleistocene mammals and are probably the source deposits from where the fossils were exhumed and/or transported out to the river channel.

Despite the few recovered specimens, the high relative abundance of osteoderms and teeth is related to the large number of these elements in mammal skeletons. Furthermore, osteoderms, teeth, calcanea and phalanges are more easily moved by hydraulic flow when compared with larger and heavier elements (Behrensmeyer, 1975; Frison and Todd, 1986), increasing the probability of them being introduced to the river channel.

The disarticulated condition and high transport potential of the bones, in addition to the identification of abrasion marks on some specimens, characterize assemblages typically exposed to high hydraulic energy (Aslan and Behrensmeyer, 1996; Fernández-Jalvo and Andrews, 2003; Van Orden and Behrensmeyer, 2010). This does not mean, however, that the fossils were necessarily transported very distant from their source areas, as suggested by actualistic studies involving fluvial transport. Although the duration and distance of transportation are intuitively considered variables associated with the degree of abrasion, at least relative to distance, this correlation is not straightforward. Actualistic experiments in natural fluvial systems have shown that lighter bones can move long distances without exhibiting significant abrasion, while stabilized heavier bones can be "sandblasted" and show greater abrasion (Aslan and Behrensmeyer, 1996; Van Orden and Behrensmeyer, 2010). Moreover, the experiments performed by Aslan and Behrensmeyer (1996) in the East Fork River in Wyoming showed that most of the experimental bones travelled less than 1000 m from their source of origin during the study.

The samples analyzed here from Bahia come from the Toca dos Ossos Cave, a limestone cave located near the municipality of Ourolândia. The cave consists of a main stream passage associated with ramifications, exhibiting a maze pattern (Cartelle, 1992; Lessa et al., 1998; Auler et al., 2006). A diverse and abundant mammal paleofauna was found in the upper and lower levels of the cave.

Auler et al. (2006) argued that the predominant abundance of large species in the Toca dos Ossos Cave was explained by the high influence of runoff events in the accumulation of fossils. This is suggested by the fact that bones are found disarticulated and broken, the absence of atypical fossil deposits at some pitfalls, the recurrent association of fossils and fluvial sediments in the areas subject to flooding, and a bias towards the preservation of larger and heavier bones probably due to selective transportation favoring the removal of smaller and lighter elements (Auler et al., 2006).

2.2. Isotopic paleoecology and ¹⁴C AMS dating

The analyses were conducted at the Center for Applied Isotope Studies, University of Georgia, USA. The hydroxyapatite was extracted from fractions of enamel (*T. platensis* from Mato Grosso do Sul, *T. platensis*, *P. major*, *N. platensis* from Bahia), dentine (*E. laurillardi* from Bahia) and bones (*E. laurillardi* from Mato Grosso do Sul, *H. paulacoutoi* and *Glyptotherium* sp.). In addition to the isotopic analysis, some of the specimens studied here were dated by ¹⁴C AMS (*E. laurillardi* and *T. platensis* from both states, and *N. platensis* from Bahia).

Although bone tissue is more susceptible to diagenesis, recent studies have shown that data extracted from it can be reliable, just as that from dentine and enamel (Lee-Thorp and Sponheimer, 2003; Cherkinsky, 2009; MacFadden et al., 2010). Mineral composition of enamel is hydroxyapatite (>95%), the inorganic material in the skeleton of vertebrates most resistant to diagenesis (MacFadden et al., 2010) and well-suited for reconstructing paleodiet from vertebrate fossils. Sullivan and Krueger (1981) show that stable carbon isotope values extracted from the purified mineral (inorganic) phase of skeleton remains were comparable in reliability to those extracted from the purified organic phase, both resulting in good results for isotopic analysis.

Here, we used a technique that separates the bioapatite fraction from diagenetic carbonates, by utilizing diluted acetic acid and bone preparation (Cherkinsky, 2009).

The stable isotope ratios δ^{13} C and δ^{18} O were measured from separated aliquotes using mass spectrometer Delta V combined with gas bench. The results reported relative to V-PDB with the standard deviation 0.2‰ or better.

Carbon isotopic data (δ^{13} C) enable paleoenvironmental inferences and reconstructions of landscape configurations by identifying the dominant plant groups, by recognizing the isotopic signatures of their photosynthetic pathways recorded in animal tissues through the composition of the animals' diet (Rundel et al., 1989; Clementz, 2012), which indicate the presence of C₃ plants (trees, shrubs, forbs, herbaceous dicotyledonous, leaves, fruits and cool to temperate climate latitudes and high-altitude grasses), C₄ plants (grasses and some monocotyledonous and pteridophytic trees from tropical/temperate environments) and CAM plants (succulent Crassulaceae).

Both C₃ and C₄ cycle pathways, utilized by the largest number of plants, fractionate carbon in different forms, and consequently in different proportions. In carbon isotopic analyses, a significant difference between values of C₃ and C₄ plants can be observed, in which the average value of C₃ plants is $-27 \pm 3\%$, in C₄ it is $-13 \pm 2\%$, and for CAM the values are intermediate between C₃ and C₄ (MacFadden et al., 1994; Koch et al., 1998; MacFadden, 2013; Dantas and Cozzuol, 2016).

The ¹³C values of carbonate from bones and teeth of the species were calculated based on the study of Tejada-Lara et al. (2018). The enrichment of studied taxa varied from 13.36‰ to 14.35‰, thus we opted to use the value for megamammals studies: 14‰ (*e.g.* Cerling and Harris, 1999).

Information obtained through oxygen isotopic analyses (δ^{18} O) can allow interpretations of aspects of the abiotic environment, such as conditions prevailing in the environment (*e.g.* precipitation and humidity; MacFadden et al., 1999; Yann et al., 2013). The oxygen isotopes are incorporated into the tissues of animals by inhaling the available atmospheric oxygen, directly by drinking surface water or indirectly by eating plants (Ayliffe et al., 1992; Bryant and Froelich, 1995; Bocherens and Drucke, 2013). References used for isotopic values were V-PDB (δ^{13} C) and V-SMOW (δ^{18} O) (Coplen, 1995).

For AMS analysis, the cleaned carbon dioxide was catalytically converted to graphite using the method of Cherkinsky et al. (2010). Graphite ${}^{14}C/{}^{13}C$ ratio was measured using the 0.5 MV Pelletron AMS instrument. The sample ratios were compared to the ratio measured from oxalic acid standard OXI (NBS-4990) to calculate radiocarbon age.

2.3. Ecological measurements

Proportions of diet were estimated through one isotope mixing model using carbon (1, 2) isotopic data.

$$\delta^{13} C_{\text{mix}} = \delta^{13} C_1 f_1 + \delta^{13} C_2 f_2 \tag{1}$$

$$1 = f_1 + f_2 \tag{2}$$

Where resources are represented by: $C_1f_1 = C_3$ plants, $C_2f_2 = C_4$ plants.

The niche breadth (*B*) of all the species was calculated by the-Levins' (1968) measure, where pi = proportion of resources consumed:

$$B = \frac{1}{\Sigma p_i^2} \tag{3}$$

These values were standardized (B_A) from 0 to 1, by the following equation, where N = total amount of resources analyzed:

$$B_A = \frac{B-1}{N-1} \tag{4}$$

3. Results

Most specimens were dated as Late Quaternary (9652–12,844 Cal yr BP) (Table 1). A *N. platensis* specimen indicated an older age, dating back to 27,473 - 26,873 Cal yr BP (Table 1).

The lowest δ^{13} C values in Mato Grosso do Sul and Bahia were observed in *E. laurillardi* (δ^{13} C = -12.77‰, -12.80‰, respectively), while the highest δ^{13} C values were observed for *T. platensis* in Mato Grosso do Sul (δ^{13} C = -4.02‰) and *E. neogeus* in Bahia (δ^{13} C = 1.70; Table 1, Fig. 2).

In Mato Grosso do Sul, *T. platensis* had a balanced diet with a higher consumption of C₄ grasses and a relative broader niche width ($B_A = 0.85$), while *E. laurillardi* had a higher consumption (almost exclusive) of C₃ plants, and consequently the narrowest niche width ($B_A = 0.04$). *Glyptotherium* sp. and *H. paulacoutoi* presented intermediate values of mixed balanced diets and consequently broader niche widths ($B_A = 0.99$ and 0.87, respectively).

In Bahia, *E. neogeus* (both specimens) had the lowest niche width among all species ($B_A = 0.00$), with an exclusive C₄ diet, followed by *E. laurillardi*, with an almost exclusive C₃ diet ($B_A = 0.02$), *T. platensis*, predominantly C₃ plant-feeder ($B_A = 0.06$ and $B_A = 0.17$), *N. platensis*, predominantly C₄ grazer ($B_A = 0.15$). *P. major*, another *T. platensis*, and two other *N. platensis* specimens presented balanced consumption of both resources and broader niche widths ($B_A = 0.96$, 0.89, 0.96 and 0.81, respectively) (Table 1; Fig. 3).

All individuals from Mato Grosso do Sul exhibit isotopic oxygen values of about 24‰ (mean 24.69 \pm 1.23‰), while in Bahia some species showed remarkable higher oxygen values (*e.g. E. neogeus*, *N. platensis* and *T. platensis*; mean 27.81 \pm 2.41‰).

4. Discussion

4.1. Isotopic paleoecology (δ^{13} C) and niche breadth (B_A)

Our results largely corroborate previous findings regarding the isotopic paleoecology of megamammals from BIR, but also add unusual information to some species. We confirm the higher δ^{13} C values referred to as *E. neogeus* in Bahia, indicating a grazer C₄ diet, as formerly reported (*e.g.* MacFadden, 2013; Dantas et al., 2017). On the other hand, according to previous studies for northeast Brazil (northern portion of BIR), a predominantly C₃ diet was attributed to *P. major*, which lived in forest border areas or had a preference for shrubs in open areas (Marcolino et al., 2012). Our results showed a generalist diet with a preference for C₄ grasses for this species, suggesting their occurrence in open areas and contradicting the premises that this species did not feed on C₄ grasses (Chaves, 2000; Marcolino et al., 2012).

N. platensis occurred in South America between at least 530 ka and 6 ka (Dantas et al., 2013b) and had lived, at least, between 120 ka to 12 ka in the BIR (Dantas et al., 2017). It is usually considered a generalist species, with diets composed of a mixture of C_4 and C_3 plants (Sánchez et al., 2004; Asevedo et al., 2012; Dantas and Cozzuol, 2016; Dantas et al., 2017), with apparent altitudinal and latitudinal gradient of C_3/C_4 grasses (Prado et al., 2001; Asevedo et al., 2012). *N. platensis* for Toca dos Ossos, Bahia, presented mixed-diet based on two specimens and a predominantly C_4 diet based on one specimen.

For the BIR, there was no published isotopic data for *Glypto*therium sp. and *H. paulacoutoi* available, until this present study. Inferences about the diet of Cingulata have been primarily studied by ecomorphology and morphogeometry (*e.g.* Pérez et al., 2000; Fariña and Vizcaíno, 2001). A recent study found a C_3/C_4 mixed diet for *Glyptotherium* sp. in Mexico, with a high consumption of C_4 plants of an open-habitat living species (Pérez-Crespo et al., 2012). Our data for *Glyptotherium* sp. also points to a mixed diet, with a balanced consumption of resources. Similarly, *H. paulacoutoi*, also presented a mixed diet, but with a higher consumption of C_3 plants.

E. laurillardi is interpreted by some authors as a generalist species (*e.g.* Dantas et al., 2017), able to cross the Americas and considered a Panamerican species (Cartelle and Iuliis, 1995) due to

Table 1

Proportions of food resources (piC_3 plants and piC_4 grass), isotopic values for $\delta^{13}C$ (‰) and $\delta^{18}O$ (‰), calibrated age and standardized niche breadth (B_A) for megamammals from Toca dos Ossos, Bahia, and Miranda River, Mato Grosso do Sul. ^(e): enamel, ^(d): dentine, ^(b): bone.

Locality/taxa	Sample	$p_i C_3$	p_iC_4	δ^{13} C (‰VPDB)	$\delta^{18}O$ (‰VSMOW)	Age (Cal yr BP)	B _A	Reference
Toca dos Ossos/BA								
E. neogeus	Uncatalogued ^(e)	_	1.00	1.10	29.46	_	0.00	MacFadden et al. (1999)
	Uncatalogued ^(e)	-	1.00	1.70	30.60	_	0.00	MacFadden et al. (1999)
N. platensis	Uncatalogued ^(e)	0.66	0.34	-8.20	30.80	_	0.81	Sánchez et al. (2004)
	Uncatalogued ^(e)	0.43	0.57	-5.00	28.95	_	0.96	Sánchez et al. (2004)
	T06 ^(e)	0.07	0.93	0.02	27.26	27,473-26,873	0.15	our data
T. platensis	U96148 ^(e)	0.97	0.03	-12.60	26.96	_	0.06	MacFadden et al. (1999)
	U96149 ^(e)	0.62	0.38	-7.70	29.46	_	0.89	MacFadden et al. (1999)
	T07 ^(e)	0.92	0.08	-11.82	25.09	10,790-10,664	0.17	our data
P. major	LPUFS5219 ^(e)	0.43	0.57	-5.07	25.68	_	0.96	our data
E. laurillardi	UGAMS34131 ^(d)	0.99	0.01	-12.80	23.80	12,844-12,214	0.02	our data
Miranda River/MS								
E. laurillardi	UGAMS 34,133 ^(b)	0.98	0.02	-12.77	23.74	10,583-10,059	0.04	our data
Glyptotherium sp.	UGAMS 34,134 ^(b)	0.52	0.48	-6.29	25.15	_	0.99	our data
T. platensis	UGAMS 34,132 ^(e)	0.36	0.64	-4.02	23.63	10,073-9652	0.85	our data
H. paulacoutoi	UGAMS 34,135 ^(b)	0.63	0.37	-7.77	26.22	-	0.87	our data



Fig. 2. Scatter-plot of δ 13C values of the megafauna species from Bahia and Mato Grosso do Sul States.



Fig. 3. Standardized isotopic niches width of the megamammals from Toca dos Ossos Cave, Bahia and Miranda River, Mato Grosso do Sul.

its wide distribution and good adaptation to diverse habitats. Our results suggest a specialist browser diet with a preference for C_3 plants in both studied areas.

A mixed feeding diet is often attributed to *T. platensis* in South America (*e.g.* MacFadden, 2005; Dantas et al., 2013a, 2017). In this study, two samples present a predominant C_3 diet and one sample a mixed-diet in Bahia, while one sample indicated a predominant C_4 diet in Mato Grosso do Sul. This inference of a high consumption of C_4 grasses for *T. platensis* was already found in southern Brazil (*e.g.* Lopes et al., 2013).

Data from MacFadden (2005) and Dantas et al. (2017) in combination with ours may indicate that *T. platensis* was a generalist adapted to feeding on the predominant type of vegetation. This pattern of animal adaptations in foraging habitats and diet to environmental changes is also debated for large herbivores in Europe (Hofman-Kamińska et al., 2019). It could be justified by food shortages or as a consequence of specific ecological pressures (*e.g.* competition with other species), possibly influenced by climate oscillations that occurred during the Pleistocene and/or expansion of C₄ grasses and dry woods due to fire regimes. Fire regimes can occur naturally through vegetation – a characteristic of *Cerrado stricto sensu* in Brazil for example (Miranda et al., 2009). Nevertheless, further studies and expansion of the number of samples analyzed are necessary to clarify this question. Regardless of the exact circumstances that generated these patterns, the feeding habits found for *T. platensis* in Mato Grosso do Sul indicate high ecology plasticity, which allowed it to inhabit in different environments. This could represent an important factor to take into

consideration when trying to elucidate paleobiogeographic patterns in the distribution of megamammals in Brazil and even in South America.

The niche width in Bahia showed that *E. neogeus* was the most specialist species ($B_A = 0.00$), with a restricted diet composed exclusively of C₄ plants, and *E. laurillardi* as another specialist, but with a diet composed almost exclusively of C₃ plants ($B_A = 0.02$), which could have been problematic in competitive scenarios.

In Mato Grosso do Sul, *E. laurillardi* and *T. platensis* occupied more differentiated niches, which would have facilitated possible coexistence of both species in this region, and low probability of competition for resources.

4.2. Paleoenvironmental reconstitution

Our results show that although *T. platensis* was found in Mato Grosso do Sul and Bahia at the same time, during the Late Pleistocene, feeding behavior was different in each region, which could be the result of different climate patterns and vegetation configurations, or ecological plasticity resulting in opportunistic adaptations to different vegetation types in distinct areas, comparable to latitudinal variations in diets of gomphotheres and horses across the Americas (*e.g.* MacFadden et al., 1999; Prado et al., 2001).

In Mato Grosso do Sul, all individuals presented isotopic oxygen values about 24‰ (δ^{18} O = 24.69 ± 1.23‰), while in Bahia some species showed significantly higher oxygen values (*e.g. E. neogeus*, *N. platensis* and *T. platensis*) and a higher δ^{18} O mean value of 27.66 ± 1.29‰. This pattern could suggest that (1): the environments in Mato Grosso do Sul were more humid than those of Bahia during the Late Quaternary, especially during the Late Pleistocene, or (2): that the megamammals from Mato Grosso do Sul State obtained water by drinking from rivers and lakes subject to lower evaporation and consequently not δ^{18} O-enriched waters.

Paleoclimate inferences can be suggested observing and interpretating our dated specimens. *T. platensis* presented distinct oxygen values in both areas in synchronous time, presenting lower δ^{18} O values in Mato Grosso do Sul and indicating a differential climate pattern during this time in Brazil. *N. platensis* presented very distinct δ^{18} O values when compared with all the dated taxa. *N. platensis*, inferred as a specialist C₄ feeder, presented the highest δ^{18} O value (among our new data) and was dated as 27,473- 26,873 Cal years, the oldest age among our dated specimens. This is congruent with the distribution of dry forest habitats during the Last Glacial Maximum and reinforces the association of this species with this type of vegetation, as proposed by Dantas et al. (2013b).

We may suppose that it is more likely that this pattern is correlated to climate changes, when drier environments configurated Bahia in some part of the Pleistocene when compared with the moment of our species.

Our results also agree with previous studies that indicate the existence of a humid corridor in this region based on studies of stalagmites (e.g. Novello et al., 2017). However, additional studies are needed on materials from Mato Grosso do Sul, in order to have more accurate comparisons of oxygen values, considering the absolute ages in which these animals lived and what their palaeoclimatic scenario would be at the given time. The high oxygen isotopic values for E. neogeus, N. plastensis and T. platensis in Bahia, in contrast to those found in individuals from Mato Grosso do Sul that are lower (Table 1), can (1): reflect paleoclimate differences between these locations, (2): indicate a common water source with constant isotopic content for Mato Grosso do Sul species and distinct water sources, such as rivers (depleted) or lakes (enriched), for species from Bahia, or (3): indicate distinct time periods with distinct isotopic compositions of the available local water for species from Bahia. The fact that this pattern was recorded by individuals referred to different taxonomic groups makes it unlikely that it was produced by intrinsic physiological factors (Kohn et al., 1996).

In short, our results corroborate a savanna-like vegetation with fragments of forests (sparse trees) for both locations in the BIR region (Figs. 4 and 5), with a probable abundance of C_4 grasses in open landscapes and wetter climatic conditions in Mato Grosso do Sul State (currently predominanted by the phytogeographical domain Cerrado) than Bahia State (currently predominanted by the phytogeographical domain Caatinga).

The presence of BIR megamammals found in the BIR and in other regions of Brazil (*e.g.* São Paulo State Ghilardi et al., 2011, Rio Grande do Sul Lopes et al., 2013 and also other countries) suggest that the central point of the BIR should not be only the sharing of taxa, but climate and vegetation conditions. Especially because both ecosystems, *Cerrado* and *Caatinga* domains, are covered by a mosaic of microregions - especially the Cerrado (the "South American savanna"), which is distributed in mainly the whole of Central Brazil and can reach other regions, comprising complex vegetations that, in the late Pleistocene, presented different responses to climate changes (Salgado-Labouriau, 1997).

Dantas and Cozzuol (2016) recognized different environmental conditions at two distinct moments in the BIR: 1) from 93-47 ka, when a warmer and drier period is recognized, with a possible connection of Caatinga and Cerrado; and 2) from 40-10 ka, when a colder and wetter period is recognized, with a possible connection of BIR with the Amazon and Atlantic Forests. In Brazil, as well as in most of South America, in the Middle and Late Pleistocene the megafauna experienced long-term environmental changes related to periodic interglacial and glacial conditions as well which promoted the expansion and retraction of vegetation types and increases-decreases of mammalian biomass, due to migrations events (Cione et al., 2007). Such events are discussed in Prado et al. (1987), Tonni et al. (1999), and Carlini et al. (2004), where the Late Pleistocene of the Pampean region is described as an inadequate average winter temperature for megamammals that resulted in migrations to Brazil and other territories to the north of the Pampas.

We interpret that it is possible that mammal individuals migrated from the northeast of BIR, a region highly influenced by climate fluctuations in intertropical South America during the Late Pleistocene (Ab'Sáber, 1957), during drier conditions (periods of reduced rainfall in the northeast) to areas of most moisture, such as the Amazoni Basin (e.g. Haffer, 1969) and probably mid-west Brazil - Mato Grosso do Sul included (Barbosa, 2012, 2016). Perhaps the Cerrado was already more humid than the Caatinga when these animals lived, or the Pantanal was already in formation. Bezerra (1999) characterized the Late Pleistocene in Mato Grosso do Sul as an unstable period, predominantly dry interspersed by fluvial phases, and the Holocene as a humid period with the establishment of flood zones (Pantanal), from the individualization of "lake systems". Unfortunately, isotopic data, especially for megamammals, from Mato Grosso do Sul are scarce, but further isotopic analysis in a bigger dataset from this area and the midwestern Brazil in general could help to reveal this pattern.

Besides Cartelle (1999), in the view of outlining the concept of the BIR, disregarded species that had wide geographic distributions (*e.g. Smilodon populator* Lund, 1842), but considered *E. laurillardi* as an autochthonous species, despite being one of the most well distributed species in the Americas (Cartelle and Iuliis, 1995). *T. platensis* is considered an allochthonous species, which occurs from the Pampean (*e.g.* Carlini et al., 2004) to intertropical Amazon (*e.g.* MacFadden, 2005).

In this context, if Mato Grosso do Sul is included in the BIR, it is



Fig. 4. Reconstruction of the Late Pleistocene environment of Mato Grosso do Sul State. Artist Júlia d'Oliveira.

expected that: 1) allochthonous BIR species followed this migration route, which integrates Mato Grosso do Sul as an Intertropical region, or 2) they followed a different migration route from the northeast BIR to the south, which could integrate Mato Grosso do Sul as a refuge area, due to factors that are still not understood and studied.

It is necessary to reflect on the BIR definition and its limits in the light of standardized data access, and additional paleoecological and statistical studies should be performed to evaluate these hypotheses, especially including other regions (within and outside the BIR) and not only large-body mammals. This could reveal unknown patterns of migration based on size and diet preferences, and increase the resolution of the delimitation of zoogeographic regions by potentially expanding the number of endemic taxa.

5. Conclusions

Carbon isotopic analyses of fossil teeth and bones of megammamals from two locations in the Brazilian Intertropical Region (BIR), Mato Grosso do Sul and Bahia states, indicate three different feeding styles for the individuals recovered in both locations: a mixed feed diet, including C_3 and C_4 grasses, a specialized grazing and a specialized browser habits. Moreover, there is a noteworthy difference in oxygen values, higher in specimens from Bahia when compared with those of Mato Grosso do Sul, which suggests a wetter climate in Mato Grosso do Sul and drier conditions in Bahia, or differential enrichment in waters sources due to evaporation in the latter.

Different feeding diets were inferred for *T. platensis* in each locality. In Mato Grosso do Sul, whereas *E. laurillardi* was a specialist C_3 feeder in both areas, *T. platensis* was a preferential C_3 feeder in Bahia, and presented a more balanced diet in Mato Grosso do Sul with preference for C_4 plants.

The notorious differences found in each region for this species can reflect: (1) ecological pressures that affected its environments (*e.g.*competition, food shortage); or (2) ecological plasticity of this species with opportunistic adaptation due to latitudinal variations of vegetation. Through this scenario, it can be inferred that these megamammals from Mato Grosso do Sul and Bahia states inhabited a mosaic of a diverse landscape, with forested landscapes and dry grasslands in savanna-like environments, and also stimulates the investigation of possibilities of ecological interactions that could influence their foraging and diet habits.

In short, in the present study we unveil that the same faunistic composition in different geographical areas is not enough to delimit the ecosystems of the BIR, and the climate is an important factor to be considered concerning the delimitation of restricted areas. The extrapolation of the BIR as a paleozoogeographic and phytogeographic region, as proposed by Cartelle (1999), may be problematic. The BIR is a mosaic of microregions in a large territory with very distinct geographical complex domains and different climate conditions that cannot be condensed as it has been



Fig. 5. Reconstruction of the Late Pleistocene environment of Bahia State. Artist Júlia d'Oliveira.

considered. We reinforce the necessity of more works in these and other regions of the Brazilian Intertropical Region (BIR) and a bigger data set, focusing on larger collections and analysis of more species.

Hence, it is possible that the BIR: (1) could be larger than that proposed in previous models (*e.g.* Cartelle, 1999); (2) with other limits still unknown; or (3) even does not exist at all.

Moreover, we propose distinct paleoclimate conditions in Brazil during the Late Pleistocene (about 10.000 years BP). Our interpretations suggest distinct vegetation configurations in distant areas (northeast and mid-west of Brazil). Moreover, we suggest the existence during the Late Pleistocene of a moisture corridor from the Atlantic ocean reaching the mid-west and south of Brazil but excluding the northeast.

Conflicts of interest

We declare we have no competing interests.

Funding

Isotopic analyses were possible with funds from Conselho Nacional de Desenvolvimento Científico e Tecnológico [CNPq proc. 404684/2016-5]. Dating analyses were possible with funds from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) by the first author's PhD scholarship.

Acknowledgements

We are thankful to the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for first author's master's scholarship, for MATD research fellowship (PQ/CNPq 308122/2016-0) and for the financial support for isotopic analyses (Universal, proc. 404684/2016-5). We would also like to thank Júlia Oliveira and Gabriel de Carvalho for the paleoart reconstructions. We are grateful to Dr. Aline M. Ghilardi, Dr. Marcelo Adorna Fernandes, Dr. Ireneu Bianchini Junior and Dr. Felisa Smith for the critical review of the manuscript. We would also like to thank the Programa de Pós-Graduação em Ecologia e Recursos Naturais (PPGERN/UFSCar) for the financial support, which made it possible to carry out preliminary results of this work for scientific events. Thanks to the editor Dr. José Carrión, the reviewer Dr. Alex Hubble and the anonymous reviewer for the suggestions and constructive criticism that helped to improve the quality of this manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2019.105864.

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