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ISOTOPIC ANALYSIS ($\delta^{13}\text{C}$, $\delta^{18}\text{O}$) OF
PLEISTOCENE MEGAFUNA IN BRAZILIAN
INTERTROPICAL REGION: PALEOECOLOGICAL
AND PALEOENVIRONMENTAL
INTERPRETATIONS

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Profa. Dra. Mirian Liza Alves Forancelli Pacheco

Remember when you were young?

You shone like the sun

Shine on, you crazy diamond!

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RESUMO

A partir de reconstrução paleoecológica baseada em análises isotópicas de carbono nos estados da Bahia e Mato Grosso do Sul, este recentemente inserido na Região Intertropical Brasileira (RIB), foi possível inferir questões ecológicas de megamamíferos dessas áreas, tais como os recursos consumidos (plantas C₃ e C₄), largura de nicho e sobreposições de nichos entre espécies. A organização da dinâmica ecológica dos animais estudados em Mato Grosso do Sul é revelada com *Holmesina paulacoutoi* ocupando a maior largura de nicho dentre os indivíduos com uma dieta equilibradamente balanceada, enquanto *Toxodon platensis* é o de nicho mais estreito, apresentando alto consumo de gramíneas C₄. *Glyptotherium* sp. e *Eremotherium laurillardi* apresentaram dietas balanceadas de plantas C₃ e C₄. No estado da Bahia, *N. platensis* apresentou a maior largura de nicho, com dieta mista, e *Equus neogeus* a mais estreita, com dieta composta exclusivamente por gramíneas C₄. Consequentemente, o valor de sobreposição de nicho desses dois organismos é o mais baixo. *E. laurillardi* e *T. platensis* apresentaram dietas balanceadas, com predominância de plantas C₃, enquanto *Palaeolama major* predominou de gramíneas C₄. Os valores de oxigênio mostraram uma diferença climática relevante em ambas as áreas, podendo inferir que na Bahia as condições ambientais eram mais secas e talvez mais quentes do que no Mato Grosso do Sul durante algum momento do Pleistoceno Superior. Dentro de uma notória diferença no comportamento alimentar encontrada em uma das espécies em comum de cada área de estudo (*T. platensis*), é reconhecida a grande plasticidade ecológica dessa espécie, assim como é possível explorar possíveis pressões ecológicas e dinâmicas ambientais que ocorreram no Brasil durante momentos paleoclimáticos específicos do Pleistoceno Superior, caracterizando mudanças de comportamento e estratégias ecológicas das suas comunidades de megamamíferos.

Palavras-chave: Paleoecologia, Largura de nicho, Paleoclima, Estratégias ecológicas

ABSTRACT

By paleoecological reconstruction based on carbon isotopic analysis in Bahia State and Mato Grosso do Sul State, recently inserted in the Brazilian Intertropical Region (BIR), it was possible to infer ecological aspects of megamammals from these areas, as well as the resources consumed (plants C_3 and C_4), niche width and niche overlaps between species. The organization of the ecological dynamics of the animals studied in Mato Grosso do Sul State is related to *Holmesina paulacoutoi* with the highest niche width, with a balanced diet, while *Toxodon platensis* is the one with the narrowest niche width, presenting high consumption of C_4 grasses. *Glyptotherium* sp. and *Eremotherium laurillardi* showed a balanced diet of C_3 and C_4 plants. In Bahia State, *N. platensis* presented the highest niche width, with a mixed diet, and *Equus neogeus* the narrowest one, with an exclusive C_4 diet. Consequently, the niche overlap for these two individuals was the lowest. *E. laurillardi* and *T. platensis* presented mixed-feeding diets, with predominance of C_3 plants, while *Palaeolama major* had predominance of C_4 grasses. The oxygen values showed a relevant climatic difference in both areas, being able to infer that in Bahia State the environmental conditions were drier and hotter than in Mato Grosso do Sul State, during some age of the late Pleistocene. Within a notorious difference in the feeding behavior found in one of the common species of each locality (*T. platensis*), the great ecological plasticity of this species is recognized, as well as it is possible to explore possible ecological pressures and environmental dynamics that occurred in Brazil during specific paleoclimate moments in the late Pleistocene, characterizing behavioral changes and ecological strategies of its megamammal communities.

Keywords: Paleoecology, Niche width, Paleoclimate, Ecological strategies

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1 CHAPTER 1: INTRODUCTION

1.1. Pleistocene South American megafauna

The Pleistocene epoch is within the Quaternary period (Figure 1), the present period of Earth's life. Pleistocene embraces the last 2.6 million of years until ~11 thousand years, what brand the Pleistocene-Holocene transition. During Quaternary, life documented high diversity of landscapes, tectonic, geographic, environmental and climate changes (Ortiz-Jaureguizar & Cladera, 2006; Ehlers et al., 2011; Bacon et al., 2016), and the origin and evolution of *Homo sapiens* (e.g. Stringer et al, 2016). Diversity of megamammals throughout America, pre-historic human migrations to America, they coexistence with megafauna and the recent extinction of this represented fauna are still subject of researches and debates (e.g. Dillehay, 2002; Barnosky et al., 2004; 2016, Haynes, 2018; Smith et al., 2018).

Along the Cenozoic era, South America was mostly of time an island and it resulted in characteristic biotas and endemic species of this continent. Some of the most important biogeographic events that occurred in Cenozoic South America and originated peculiar flora and fauna were the disconnection with Antarctica, sea-level changes and formation of the Isthmus of Panama (Ortiz-Jaureguizar & Cladera, 2006; Prevosti & Forasiepi, 2018). Connection of North and South America, due to the Isthmus of Panama, portion of land that linked the continent around ~3.5–2.8 million of years during the Late Pliocene (Webb, 1985, 1991; Bacon et al., 2015; O'Dea et al., 2016) was crucial for diversity of American mammals and ecological dynamics of each community. Several taxa migrated from North to South America and vice versa. This important event of dispersion is named “the Great American Biotic Interchange” – GABI (Simpson 1980; Webb 1985).

Some of South American mammals which migrated to North America are the extant armadillo *Dasypus novemcinctus* Linnaeus, 1758 and the extinct ground sloth *Megalonyx* Harlan 1825 and *Glyptodon* Owen 1939. From North to South America can be list the feline *Smilodon* Lund 1841, the artiodactyl *Palaeolama* Gervais 1869 and the gomphothere *Cuvieronius* Osborn 1923. Besides the role on the transition of land-mammal species, the GABI was also important for other taxa migrations, like reptiles, amphibians (Vanzolini & Heyer

1985) and flightless birds (Pelegriin et al., 2018), as well as for oceanic circulation, climate and atmospheric contexts.

Representatives of the Brazilian Pleistocene megafauna were initially and deeply studied by Lund (e.g. Lund 1840) and Paula Couto (e.g. Paula Couto 1979). Individuals belonging to the term of “megafauna” are basically classified about its size (body mass > 44 kg Barnosky et al., 2004, body mass > 1000 kg; Prevosti & Vizcaíno 2006). Causes of its extinction in American continent is very discussed, with most notorious possibilities explained by climate change (e.g. Rabanus-Wallace et al., 2017), such as expansion of humid forests characteristic of Holocene (De Vivo & Carmignotto, 2004), human interaction (Fariña et al., 2014), and combination of them (Barnosky & Lindsey, 2010; Haynes, 2018). South America experienced the major loss of animal taxa (Barnosky et al., 2004), losing entire orders, such as Notoungulata and Litoptern: ungulates who disappeared and left no line of descendants which we can compare and restore its ecology.

Consequences in modern ecosystem are also debated. These megamammals played an important role on landscape structure and ecosystem functions (Bakker et al., 2015; Barnosky et al., 2016), on nutritional composition of soil, water and atmospheric (Doughty et al, 2013; 2016) and its absence certainly affected ecologically the planet local, regionally and globally (Smith et al., 2015; Malhi et al., 2016; Galetti et al., 2017; Onstein et al., 2018).

Animals studied here (Figure 2) are all large-bodied herbivorous mammals, from orders still extant to others completely extinct. Compose this work the giant ground sloth *Eremotherium laurillardii* Lund 1842, with a Panamerican distribution (Cartelle & De Iuliis, 1995), the giant armadillo *Glyptodon* sp. and its relative *Holmesina paulacoutoi* Cartelle and Bohorquez 1985, the camelid *Palaeolama major* Liais 1872, the horse *Equus (Amerhippus) neogeus* Lund 1840, and the extinct proboscidean *Notiomastodon platensis* Ameghino, 1888. All individuals are well or new already known for the Brazilian Intertropical Region (BIR), as well as others regions in South America (e.g. Prado et al., 2011; Dantas et al., 2013b).

Phanerozoic	Cenozoic	Quaternary	Holocene
			Pleistocene
		Neogene	Pliocene
			Miocene
		Paleogene	Oligocene
			Eocene
	Mesozoic	Cretaceous	
			Jurassic
			Triassic
	Paleozoic	Carboniferous	
Devonian			
Silurian			
Ordovician			
Cambrian			
Precambrian	Proterozoic		
	Archean		

Figure 1. Geological table with eras, periods and epochs within Quaternary. Adapted from International Chronostratigraphic Chart (2018).

XENARTHRA	NOTOUNGULATA	PROBOSCIDEA
TARDIGRADA	TOXODONTIA	Gomphotheriidae
Megatheriidae	Toxodontidae	<i>Notiomastodon platensis</i>
<i>Eremotherium laurillardii</i>	<i>Toxodon platensis</i>	
CINGULATA	ARTIODACTYLA	PERISSODACTYLA
Glyptodontidae	TYLOPODA	Equidae
<i>Glyptodon</i> sp.	Camelidae	<i>Equus neogeus</i>
	<i>Palaeolama major</i>	
Pampatheriidae		
<i>Holmesina paulacoutoi</i>		

Figure 2. List of species studied: paleontological systematic.

1.2. Brazilian Intertropical Region

The Brazilian Intertropical Region (BIR) was initially defined by Cartelle (1999) as a zoogeographic region which includes 12 Brazilian states, from northeast of country: Bahia (BA), Sergipe (SE), Pernambuco (PE), Alagoas (AL), Paraíba (PB), Rio Grande do Norte (RN), Ceará (CE), Piauí (PI), southeast of country: Minas Gerais (MG), Espírito Santo (ES), Rio de Janeiro (RJ), and central-west of country: Goiás (GO). Current ecosystem of these regions is Cerrado *stricto sensu* (dry/wet season's alternation) and Caatinga, warm and dry ambient. These phytophysiognomies are currently more similar to savannas, and it is presumed that along the Pliocene it were an open dry Savanna-like ambient.

Cartelle defines BIR as a region with presence of autochthonous (endemic of intertropical region) and allochthonous (originated in temperate regions) Pleistocene megamammals (20,000–10,000 years BP). Some of autochthonous species are *Eremotherium laurillardi* Lund 1842 and *Holmesina paulacoutoi* Cartelle and Bohorquez 1985, and some of allochthonous species include *Toxodon platensis* Owen 1837, *Equus (Amerhippus) neogaeus* Lund 1840, and *Palaeolama major* Liais 1872, all specimens studied in this work.

São Paulo (SP), the only southeast' state of Brazil excluded in BIR, is considered by Cartelle (1999) and Ghilardi et al. (2011) as a transition zone – with presence of species from BIR and from the Pampean region (Rio Grande do Sul – Brazil, Uruguay and Argentina), two different climatic and ecological areas. Oliveira et al. (2017) highlights the taxonomical affinity of Mato Grosso do Sul State with BIR and São Paulo, and considered that Mato Grosso do Sul should be included in BIR, corroborated by Pansani et al. (2016). In this present work the BIR is considered including Mato Grosso do Sul State (Figure 3), and specimens of this State is, unprecedented, isotopically analyzed and ecologically discussed.

Recent studies have been made an effort to better understand the paleoecology of megamammals from BIR by diverse paleoecological methods and procedures, such as dental micro-wear (e.g. Asevedo et al., 2012) and stable isotopes (e.g. Dantas et al., 2013a; Pereira et al., 2013; França et al., 2014; Dantas et al., 2017).



Figure 3. Map of paleozoogeographic zones in Late Pleistocene of Brazil (grey). Brazilian Intertropical Region (BIR) in purple, Transition Zone (São Paulo) in orange and part of Pampean Region (Rio Grande do Sul, Uruguay and Argentina) in yellow.

1.3 The use of isotopes in Paleoecology: “you are what you eat”.

Stable isotope analysis in Paleoecology has been used to infer diet ($\delta^{13}\text{C}/\delta^{12}\text{C}$ and $\delta^{15}\text{N}/\delta^{14}\text{N}$) and paleoenvironment ($\delta^{18}\text{O}/\delta^{16}\text{O}$) by measures of fossil tissues and bones, due to composition of the life time diet of an organism reflected isotopically in they tissues (Phillips, 2012). Stable isotopes are different chemical forms of the same element, differing in number of neutrons in its nucleus and, consequently, displaying different atomic masses. Each isotope abundance of an element in nature is also different, heavier stable isotopes usually are rarer than lighter ones (Ben-David & Flaherty, 2012).

The use of stable isotope analysis can help to estimate proportional contributions of sources in an animal’s assimilated diet (Phillips, 2012), and it is been well working specifically in Mammalogy (Crawford et al., 2008; Ben-David & Flaherty, 2012). The isotopic signature is firstly captured in primary consumers and reflected along next trophic positions. When analyzed diet to estimate proportional contributions of each food resource is interpreted mathematical mixing models – a potential but limited tool that has been studied

and improved (Phillips 2012; 2014; Dantas et al. 2018, *submitted*). Besides diet, other's ecological factors has been under study based on stable isotopes analyses, such as niche dimensions, overlap niches and food web ecology (Bearhop et al., 2004; Newsome et al., 2007; Flaherty & Ben-David, 2010; Rossman et al., 2016).

It is common to use $\delta^{15}\text{N}$ isotopes for study of carnivore's diet and food webs (e.g. Kelly, 2000; Layman et al., 2007; Bocherens et al., 2016; Krajcarz et al., 2016), while for reconstruction of an herbivore diet it is only necessary $\delta^{13}\text{C}$ isotope values, given that these animals only consumed autotrophic beings (e.g, Cerling & Harris, 1999; Bocherens et al., 2017).

Recent works about Paleoeecology of Pleistocene megamammals of North (e.g. Bravo-Cuevas et al., 2017; Carlson et al., 2017) and South America (e.g. Domingo et al., 2012; Bocherens et al., 2016; Dantas et al., 2017; Mendoza et al., 2018) performing isotopes analyses insights paleoenvironment inferences such as diet, habitats and ecological niches, paleoclimate conditions and landscape configurations.

Most common use of stable isotopes in ecological studies is carbon ($\delta^{13}\text{C}$), a very effective mechanism to investigate diet. In terrestrial ecosystem, the main source of carbon is in photosynthesis performed by plants. This biochemical mechanism occurs in three different metabolisms: 1) Calvin Cycle in C_3 plants, 2) Hatch–Slack pathway in C_4 plants and 3) Crassulacean acid Metabolism (CAM) pathway in CAM plants. C_4 and CAM plants have advantage over C_3 plants in warmer, drier and more arid ambients, due to physiological adaptations. C_3 plants, in contrast, has advantage in tropical, humid and shaded ambients with low temperatures, such as forests (Ambrose & DeNiro, 1986).

C_3 plants are predominant in terrestrial vegetation and it includes trees, shrubs, herbs and some high-latitude grasses, while CAM, most succulents, is the smaller proportion (MacFadden et al., 1994; 1999; Kohn, 2010). Both C_3 and C_4 cycle pathways fractionate carbon in different forms, consequently, in different proportions. This way, is known an average of $\delta^{13}\text{C}$ for C_3 plants around -27‰ and $\delta^{13}\text{C}$ for C_4 plants around -13‰, while CAM plants present intermediate values (MacFadden et al., 1994; Koch 1998).

$\delta^{18}\text{O}$ values, usually measured in phosphate of tissue (PO_4^{3-}), are related to environmental and meteoric water, through oxygen breathed, drinking water

or water present in plants eaten (D'Angela & Longinelli, 1990; Bocherens & Drucker, 2013). Different $\delta^{18}\text{O}$ values can infer seasonal variations and temperature changes. More positive $\delta^{18}\text{O}$ values are associated with warmer temperatures, when more negative $\delta^{18}\text{O}$ values are associated with cooler temperatures (MacFadden, 1999; Bocherens & Drucker, 2013). As long as evapotranspiration is higher in C_4 plants (drier and warmer ambients), it is expected higher $\delta^{18}\text{O}$ values for grazers (Kohn et al., 1996), herbivore animals which live in open warm areas and ingest most of grasses and remove all biomass from vegetation in its feeding.

1.4. Regional Setting

1.4.1. Bahia State, Brazil

Toca dos Ossos Cave ($10^{\circ}55'52''\text{S}/41^{\circ}03'24''\text{W}$), is in the city of Ouro-lândia, in Bahia State, northeast of Brazil (Figure 4 and 5). The Cave has paleontological, archaeological and speleological importance, highlight the several findings of large mammalian fossil bones, such as edentulous mega herbivores (Cartelle, 1992). It is inserted in limestone mass of Caatinga Formation (Cartelle, 1992; Lessa et al., 1998), distributed along the Salitre, Verde and Jacaré river valleys, with fluvial origin (Cartelle, 1992). It is also noted that in this cave there is fossil associated with fluvial sediments, what can infer a deposition mechanism of fossil's input into the cave (Auler et al., 2003).

Its conduits occur on several levels, all of which contain fossils, with more complete skeletal presences at superior level and greater presence of disjointed pieces at bottom levels (Cartelle, 1992).

Fossils here studied (*Palaeolama major* and *Eremotherium laurillardii*) were collected by Mário A. T. Dantas, co-advisor of the author, and available to this study. Besides it, it was studied three other taxa whose isotopic values is already available in the literature: *Equus neogaeus* (MacFadden et al., 1999), *Notiomastodon platensis* (= *Stegomastodon waringi*; Sánchez et al., 2004; Mothé et al., 2012) and *Toxodon platensis* (MacFadden, 2005).

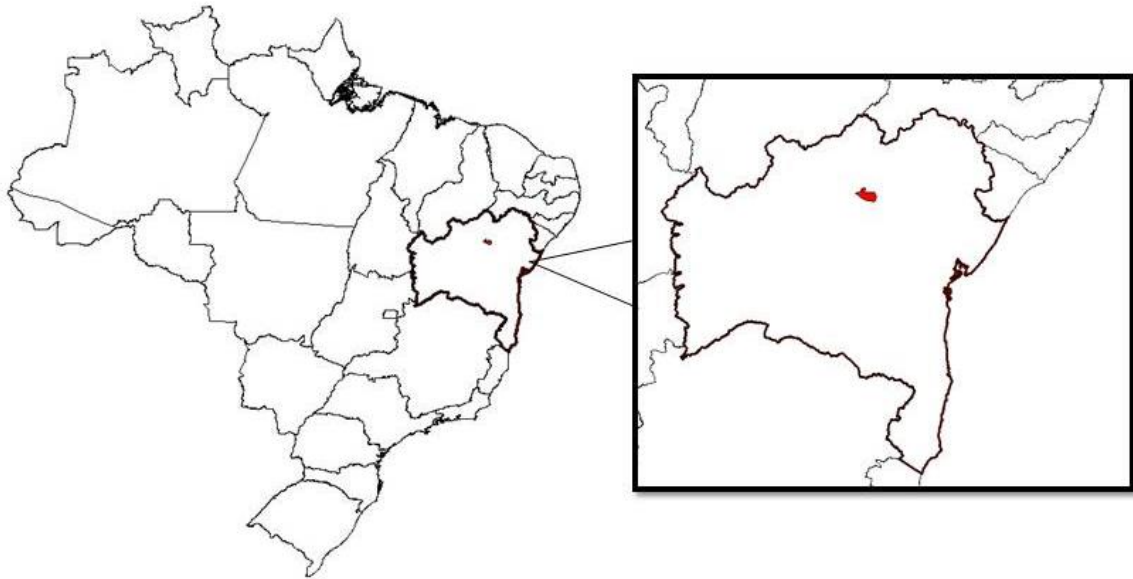


Figure 4. Brazil, highlighting Bahia State, in red Ourorândia municipality.

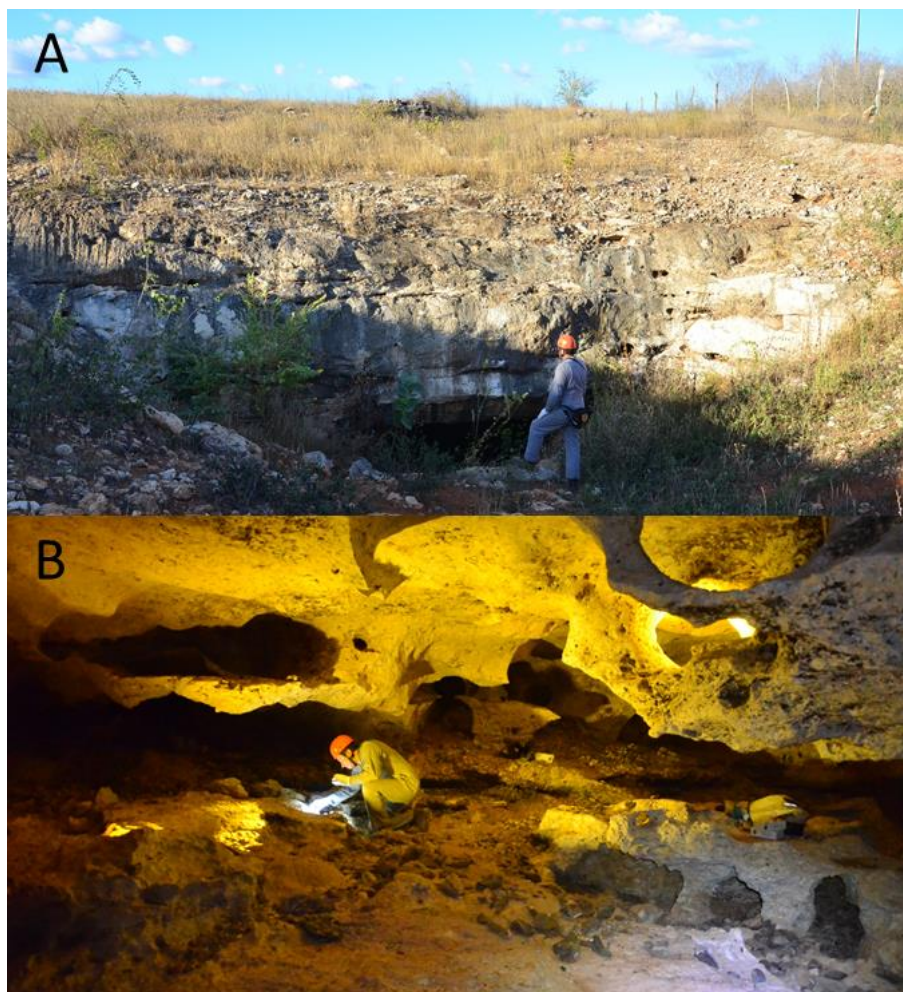


Figure 5. Toca dos Ossos Cave, outside (A) and inside (B) the cave. Photo: Ricardo Fraga (2015).

1.4.2. Mato Grosso do Sul State, Brazil

Miranda River (20°14'27.30"S/56°23'59.30"W) is a water course of Mato Grosso do Sul State, southwestern of Brazil (Figure 6 and 7). It is a tributary of the Paraguay River, a major river in south-central South America, and there's as a main affluent the Aquidauana River.

In Pantanal Formation, a Quaternary basin in Mato Grosso do Sul and Miranda River region, there are records of Pleistocene megamammals along its territory, including calcareous caves (Scheffler et al., 2010) and extant animals typical of open vegetation (Perini et al., 2009). For interpretations of specimens' fossil presents and its characteristics, a possible scenario for Pleistocene-Holocene in Mato Grosso do Sul (Serra da Bodoquena) was typical region with open vegetation and wetlands, with megafauna associated with medium and small sized mammal communities (Salles et al., 2006; Perini et al., 2009).

Besides Mato Grosso do Sul State has a large fossiliferous potential in Pleistocene megafauna, few studies on this locality has been made, and mostly of all focus on taxonomical and register of occurrences, missing paleoecological data for these animals. Here it is made the first paleoecological investigation based on isotopic analyses for megamammals from Mato Grosso do Sul State.

Fossils here studied were collected by this author and Alessandro Marques de Oliveira, in 2014 (Figure 7), thanks to solidarity of a resident who donated us the material, Manoel Messias A. Silva. Taxonomical identifications and other paleontological comments are found in Pansani et al. (2016).

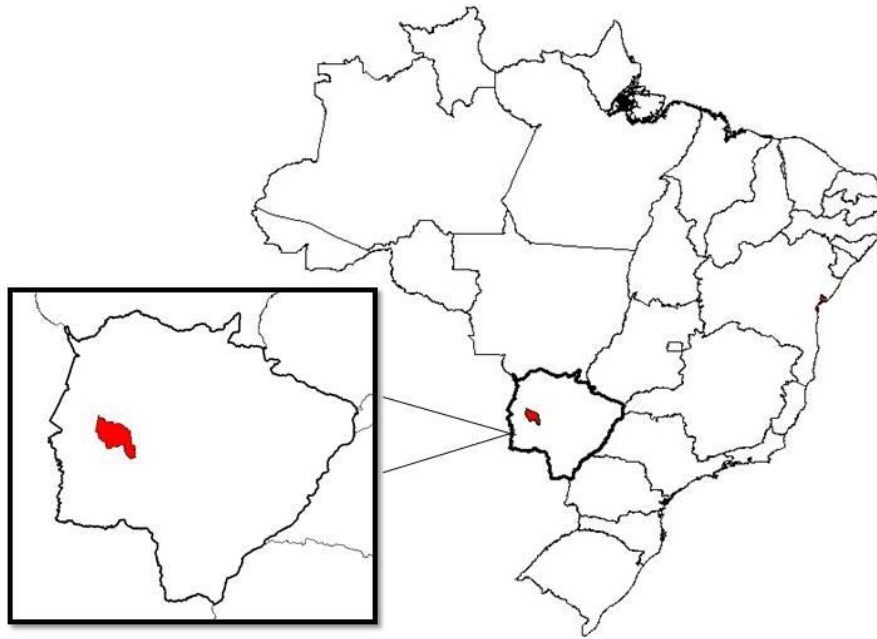


Figure 6. Brazil, highlighting Mato Grosso do Sul State, in red Miranda municipality.



Figure 7. Miranda River, locality where it was collected material here studied.
Photo: Pansani et al., (2016).

1.5. Perspectives, goals and approaches

In view of the context explored, this work recognizes the importance that Brazilian Intertropical Region (BIR) has in the understanding of Brazilian and South American Pleistocene megamammals. Owing Mato Grosso do Sul State had recently been added to this paleobiogeography region, and due to its few paleoecological and none isotopic studies of its paleofauna, the first purpose of this work was to generate isotopic data for its megamammals, cooperating with the knowledge of ecological aspects of the megafauna from this region and the environment where they lived. Additionally, do the same to megamammals from Bahia State (by new and already available taxa), and finally compare these two localities, in terms of paleoclimate conditions and feeding behavior of similar species.

To examine if these both regions was similar or different in paleoclimate and paleoecological aspects, the main goal of this work is to test the hypotheses that (1): the diet behavior of megamammals species from Mato Grosso do Sul State was likely than megamammals species from Bahia State, especially the same individuals present in both areas (none or few differences), and (2): the climate conditions (temperature, humidity) was similar in both areas at some age during the late Pleistocene, once these two areas are within a greater paleobiogeographic region (the Brazilian Intertropical Region).

For this purpose, analysis and interpretations were based on stable isotopic techniques and mathematical and ecological models, thanks to possibility of send the material to Center for Applied Isotope Studies, University of Georgia, and thus possible to explore the results obtained through an isotopic calculation methodology where it is analyzed the proportion of two resources (C_3 and C_4 plants) in herbivorous diets.

This work was submitted as a paper (Chapter 2) to the scientific journal "Palaeogeography, Palaeoclimatology, Palaeoecology" in November 2018.

1.6. General considerations

Carbon carbon isotopic analyses of fossil tooth and bones of megamammals from two localities in the Brazilian Intertropical Region (BIR): Mato Grosso do Sul and Bahia States, indicate a predominantly mixed-feeding diet style for mainly individuals recovered in both localities, including C_3 and C_4

plants. Highlights the diet of *T. platensis*, which is balanced C₃/C₄ mixed in Bahia State, but predominantly C₃ in Mato Grosso do Sul State. This pattern may indicate a good adaptation owing to different landscape configurations, in terms of vegetation, in both areas. This species appears to have had an ecological flexibility and plasticity, being able to exist in environments despite the unavailability of certain food items or other possible ecological pressures. And with this advantage, it's questionable if only climate change has been able to cause the extinction of these organisms (megafauna). And if so, how drastic it should have been. Although this is a first step with a low N, our results and interpretations proposes that studies with a bigger set of data and locations in the BIR should be performed. A better understanding of the paleoecology of these megamammals in the late Pleistocene-early Holocene can represent important information when trying to elucidate paleobiogeographic patterns in the distribution of megamammals in Brazil and South America.

Moreover, there is a noteworthy difference in average oxygen values, higher in specimens from Bahia State when compared with those of Mato Grosso do Sul State, suggesting a colder and wetter climate for Mato Grosso do Sul State and warmer conditions for Bahia State. Different feeding diet behaviors were observed for *T. platensis*, which presented a diet consisting of predominantly consumption of C₄ grasses in Mato Grosso do Sul State, while in Bahia it presented a consumption of both resources (C₃ and C₄ plants). This notorious difference found in each region for this species can reflect casual ecological pressures or environmental dynamics that occurred on the environment, resulting in behavior changes and ecological strategies.

Niche width for Bahia State show *E. neogeus* as a specialist grazer, with lowest niche width. All other species are generalists with intermediate niche widths. *N. platensis* has the broadest niche width (Figure 7). In Mato Grosso do Sul State, a role of specialist is performed by *T. platensis*, with the lowest niche width. Other species are generalists with similar broad niche widths (Figure 8).

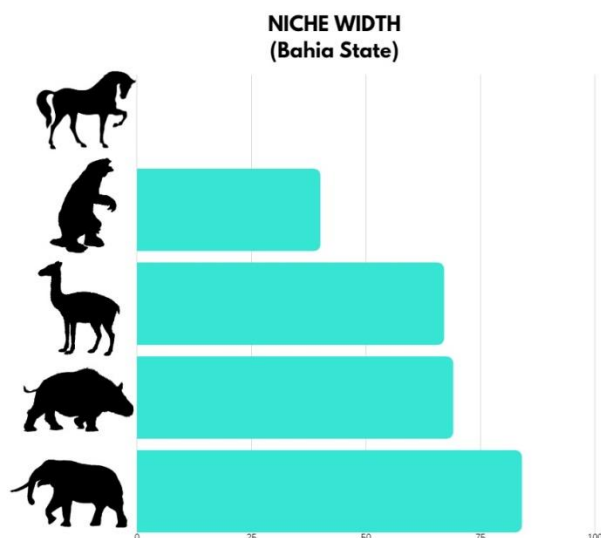


Figure 8. Niche width for specimens from Bahia State. *E. neogeus* ($BA = 0$), *E. laurillardii* ($BA = 0.40$), *P. major* ($BA = 0.67$), *T. platensis* ($BA = 0.69$) and *N. platensis* ($BA = 0.84$).

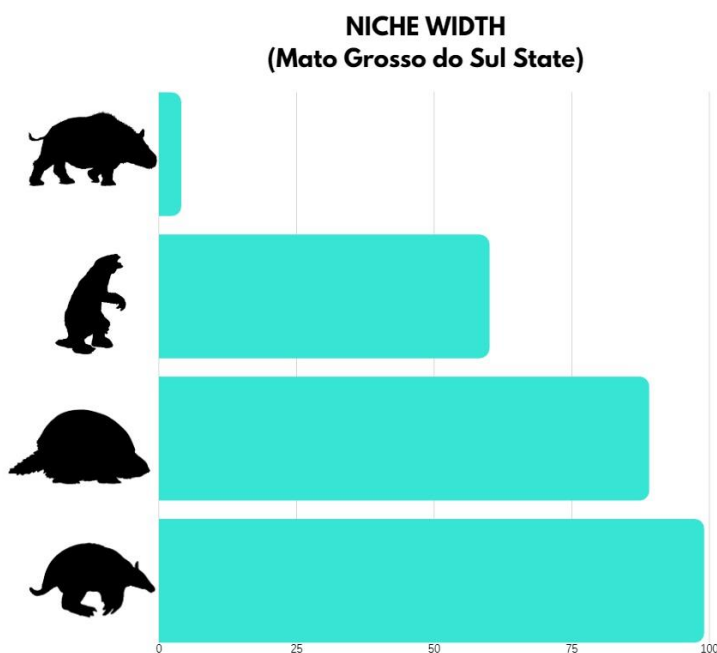


Figure 9. Niche width for specimens from Mato Grosso do Sul State. *T. platensis* ($BA = 0.04$), *E. laurillardii* ($BA = 0.60$), *Glyptotherium* sp. ($BA = 0.89$), *H. paulacoutoi* ($BA = 0.99$).

Deepening the possibilities of the results from this work by oxygen analyses, we can also suggest the possibility that Mato Grosso do Sul State acted as a refuge area or a contact zone during the late Pleistocene, during moments of alternation of wet and dry climates in the tropical regions, especially

for the northeast of the BIR. Based on the refuge theory (Haffer 1969), in front of climate fluctuations, forests retreated to small areas with constant humidity and geographical isolation during the Quaternary Ice Ages in South America (e.g. Ab'Sáber, 1977, 2006). It is possible that mammal individuals migrated from northeast of BIR, a region highly influenced by the intertropical climate fluctuations at late Pleistocene (Ab'Sáber, 1957), during drier and warmer conditions and periods of reduced rainfall in the northeast to areas of most moisture, such as the Amazonia Basin (e.g. Haffer 1969) and probably the Midwest Brazil – Mato Grosso do Sul State included (Barbosa et al., 2012; 2016). The suggestion of a possible route of migration to this geographic area (acted like a refugee area) can be reasonable and supported when compared to the late Pleistocene of Pampean region migration - when it is possible that species migrated into Intertropical regions due to adverse and extremes climate conditions in the south Pampean (e.g. Prado et al., 1987, Tonni et al., 1999).

Through the scenario explored above, it is possible to infer that these megamammals from Mato Grosso do Sul and Bahia States lived in a mosaic of a diverse landscape, composed by dry grasslands and leafy vegetation, but different climate patterns. We reinforce the necessity of more studies in these and other areas within the Brazilian Intertropical Region (BIR), a bigger set of data focusing on larger collections and paleoecological analysis of new species, and future dating.

The inferences of this study presents unpublished data for the region of Mato Grosso do Sul State, in the Brazilian Intertropical Region, and highlights a paleoenvironmental and paleoecological variability within the Brazilian Intertropical Region. Besides to point out the importance of deepening the paleoecological studies in this region, raises the question if the sharing of species is enough to define the BIR regions, as well it is currently defined. Similar studies in even other Brazilian sites (outside the BIR) may contribute to the refinement of paleobiogeographic delimitations.

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2 CHAPTER 2: SCIENTIFIC PAPER

This chapter is the paper submitted for “Palaeogeography, Palaeoclimatology, Palaeoecology” journal (November 2018).

Isotopic paleoecology ($\delta^{13}\text{C}$, $\delta^{18}\text{O}$) of Late Pleistocene megafauna from Mato Grosso do Sul and Bahia (Brazilian Intertropical Region)

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Declarations of interest: none

Abstract

Eremotherium laurillardi, *Toxodon platensis*, *Notiomastodon platensis*, *Equus neogeus*, *Palaeolama major*, *Holmesina paulacoutoi* and *Glyptotherium* sp. are some of megamammals that inhabited the Brazilian Intertropical Region (BIR) during the Late Pleistocene. Isotopic Paleoecology (diet, niche width and niche overlap) of these specimens was assessed by $\delta^{13}\text{C}$ analyses. Our results suggest a generalist diet for most species. *E. laurillardi*, *H. paulacoutoi* and *Glyptotherium* sp. were balanced mixed feeders in Mato Grosso do Sul State, as well as *E. laurillardi* and *N. platensis* in Bahia State. *E. neogeus* and *P. major* were predominant grazers in Bahia State, with high consumption of C_4 grasses. A differential diet pattern was found for one megamammal species: *T. platensis*, a specialist grazer in Mato Grosso do Sul State but a mixed feeder in Bahia State. These results points out to the possibility of distinct ecological pressures or specific vegetation and climate conditions in both regions. Diet reconstructions ($\delta^{13}\text{C}$) for both localities in the BIR suggest an open savanna-like landscape with fragments of forest. $\delta^{18}\text{O}$ values revealed can distinct climate conditions in these areas, indicating wetter conditions for Mato Grosso do Sul State and corroborating the existence of a moisture corridor in central and southern South America. Also from this, our approach suggests that the definitions of BIR should be revised to include more refined climate data, and other zoogeographic regions around the world could consider the same.

Key words: isotopic analyses, megamammals, niche width, niche overlap, ecological strategies

1. Introduction

South American megafauna was originally composed of several endemic taxa (*e.g.* *Toxodon* Owen 1837, *Glyptodon* Owen 1839, *Holmesina* Simpson 1930, *Pampatherium* Ameghino 1875, *Glossotherium* Owen 1840, *Mylodon* Owen 1859, *Eremotherium* Spillmann 1948) and North American taxa (*e.g.* *Notiomastodon* Cabrera 1929, *Smilodon* Lund 1841, *Equus* Linnaeus 1758, *Palaeolama* Gervais 1869) which advanced to South America through a dispersion event known as Great American Biotic Interchange - GABI (Webb, 1985, 2006, Prado and Aberti 2014, Bacon et al., 2016). American megafauna greatly disappeared along with the Late Quaternary Extinctions - LQE (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).

Brazilian Intertropical Region (BIR; Figure 1) is a paleozoogeographic region defined by Cartelle (1999) that includes 12 Brazilian States and where dry seasonal forests and savanna-like environments persisted between 20,000 and 10,000 years ago. Recently, the BIR has been expanded to include Mato Grosso do Sul State, located in the Central-Western of Brazil, because of the discovery of many taxa common to both regions (*e.g.* Pansani et al., 2016; Oliveira et al., 2017). The Mato Grosso do Sul State is an important region for the study of the evolution, paleoecology, paleoenvironment and extinction of mammals because of its still understudied fossil richness, especially Quaternary megamammals (*e.g.* Salles et al., 2006; Perini et al., 2009; Oliveira et al., 2017) and the high diversity of medium and large bodied extant mammals (47 species, Tomas et al., 2017). Also, the present 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), thus an interesting place to investigate paleoecological aspects of extinct megamammals.

The feeding ecology and ecological dynamics of the Pleistocene megafauna of the Brazilian Intertropical Region have been recently studied based on different methodologies, including the study of stable isotopes (*e.g.* Asevedo et al., 2012; 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 informations 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 Drucker, 2013). This approach can help us better understand and corroborate studies on the evolution of megafauna and their ecological relation to the environment, often in combination with different methods, such as analysis of functional morphology, ecomorphology, palynology and paleobotanic (*e.g.* Van deer Hammen, 1974; Ferraz-Vincentini 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 plant community is the most sensitive indicator of climate in terrestrial environments, especially because it is deeply affected by climate conditions such as rainfall regimes (Feng et al., 2013), and the biodiversity responds to this (Norberg et al., 2012). Changes in disturbance regimes are a natural phenomenon in current ecosystems, but climate changes can show some ecological consequences (Dale et al., 2001), including the migration of tolerant species to specific areas and trophic cascades effects through bottom-up disturbances by complex interactions (Walther, 2010). The

understanding of in what manner climate affects modern vegetation can shed light on how climate affected vegetation changes in the past, using the reconstruction of paleodiet and paleoecology of extinct fossil species as paleoenvironmental proxies.

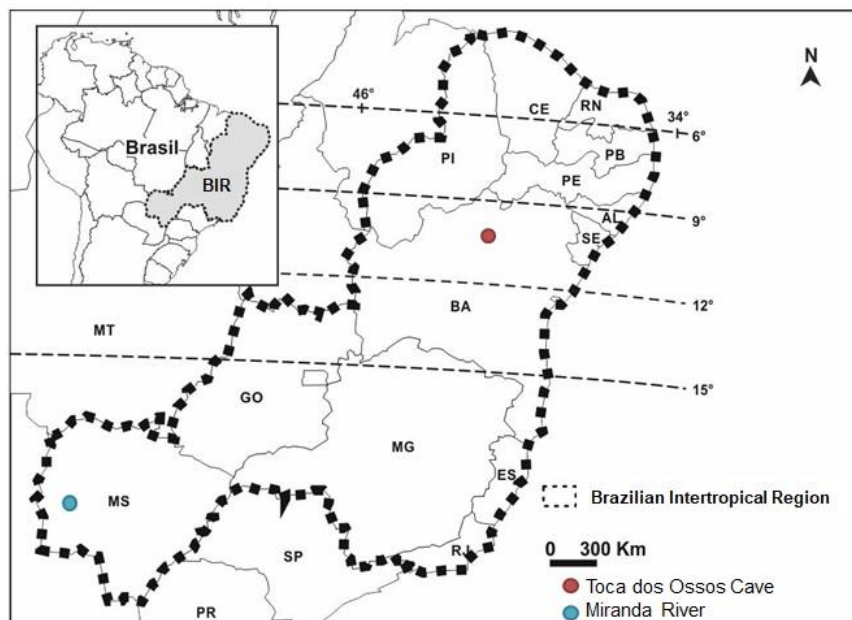


Figure 1. Brazilian Intertropical Region (BIR), accepted here including Mato Grosso do Sul State (adapted from Dantas et al., 2017).

The main goals of this work are: 1) to investigate the diet and ecological aspects of megamammals recovered from Miranda River in Mato Grosso do Sul State and Toca dos Ossos Cave in Bahia State based on $\delta^{13}\text{C}$ analyses; 2) investigate the climate condition of two areas within the Brazilian Intertropical Region based on $\delta^{18}\text{O}$ analyses and 3) to compare the paleoecology of the species analyzed and the paleoenvironmental conditions of both areas. Unfortunately, without the dating of material it is difficult to compare the results during an exactly age in the Pleistocene. However, due to the existence of dating of Late Pleistocene megamammals in regions in Brazilian Central-West, near Mato Grosso do Sul State (e.g. Goiás Paulo and Bertini (2015) and Mato Grosso Vialou and Vialou (2009), and for the cave where our specimens were collected

in Bahia State (e.g. Cartelle, 1992, MacFadden 1999, 2005) we consider here as a hypothesis that all species from Mato Grosso do Sul and Bahia State are from that same range of Late Pleistocene.

2. Material and methods

2.1. Samples choice and aspects

Samples of four species (*Eremotherium laurillardi* Lund 1842, *Glyptotherium* sp., *Holmesina paulacoutoi* (Cartelle and Bohorquez 1985), and *Toxodon platensis* Owen 1837) from Miranda River, Mato Grosso do Sul State (20°14'27.30"S/56°23'59.30"W), and two species (*Palaeolama major* Liais 1872 and *E. laurillardi*) from Toca dos Ossos Cave, Ouroelândia, Bahia State (10°55'52"S/41°03'24"W), both in Brazil, were analyzed for their isotopic ($\delta^{13}\text{C}$, $\delta^{18}\text{O}$) content.

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 State are allocated at "Laboratório de Estudos Paleobiológicos" (LEPBio), in Universidade Federal de São Carlos *campus* Sorocaba, Sorocaba, São Paulo, Brazil. Material of *E. laurillardi* (LEG 1636) from Bahia State and *P. major* (LPUFS 5219) are allocated at "Laboratório de Ecologia e Geociências" (LEG) of Universidade Federal da Bahia (IMS/CAT, Vitória da Conquista, Bahia, Brazil) and "Laboratório de Paleontologia" of Universidade Federal de Sergipe (LPUFS, São Cristovão, Sergipe, Brazil), respectively.

The fossils from the Mato Grosso do Sul State 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. In total, ten specimens were collected and identified, consisting of one calcaneus and 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, 2006; Scheffer et al., 2010; Oliveira, 2013; Oliveira et al., 2017) and riverbank outcrops along the Miranda River (Scheffer 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 low quantity of recovered specimens, the high representation of osteoderms and teeth is favoured by their greater numbers 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 taphonomic experiments involving fluvial transport (Aslan and Behrensmeyer, 1996).

The samples analyzed here from the Bahia State 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 has been found in the upper and lower levels of the cave. Isotopic data of some of these recovered taxa has been previously published and are included in the

present study (MacFadden et al., 1999; Sánchez et al., 2004; MacFadden, 2005), while a tooth referred to *Palaeolama major* and a tooth referred to *Eremotherium laurillardii* are here analyzed for the first time. 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 runoffs 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 flood prone areas, and a bias towards the preservation of larger and heavier bones probably due to selective transportation favouring the removal of smaller and lighter elements (Auler et al., 2006).

2.2. Isotopic Paleoecology

Analyses were conducted at the Center for Applied Isotope Studies, University of Georgia, USA. The hydroxyapatite was extracted from fractions of enamel (*T. platensis*, *P. major*), dentine (*E. laurillardii* from Bahia) and bones (*E. laurillardii* from Mato Grosso do Sul, *H. paulacoutoi* and *Glyptotherium* sp.). Although bone tissue is more susceptible to diagenesis, recent studies have shown that data extracted from it can be reliable, as well as that from dentine and enamel (Lee-Thorp and Sponheimer, 2003; MacFadden et al., 2010; Pérez-Crespo et al., 2012; Dantas et al., 2017).

Here, we used a technique that separates the bioapatite fraction from diagenetic carbonates, by utilizing diluted acetic acid and preparation of bone (Cherkinsky, 2009). To remove these diagenetic carbonate compounds the bone is soaked overnight in 1N acetic acid, then washed free of acetic acid by repeated decantation. Loose or extraneous material is discarded and the bone sample is dried at ~ 70°C.

After drying, a sample is selected for further preparation. The bone is gently

crushed to small fragments less than 1 mm but not to a fine powder, for further cleaning. The powdering of the poor preserved bone leads to completed dissolving collagen and destruction of structure bioapatite. The bone fragments are again reacted with 1N acetic acid in a 250-ml Erlenmeyer flask, periodically evacuated to remove air and/or CO₂ from micropores, after which the flask is returned to atmospheric pressure to force fresh acid into microspaces of the sample. This process of evacuation and repressuring is continued at about 20 minutes intervals until no substantial release of gas as fine foamy bubbles occurs, even at the vapour pressure of water. The process of evacuation and repressurization to atmospheric pressure should be repeated at least 4-5 times, the last reaction being overnight (20+ hours) under atmospheric pressure, because the reaction of acidification of bioapatite by acetic acid could continue in the vacuum.

Once the evolution of fine gas bubbles has ceased (virtually an end point to the reaction) it can be assumed that all secondary or surface exchanged carbonates have been removed. The completely cleaned bone sample is then washed free of acetic acid by repeated soaking and decantation with demineralised water and then vacuum-dried. The sample is now ready for isotopic analysis of carbon in bioapatite and for collagen extraction.

For analysis of carbon isotopes in bioapatite approximately 100-500 mg of the cleaned bone powder is transferred to a vacuum flask and evacuated to remove air. The chemically cleaned sample was then reacted under vacuum with 100% H₃PO₄ to dissolve the bone mineral and release carbon dioxide from bioapatite for carbon and oxygen isotope ratio analysis.

The released CO₂ is purified by cryogenic separation and collected in sealing tubes for AMS and stable isotope analyses. Bioapatite carbon content in modern bone is about 1% and about 0.8% in the modern enamel. However, in archaeological samples after

treatment with acetic acid this value should be in the range 0.4-0.7%; therefore 100 mg of bone should yield about 0.4-0.7 mg of carbon. If yield are much higher it is probable that diagenetic carbonates were not completely removed.

The stable isotope ratios $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ 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 ($\delta^{13}\text{C}$) 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 composition of animal's diet (Rundel and Ehlering, 1989; Clementz, 2012), dominated as C_3 plants (trees, shrubs, forbs, herbaceous dicotyledonous, leaves, fruits and high latitude and high-altitude grasses), C_4 plants (grasses and some monocotyledonous and pteridophytic trees from tropical/temperate environments) and CAM plants (succulent Crassulaceae).

Both C_3 and C_4 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 C_3 and C_4 plants can be observed, in which the average value of C_3 plants is -27 ± 3 ‰, in C_4 is -13 ± 2 ‰, and for CAM the values are intermediate between C_3 and C_4 (MacFadden et al., 1994; Koch et al., 1998; MacFadden, 1999; Dantas and Cozzuol, 2016).

The ^{13}C 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 usually value for megamammals studies: 14‰ (e.g. Cerling & Harris, 1999).

Informations uncovered by oxygen isotopic analyses ($\delta^{18}\text{O}$) can allow

interpretations of aspects of the abiotic environment, such as conditions prevailing in the environment (*e.g.* temperature, precipitation and humidity; MacFadden et al., 1999; Yann et al., 2013). The oxygen isotopes are incorporated into the tissues of animals through consumption of the available atmospheric oxygen, directly by drinking surface water or indirectly by eating plants (Ayliffe et al., 1992; Bryant and Froelich, 1995; Bocherens and Drucker, 2013).

Reference used for isotopic values were V-PDB ($\delta^{13}\text{C}$) and V-SMOW ($\delta^{18}\text{O}$) (Coplen, 1995). 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; and MacFadden, 2005). Suess Effect (+2%; Keeling, 1979) was considered to estimate the proportion of consumed food resources, because of the decrease of ^{14}C in atmospheric CO_2 due the high combustion emissions by fossil fuels.

Proportions were estimated through one isotope mixing models that include a refinement of proportion of food types resources using carbon and oxygen isotopic data:

$$\delta^{13}\text{C}_{\text{mix}} = \delta^{13}\text{C}_1f_1 + \delta^{13}\text{C}_2f_2 \quad (1)$$

$$1 = f_1 + f_2 \quad (2)$$

Where resources are represented by: $\text{C}_1f_1 = \text{C}_3$ plants, $\text{C}_2f_2 = \text{C}_4$ plants.

Niche breadth (B) of all the species was calculated by the Levins' (1968) measure, where p_i = resources consumed:

$$B = \frac{1}{\sum p_i^2} \quad (3)$$

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

$$B_A = \frac{B-1}{N-1} \quad (4)$$

The niche overlap of all species from each location was calculated considering Pianka's (1973) equation, where p_{ij} = sum of resources of one specie and p_{ik} = sum of resource of another species:

$$O_{jk} = \frac{\sum p_{ij} \cdot p_{ik}}{\sqrt{\sum p_{ij}^2 \cdot \sum p_{ik}^2}} \quad (5)$$

When the result of the equation is equal to zero (0), it is interpreted that there is no niche overlap. When the result is equal to one (1), it is interpreted that there is total overlap (*e.g.* Dantas et al., 2017). From intermediate values, it is possible to infer if there was low (<0.3), intermediate (0.30 < x <0.70) or high (> 0.7) niche overlap between the animals.

Table 2. Results of Paleoecology of megamammals from both localities within Brazilian Intertropical Region.

Locality/taxa	N	Pi		mean±s		B _A	O				
		C ₃ plants	C ₄ plants	δ ¹³ C (‰)	δ ¹⁸ O (‰)						
Toca dos Ossos/BA							<i>En</i>	<i>Np</i>	<i>Tp</i>	<i>Pm</i>	<i>El</i>
<i>E. neogaeus (En)</i>	2	0.00	1.00	1.4±0.42	30.03±0.81	0	-	0.83	0.47	0.93	0.20
<i>N. platensis (Np)</i>	2	0.40±0.16	0.60±0.60	-6.6±2.26	29.88±1.31	0.84	0.83	-	0.88	0.97	0.71
<i>T. platensis (Tp)</i>	2	0.65±0.24	0.45±0.24	-10.15±3.46	28.21±1.77	0.69	0.47	0.88	-	0.76	0.95
<i>P. major (Pm)</i>	1	0.28	0.72	-5.07	25.68	0.67	0.93	0.97	0.76	-	0.54
<i>E. laurillardi (El)</i>	1	0.83	0.17	-12.61	24.62	0.40	0.20	0.71	0.95	0.54	-
Miranda River/MS							<i>El</i>	<i>G</i>	<i>Tp</i>	<i>Hp</i>	
<i>E. laurillardi (El)</i>	1	0.75	0.25	-11.51	25.40	0.60	-	0.76	0.33	0.88	
<i>Glyptotherium</i> sp. (<i>G</i>)	1	0.38	0.62	-6.29	25.15	0.89	0.76	-	0.86	0.97	
<i>T. platensis (Tp)</i>	1	0.02	0.98	-2.76	25.70	0.04	0.33	0.86	-	0.73	
<i>H. paulacoutoi (Hp)</i>	1	0.49	0.51	-7.77	26.22	0.99	0.88	0.97	0.73	-	

Proportions of food resources (*pi* – C₃ plants and C₄ grass), isotopic values for δ¹³C (‰) and δ¹⁸O (‰), standardized niche breadth (*B_A*) and niche overlap (*O*) between the individuals of each site, for megamammals from Toca dos Ossos, Bahia State, and Miranda River, Mato Grosso do Sul State, localities within Brazilian Intertropical Region.

3. Results

Lowest $\delta^{13}\text{C}$ values in Mato Grosso do Sul and Bahia States were observed in *E. laurillardi* ($\delta^{13}\text{C} = -11.51\text{‰}$, -12.61‰ , respectively), while highest $\delta^{13}\text{C}$ values were found for *T. platensis* in Mato Grosso do Sul State ($\delta^{13}\text{C} = -2.76\text{‰}$) and *E. neogeus* in Bahia State ($\delta^{13}\text{C} = 1.4 \pm 0.42$; Table 1, Figure 2).

The proportion of resources consumed on the diet is interpreted as related to niche width, where *T. platensis* had higher consumption of C_4 grasses and a narrower niche width ($B_A = 0.04$) in Mato Grosso do Sul State. *E. laurillardi*, *Glyptotherium* sp. and *H. paulacoutoi* presented intermediate values of mixed balanced diets and consequently broader niche widths ($B_A = 0.60$, 0.89 and 0.99 , respectively). In Bahia State, *E. neogeus* had the lowest niche width among all species ($B_A = 0$), with an exclusive C_4 diet, followed by *E. laurillardi*, predominantly C_3 plant-diet ($B_A = 0.40$), and *P. major*, predominantly C_4 diet ($B_A = 0.67$). *T. platensis* and *N. platensis* presented balanced consumption of both resources and broader niche widths ($B_A = 0.69$ and 0.84).

In Mato Grosso do Sul State, all individuals presented isotopic oxygen values around 25‰ , a mean of $\delta^{18}\text{O} = 25.48 \pm 0.26\text{‰}$, while in Bahia State some species showed significantly higher oxygen values (e.g. *E. neogeus*, *N. platensis* and *T. platensis*) and a final mean of $\delta^{18}\text{O}$ also higher, around $27.66 \pm 1.29\text{‰}$.

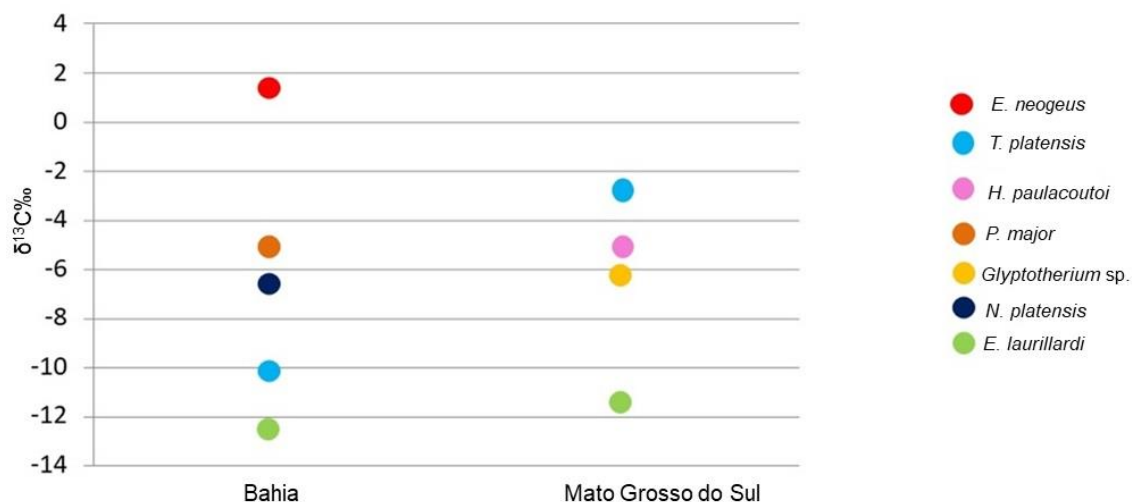


Figure 2. Scatter-plot of $\delta^{13}\text{C}$ values of the megafauna species from Bahia and Mato Grosso do Sul States.

4. Discussion

4.1. Isotopic Paleoecology ($\delta^{13}\text{C}$), niche breadth (B_A) and niche overlap (O)

Our results for Bahia State show *E. neogeus* as the most specialist species, with a restricted diet composed of C_4 plants, what can be problematic in competitive scenarios. Elseways, *N. platensis*, *T. platensis*, *E. laurillardi*, and *P. major* showed more flexible diets. Niche breadth showed lowest overlap for the horse *E. neogeus* with the giant ground sloth *E. laurillardi*, due to the high differential proportion of resources contribution on their diets. Otherwise, the highest overlap in Bahia State was between *N. platensis* and *P. major*, well sustained by their similar mixed diet with preference for C_4 grasses.

In Mato Grosso do Sul State, *Eremotherium laurillardi* and *T. platensis* occupy more differentiated niches, which facilitates possible coexistence of both species in this region. In meantime, *T. platensis* and *Glyptotherium* sp. occupy more similar niches.

Thus, if both species coexisted, and depending on their foraging behaviors, they could have competed for resources and have potentially caused an ecological competitive scenario.

E. laurillardi is commonly known 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 its wide distribution and good adaptation to diverse habitats. Our results are congruent with this hypothesis and suggest a generalist diet with preference for C₃ plants in both areas. In contrast, *T. platensis* show a curious pattern, having a mixed-feeding diet in Bahia State but a high consumption of C₄ grasses comprising almost all its diet in Mato Grosso do Sul.

A mixed feeding diet is often attributed to *T. platensis* in South America (*e.g.* MacFadden, 2005; Dantas et al., 2013; 2017), however this pattern of high consumption of C₄ grasses is unusual, and was already found in Southern Brazil (*e.g.* Lopes et al., 2013). It could be justified by food shortage or as a consequence of specific ecological pressures (*e.g.* competition with other species), possibly influenced by temperature 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 – 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 State indicate high ecology plasticity, being able to exist in different environments despite the unavailability of certain food items or other possible ecological pressures. This could represent important information when trying to elucidate paleobiogeographic patterns in the distribution of

megamammals in Brazil and even South America, once we can explore more regions and data.

In short, we present interpretations that corroborate some inferences for species recovered in Bahia State, for example, the higher $\delta^{13}\text{C}$ values referred to *E. neogeus* indicating a grazer C_4 diet (e.g. MacFadden, 1999; Dantas et al., 2017), but differ from what was expected for the other species. According to published studies for the Northeast Brazil (northern portion of BIR), a predominantly C_3 diet is attributed to *P. major*, which is characteristic of forest border areas or preference for shrubs in open areas (Marcolino et al., 2012). Our results showed a preference for C_4 grasses for this species, suggesting the occurrence of open areas.

Toxodon platensis, *N. platensis* and *E. laurillardii* are usually considered generalists, with diets composed of a mixture of C_4 (grasses and herbaceous) and C_3 (fruits leaves and barks) plants (MacFadden, 1994; MacFadden, 2005; Asevedo et al., 2012; Dantas and Cozzuol., 2016; Dantas et al., 2017), but for Toca dos Ossos, Bahia, *T. platensis* has already been considered a great consumer of C_3 plants (Dantas et al., 2017). Our unexpected results are the well-balanced diet for *T. platensis* in Bahia State but drastically focused on C_4 grasses in Mato Grosso do Sul State, depicting a higher niche width for *T. platensis* in Bahia State (Figure 3). *Notiomastodon platensis* is considered a C_4 grazer or a mixed feeder for some localities in northeast of BIR, including Toca dos Ossos, Bahia (Sánchez et al., 2004; Dantas et al., 2017), and our results corroborate mixed feeding for this taxon.

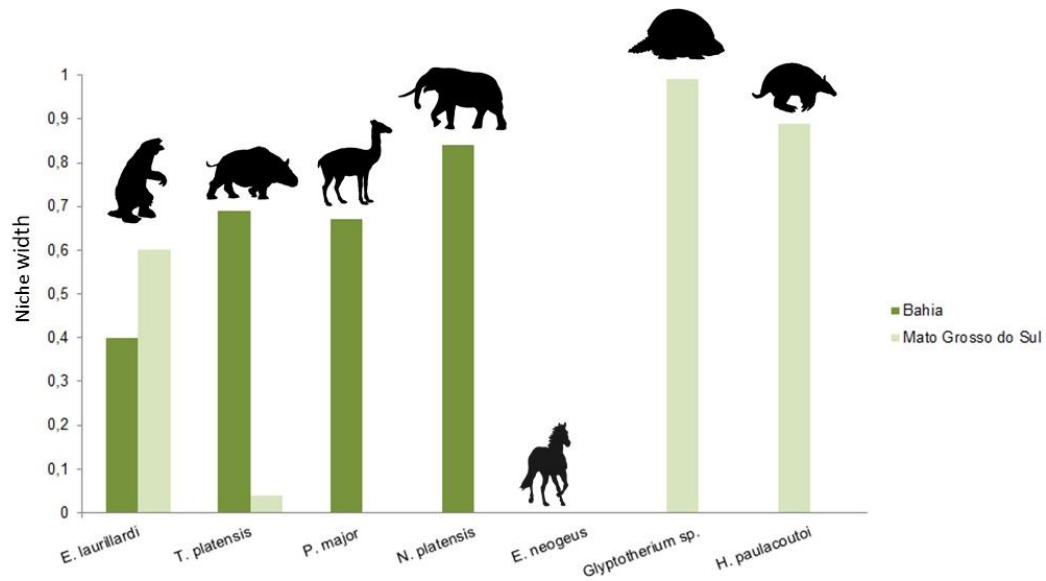


Figure 3. Isotopic niches width of the megamammals from Toca dos Ossos, Bahia State and Rio Miranda, Mato Grosso do Sul State.

Comparison of niche overlap between *E. laurillardi* and *T. platensis*, the species analyzed in both studied areas (Figures 4-5), shows that *E. laurillardi* and *T. platensis* had a lower niche overlap in Mato Grosso do Sul State and higher one in Bahia State.

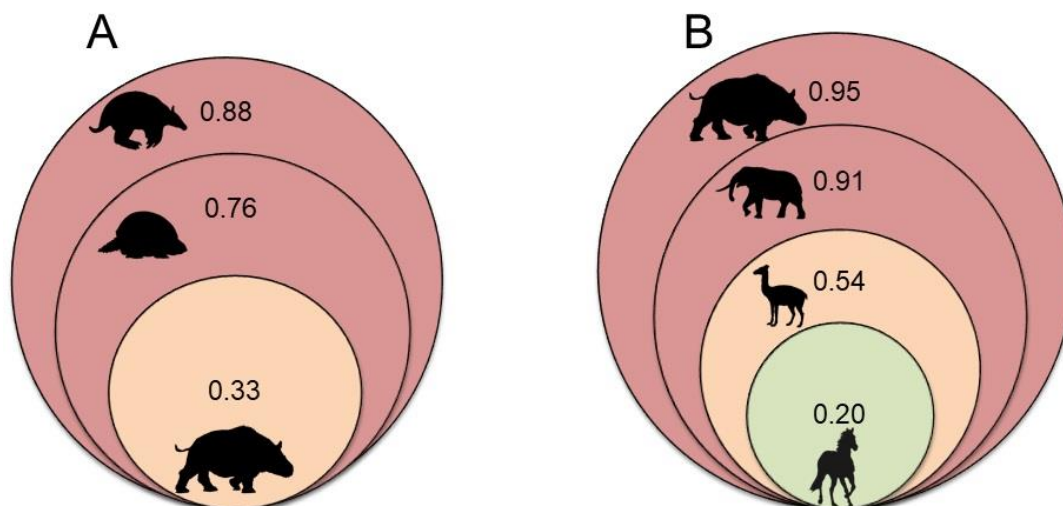


Figure 4. Niche overlaps for *E. laurillardi* in Mato Grosso do Sul State (A): *Ojk* with *T. platensis* = 0.33, *Ojk* with *Glyptotherium sp.* = 0.76 and *Ojk* with *H. paulacoutoi* = 0.88 and in

Bahia State (B): *Ojk* with *E. neogeus* = 0.20, *Ojk* with *P. major* = 0.54, *N. platensis* = 0.71, *Ojk* with *T. platensis* = 0.95. Niche overlap of *E. laurillardii* with *T. platensis* is narrower in Mato Grosso do Sul.

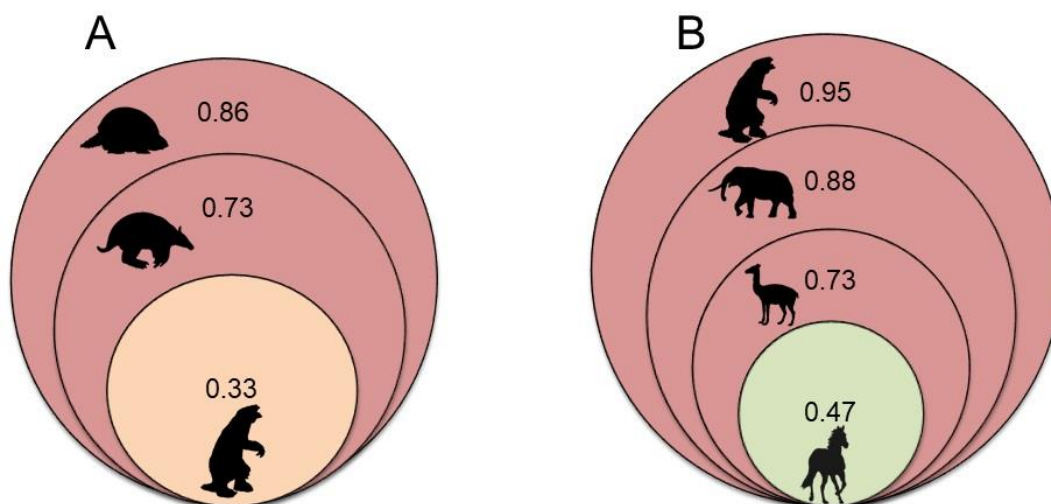


Figure 5. Niche overlaps for *T. platensis* in Mato Grosso do Sul State(A): *Ojk* with *E. laurillardii* = 0.33, *Ojk* with *H. paulacoutoi* = 0.73, *Ojk* with *Glyptotherium* sp. = 0.86, and in Bahia State (B): *Ojk* with *E. neogeus* = 0.47, *Ojk* with *P. major* = 0.73, *Ojk* with *N. platensis* = 0.88, *Ojk* with *E. laurillardii* = 0.95. Niche overlap of *T. platensis* with *E. laurillardii* is narrower in Mato Grosso do Sul.

4.2. Paleoenvironmental reconstruction

In Mato Grosso do Sul State, all individuals presented isotopic oxygen values ranging around 25‰, lower than the mean value found in Bahia, which could suggest that (1): Mato Grosso do Sul landscapes were more humid than those of Bahia during some period of the Pleistocene, or (2): that the megamammals from Mato Grosso do Sul State drank from rivers and lakes with low evaporation and consequently not enriched $\delta^{18}\text{O}$ waters.

Our results also seem to agree with previous studies that indicate the existence of a moisture corridor in this region based on studies of stalagmites (*e.g.* Novello et al., 2017). However, it is necessary additional studies and dating of 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 paleoclimatic 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 Mato Grosso do Sul individuals that are lower (Table 1), can (1): reflect paleoclimate differences between these localities, (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 Bahia State species, or (3): indicate distinct time periods with distinct isotopic compositions of the available local water for Bahia species. 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 the present study we unveil that perhaps the same faunistic composition in different geographical areas is not enough to delimit the RIB: one reason for this is that although the same animal was found in Mato Grosso do Sul and Bahia States (*T. platensis*), feeding behavior were different in each region, what could be the result of different climate patterns and vegetation configurations. Given these data, it is possible that the RIB could be larger than proposed in previous models (*e.g.* Cartelle 1999), have other limits still unknown, or even does not exist at all. It is necessary to reflect on the RIB definition and its limits in the light of standardized data access, and additional studies should be performed to evaluate these hypotheses, especially including other regions.

In short, our results corroborate a savanna-like vegetation with fragments of forests for both localities in the BIR region (Figure 6, 7), with a probable abundance of C₄ grasses in open landscapes, but wetter climatic conditions in Mato Grosso do Sul State.

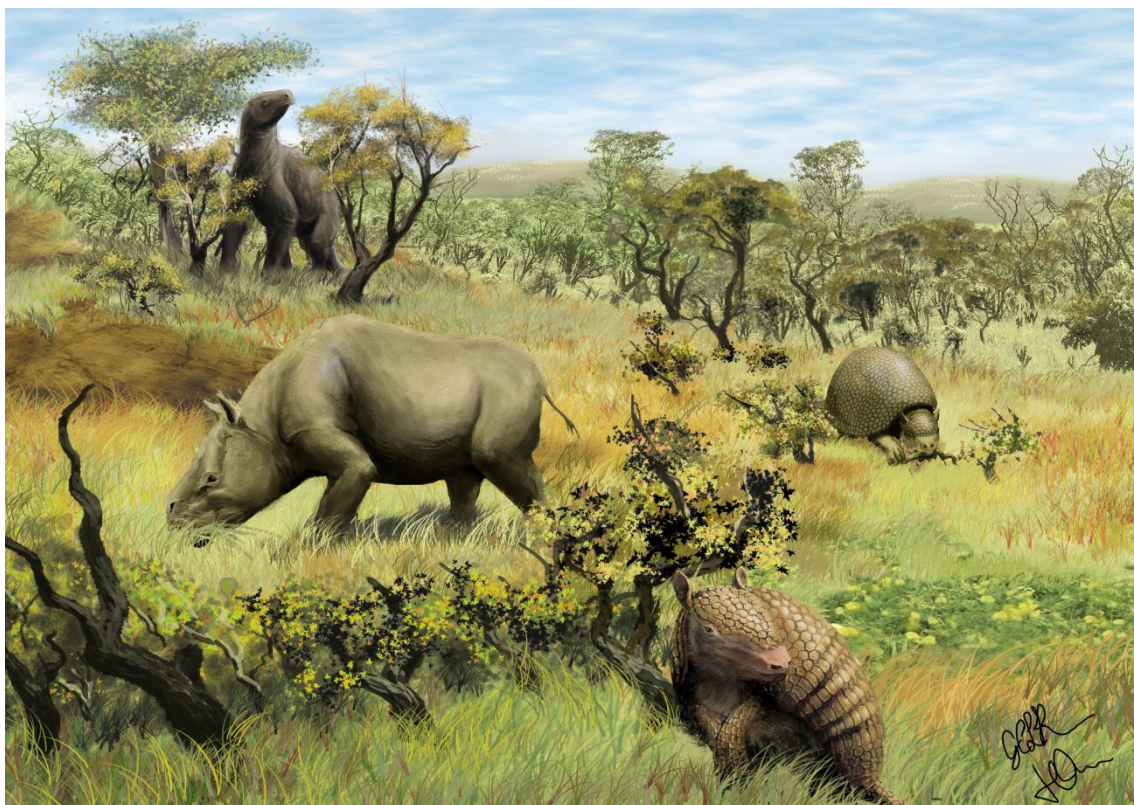


Figure 6. Reconstruction of the environment of Mato Grosso do Sul State. Art: Julia Oliveira (2018).

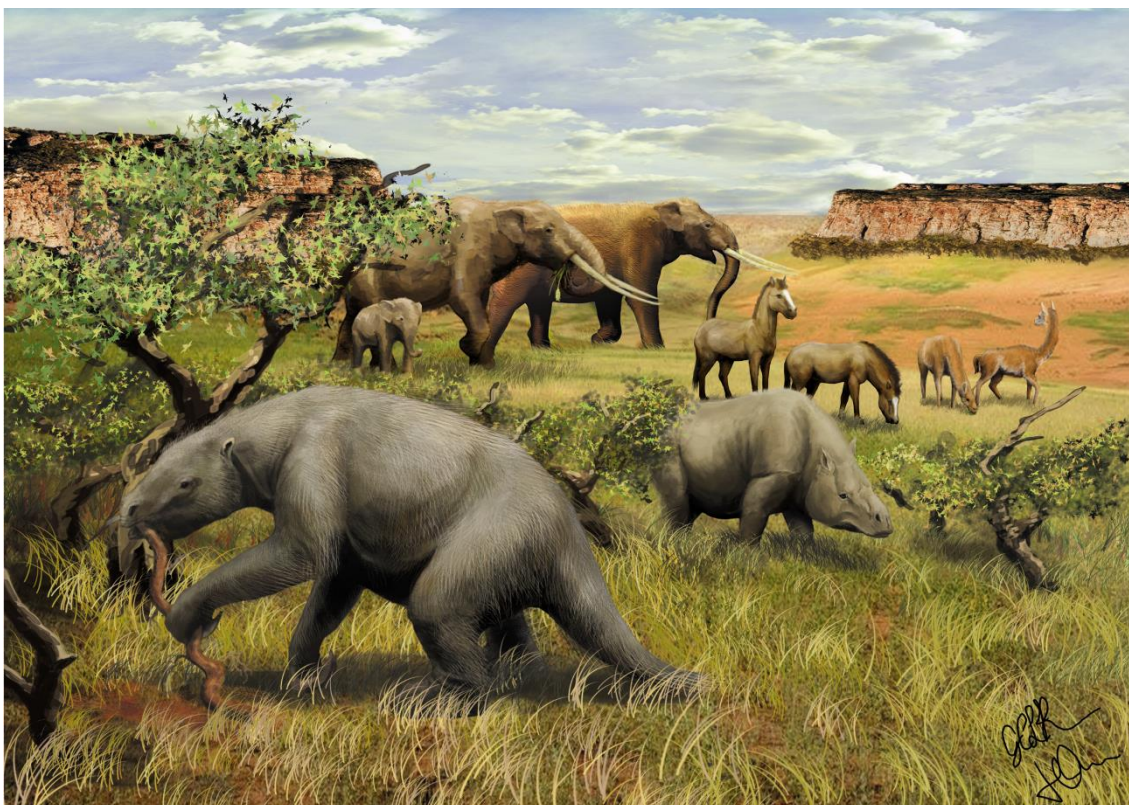


Figure 7. Reconstruction of the environment of Bahia State. Art: Julia Oliveira (2018).

5. Conclusions

Carbon isotopic analyses of fossil teeth and bones of megamammals from two localities in the Brazilian Intertropical Region (BIR), Mato Grosso do Sul and Bahia States, indicate two different feeding styles for the individuals recovered in both localities: a mixed feed diet, including C_3 and C_4 grasses, and a specialized grazing habit. Moreover, there is a noteworthy difference in oxygen values, higher in specimens from Bahia when compared with those of Mato Grosso do Sul, what can suggest wetter climate for Mato Grosso do Sul State and drier conditions for Bahia State, or differential enrichment in waters sources due to evaporation in Bahia State. Different feeding diets were inferred for *T. platensis* in each locality. In Mato Grosso do Sul State, *T. platensis* presented a diet consisting of predominant consumption of C_4 grasses, while in Bahia it

presented a balanced consumption of all resources. The notorious differences found in each region for this species can reflect (1): casual ecological pressures or environmental dynamics that occurred in its environments, resulting in behavior changes and ecological strategies or (2): opportunistic adaptation to different vegetation types in each area, what can be compared to latitudinal variations in diets of gomphotheres and horses across the Americas (*e.g.* MacFadden et al., 1999, Prado et al., 2001). Through this scenario, it is possible to infer that these megamammals of Mato Grosso do Sul and Bahia States lived in a mosaic of a diverse landscape, with forested environments and dry grasslands in savanna-like environments, especially in Bahia, and also stimulates the investigation of possibilities of ecological interactions that could influence their eating habits.

The extrapolation of the BIR as a phytogeographic region, as proposed by Cartelle (1999), may be problematic. We reinforce the necessity of more works in these and other regions of Brazilian Intertropical Region (BIR) and a bigger set of data, focusing on larger collections and analysis of more species.

The inferences of this study support significant paleoenvironmental and paleoecological variability within the Brazilian Intertropical Region and raises the question of if the sharing of species is enough to define paleobiogeographic regions. Similar studies in other areas may contribute to the refinement of paleobiogeographic delimitations.

Competing interests

We declare we have no competing interests.

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