Genesis and taphonomic biases of quaternary tank deposits of northeastern Brazil

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ABSTRACT

A taphonomic comparison among ten Quaternary tank deposits bearing megafauna remains in northeastern Brazil allowed the identification of four regional-scale taphonomic aspects controlled by climate seasonality: differential preservation of mega-mammal bones, poor physical integrity, spatial resolution (local) and time averaging (10^4 years). Sedimentary aspects, such as the high degree of packing of fossiliferous layer, indicate conditions of low clastic detrital sediment input in arid conditions. The correlation among geochronological data of tank deposits and paleoclimatic curves of northeastern Brazil suggest that the climate was arid/semi-arid characterized by seasonality between dry and rainy periods. Thus, we postulate the succession of the two paleoenvironmental and paleoecological scenarios during the Late Quaternary affectiing the formation of fossiliferous tank deposits: (i) the intensity and duration of arid periods led animals to search for water and food, and consequently, concentration and death near these water sources; and (ii) in the rainy season, carcasses, disarticulated and fragmented bones around these water sources were transported and accumulated through high-energy tractive flows, reworking previously buried skeletal material.

1. Introduction

The alternation between glacial and interglacial periods during the Quaternary has altered biomass composition and abundance in ecosystems in South America and other continents (Tonni et al., 1999). These climatic alternations that characterize the Late Pleistocene and Holocene overlap chronologically with the formation of fossil assemblages in tank deposits and extinction of large and mega-mammal fauna on the continent. In South America, two regions have a large abundance of megafauna fossil records: Argentine Pampa (see Tonni et al., 1999; Cione et al., 2003) and Brazilian Intertropical Region (BIR) (see Cartelle, 1999; Araújo-Júnior et al., 2017).

Tank deposits are among the main South American deposits containing fossil of Quaternary mammals. These are stratified sedimentary bodies that fill depressions on basement rocks in northeastern Brazil, with a great diversity of megafauna fossils when compared to other Brazilian deposits (Araújo-Júnior et al., 2013). Over the past two decades, the number of taphonomic analyses of Quaternary vertebrates in South America has increased (Auler et al., 2006; Tomassini et al., 2010; Tomassini and Montalvo, 2013), especially those focusing on tank assemblages (e.g. Santos et al., 2002; Alves et al., 2007; Araújo-Júnior et al., 2013, 2015; 2017; Faria et al., 2013). They have allowed us to understand important paleoecological and paleoenvironmental aspects, as well as the occurrence of taphonomic biases in the genesis of these fossil accumulations.

Fossiliferous tank deposits preserve skeletal remains of several representatives of the Quaternary megafauna, such as large ground sloths, glyptodonts, mastodons, toxodonts, saber-toothed cats and macraucheniids (Bergqvist et al., 1997; Cartelle, 1999). In some small and mid-sized mammalian deposits, crocodiles, lizards, birds and anurans are also preserved (Araújo-Júnior and Moura, 2014). The deposition of these deposits has been related to the action of debris flows and flash floods (Araújo-Júnior et al., 2013, 2015; 2017; Faria and Carvalho, 2019).

This type of fossiliferous deposit provides one of the best evidences for understanding paleoenvironmental and paleoecological aspects of the Brazilian Intertropical Region (BIR) during the Late Quaternary. However, these deposits preserve different paleoecological aspects of ancient ecosystems (Araújo-Júnior et al., 2011), where these differences began to be examined in last decades through taphonomic studies (Santos et al., 2002; Alves et al., 2007; Araújo-Júnior et al., 2013, 2015; 2017; Faria and Carvalho, 2019).

Currently, tank deposits have revealed a wide array of taphonomic processes responsible for the accumulation and preservation of fossils (e.g. Araújo-Júnior et al., 2013; 2015, 2017; Faria et al., 2013). Therefore, comparative taphonomic analyses among tank deposits may be crucial to better understand the paleoenvironmental and paleoecological scenarios responsible for the accumulation and preservation of skeletal remains. In this study, we present the results of taphonomic and geochronological analyses on a regional scale, which refines

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the knowledge on paleoecological and paleoenvironmental contexts of fossiliferous tank deposits in BIR.

2. Materials and methods

2.1. Comparative analyses

We performed a comparative taphonomic analysis of ten fossiliferous tank deposits using taphonomic data available in the literature (Fig. 1 and Table 1). The following taphonomic attributes taken into account: taxonomic diversity (Eberth et al., 2007), types of transport, degrees of spatial resolution (Behrensmeyer and Hook, 1992), degree of packing (Holz and Simões, 2002), degrees of physical integrity (Behrensmeyer, 1991), and sedimentological aspects of the fossiliferous layer.

Besides, deposits 1–7 (see Fig. 1 and Table 1) were compared using multivariate statistical analyses (cluster, correspondence, and principal component analyses). They were selected because their authors follow the same methodology of identification and quantification of taphonomic signatures. The taphonomic attributes avaluated in the multivariate statistical analyses were: degree of articulation and physical integrity (Behrensmeyer, 1991), weathering stages (Behrensmeyer, 1978), abrasion (Shipman, 1981), biological alterations and Fluvial Transport Index (FTI; Frison and Todd, 1986). A data matrix with the attributes described above was elaborated using their percentage values for each fossil deposit and, then, it was submitted to a cluster analysis (Q- and R-modes) using the simple arithmetic method of weighted average pairs (UPGMA) and Euclidean distance.

In the cluster among paleontological sites (Q-mode), fossiliferous deposits were clustered by their similarity in terms of taphonomic signatures in order to identify different taphonomic settings. In the R-mode analysis, the categories of taphonomic features were grouped based on the similarities of the percentages with which they occur among paleontological sites. In both analyses, we performed the bootstrap test (N = 1000) to evaluate the consistency of the clusters.

The same matrix was submitted to correspondence and principal component analyses. It was used correspondence analysis to identify x^2 distances among paleontological sites, observing which taphonomic attributes are intrinsic and extrinsic. According to Hammer (2013, pg. 97) "[...] If you data are 'well behaved', taxa [in our case, paleontological sites] typical for na association should plot in the vicinity of
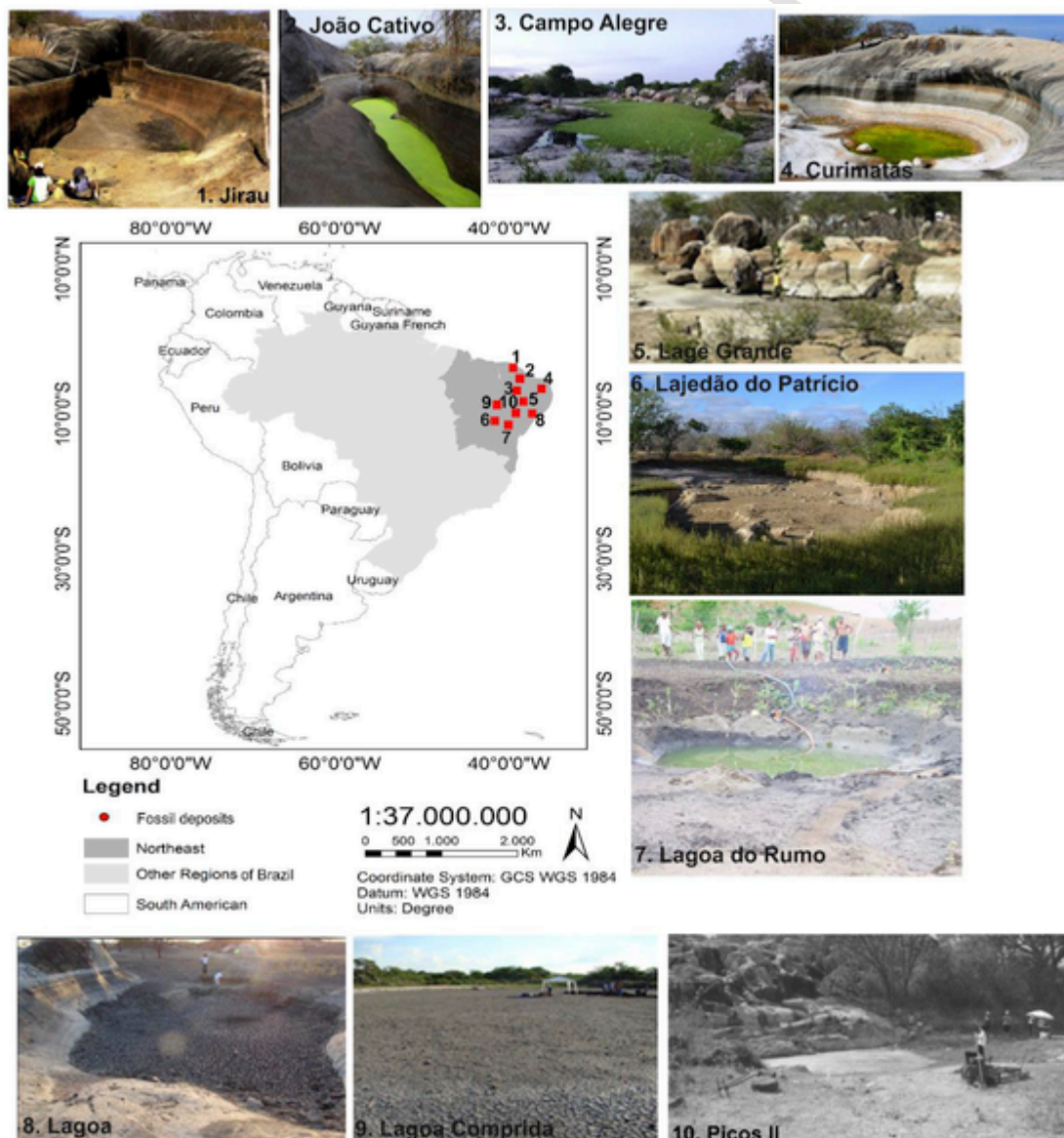

Fig. 1. Location map of analyzed paleontological sites.

Table 1
Geographic coordinates of the analyzed paleontological sites.

Paleontological site	Coordinates	Author
1. Jirau - JI - (Ceará State)	3° 21′ 23″S/39 ⁰ 42′ 20″ W	Araújo-Júnior et al. (2013)
2. João Cativo - JC - (Paraíba State)	3° 30′ 17″ S/39 ⁰ 40′ 24″ W	Araújo-Júnior et al. (2017)
3. Campo Alegre - CA - (Paraíba State)	7° 15′ 18.5″ S/36 ⁰ 44′ 26.3″	Araújo-Júnior et al. (2015)
4. Curimatãs - CU - (Paraíba State)	7° 07′ 36″ S/36 ⁰ 07′ 48″W	Araújo-Júnior et al. (2015)
5. Lage Grande - LG - (Paraíba State)	8° 25′ 27″ S/36 ⁰ 43′ 20″W	Araújo-Júnior et al. (2015)
6. Lajedão do Patrício - LP - (Bahia State)	11° 16 ′52,4″ S/ 41 ⁰35″79″ W	Faria and Carvalho (2019)
7. Lagoa do Rumo - LR - (Bahia State)	11° 52′ 07″ S/40° 07′ 11″ W	Ribeiro (2014)
8. Lagoa (Alagoas State)	09° 13′ 31″ S/37 ⁰ 14′ 94,7″ W	Silva (2008)
9. Lagoa Comprida (Pernambuco State)	08° 30′ 54″ S/41 ⁰ 00′ 18″ W	Silva (2009)
10. Picos II (Alagoas State)	07° 04′ 37″ S/41° 28′ 01″ W	Asakura et al. (2016)

that association [...]″. The tests performed provided a standard deviation R ranging from +1 to −1, where R values equal to +1 are obtained when all samples within groups are more similar to each other than other groups (Clarke and Warwick, 2001). All multivariate analyses were performed using the Paleontological Statistics version 2.17 software (Hammer et al., 2001).

Geochronological comparison was performed using the ages available in the literature for fossiliferous tank deposits in northeastern Brazil. These ages were compared to the paleoclimatic curves of Wang et al. (2004) and Cruz et al. (2009), which characterize the climate regime of northeastern Brazil for the last 90 kyr.

2.2. Terminologies

We follow Lyman (1994) in the use of the terms "specimen" and "skeletal elemento". The former correponds to an "observational unity": whether a complete bone (skeletal element) or a simple bone fragment. Skeletal element corresponds to a "discrete, natural anatomical unit of a skeleton, such as a humerus, a tibia, or a tooth". The terms "biocoenosis", "thanatocoenosis" and "taphocoenosis" also follow Lyman (1994): (i) biocoenosis, life assemblage; (ii) thanatocoenosis, death as-

semblage, derived from the biocoenosis and subsequently modified by bioestratinomic processes; and (iii) taphocoenosis, buried and preserved assemblage. We follow Behrensmeyer and Hook (1992) in the use of the terms "local and regional" assemblages. Local assemblages include fossil accumulations that represent areas and life habitats proximal to the depositional site. Regional assemblages include fossil accumulations derived from larger areas, up to entire drainge basins. Finally, terms "monotaxic", "paucitaxic", "multitaxic", "mono-dominant", and "multi-dominant" were used according to Eberth et al. (2007): (i) monotaxic, a fossil assemblage formed only by a siingle species; (ii) paucitaxic, between two and nine species; (iii) multitaxic, more than nine species; (iv) mono-dominant, an assemblage where one species accounts for 50% or more of the NISP (Number of Identifiable Skeletal Parts) or MNI (Minimum Number ofIindividuals); and (v) multi-dominant, assemblages in which two or more species account for 50% or more of the NISP or MNI.

3. Results and discussion

3.1. Comparing taphonomic features, sedimentary attributes, and taxonomic diversity

According to Table 2, all fossil concentrations are paucitaxic or multitaxic and multi-dominant, with taxonomic composition dominated by mega-mammals. According to Eberth et al. (2007), multidominant fossil assemblages are typically interpreted as resulting from reworking and then time-averaging, including bone elements concentrated by a variety of events and processes. Several paleoenvironmental scenarios are proposed for the genesis of multidominant assemblages, such as: (i) attrition in low-sedimentation-rate paleoenviroments (Badgley, 1986; Schröder-Adams et al., 2001); (ii) hidraulic reworking (Wood et al., 1988); (iii) multiple death events (attrition), but at a specific site possibly due to predation, diasease, and drought (Sunder, 1992; Sundell, 1999); and (iv) complex combination of the above phenomena (Commbs and Coombs and Coombs, 1997; Britt et al., 1997; Badgley et al., 1998). Therefore, it is likely that the fossil concentrations of tank deposits have been result o fone or more environmental processes and conditions mentioned above.

All analyzed fossil concentrations are found in sedimentary layers deposited in high-energy events (conglomerates and coarse sands with muddy matrix This indicates that the disarticulation and fragmentation processes may have been intensified by the transport and accumulation agent, although, biogenic agents and subaerial exposure may also have contributed to the generation of these taphonomic attributes. For some deposits, the degree of packing of the fossil layer range from moderately to densely packed, with a maximum thickness of 1 m. Araújo-

Table 2
Comparison of taphonomic signatures, sedimentary attributes and species diversity among tank deposits in northeastern Brazil.

Paleontological site	Species diversity	Sedimentary layer	Agent of transport	Physical integrity	Degree of packing	Depositional environment
Jirau	Multitaxic	Conglomerate	Flash floods	Fragmented/disarticulated	Moderate	Alluvial
João Cativo	Paucitaxic/multi dominant	Conglomerate	Flash floods	Fragmented/disarticulated	Densely	Alluvial
Campo Alegre	Paucitaxic/multi dominant	Conglomerate	Flash floods	Fragmented/disarticulated	Densely	Alluvial
Curimatãs	Paucitaxic/multi dominant	Conglomerate	Flash floods	Fragmented/disarticulated	Densely	Fluvial
Lage Grande	Multitaxic/multi dominant	Conglomerate	Flash floods	Fragmented/disarticulated		Fluvial
Lajedão do Patrício	Multitaxic/monodominant	Conglomerate	Debri flows	Fragmented/disarticulated	Densely	Alluvial
Lagoa do Rumo	Paucitaxic/monodominant	Conglomerate	Debri flows	Partial/disarticulated	Moderate	Alluvial
Lagoa	Multitaxic/multi dominant	Coarse sand with muddy matrix	Debri flows	Partial, complete/ disarticulated		Alluvial
Lagoa Comprida	Multitaxic/multidominant	Conglomerate	Flash floods	Fragmented		Alluvial
Picos II	Multitaxic/multidomunat	Conglomerate	Flash floods	Fragmented/disarticulated		Alluvial

Júnior et al. (2017) have attributed this characteristic to the low supply of clastic sediments and the high availability of bones in the thanatocoenosis. Fossil concentrations formed in this type of context are attritional, indicating long periods of skeletal accumulation (Behrensmeyer, 2007).

Regarding the depositional environment, we observed that most are placed in alluvial settings and few in fluvial ones. Alluvial and fluvial environments are favorable places for the concentration of fauna in periods of intense drought, due to the greater availability of resources (food and water). Due to the taphonomic characteristics of the compared fossiliferous concentrations (e.g. predominance of skeletal elements with low transport potential), we classify these as local assemblages. Araújo-Júnior (2016) explains that in fossil concentrations with such characteristics, the skeletal remains that make up the taphocoenoses are derived from thanatocoenoses near the natural tanks. As previously shown, tank deposits have their taxonomic composition influenced by stressful environmental conditions (Araújo-Júnior et al., 2017). This explains the fauna accumulation around these water reservoirs in times of environmental stress, where animals that die due to multiple factors (e.g. starvation, disease and predation) began to compose the thanathocoenoses that served as the source for the taphocoenoses.

3.2. Multivariate analyses

Our analyses of sites 1–7 revealed a wide range of taphonomic processes interacting in the genesis of fossil concentrations of tank deposits (Fig. 2), such as disarticulation, fragmentation and moderate abrasion of the specimens. In the cluster analysis among taphonomic features (R-mode) and correspondence analysis we observed two groups (Groups A and B; Fig. 3A), and three taphonomic settings (taphonomic settings A, B and C; Fig. 3B), respectively.

The most common taphonomic signatures in tank deposits are fragmented, disarticulated specimens, weathering stage 1 and moderate abrasion, represented in Group A (Fig. 3A) and taphonomic setting A (Fig. 3B). Fragmentation and disarticulation occur in a contexto of subaerial exposure prior to burial (Behrensmeyer, 1991), suggesting that bones were transported and deposited after a period of carcasses decay. This hypothesis is supported by the different stages of weather-

ing observed in the fossils as such taphonomic features are also generated in circumstances of subaerial exposure (Behrensmeyer, 1978).

All bones of the analyzed fossil concentrations are disarticulated and, besides, fragmented bones are present in large proportion. These alterations are associated with bones with a short period of subaerial exposure (weathering stages 1 and 2), indicating that the disarticulation process was intensified by taphonomic agents. Hill and Behrensmeyer (1984) explain that the process of skeletal disarticulation is continuous until stage 4 of weathering. Araújo-Junior et. al. (2013, 2015) explain that fragmentation and disarticulation in tank deposits are attributed to transport and reworking by flash-flood events. Post-fossilization breaks are well represented in the deposits; this type of break is generated by reworking events in bones that have gone through some diagenetic process (Araújo-Júnior et al., 2013). In the analyzed deposits, we observed the significant presence of perpendicular break of the diaphysis. This sort breaks is generated during the biostratinomic phase and attributed to transport or trampling, after a long period of subaerial exposure. (Cladera et al., 2004). Spiral and irregular breaks are scarce; these are caused by biotic agents when bones are fresh indicating a short period of subaerial exposure (Cladera et al., 2004). Therefore, it is evident that the process of disarticulation and fragmentation are attributed to bioestratinomic processes, where diagenetic processes and reworking also contributed to the fragmentation of bioclasts.

Moderate abrasion can be generated under two circumstances by hydraulic transport; (i) during long and moderate hydraulic transport distances, or (ii) moderate to a long time subaerial exposure over short distances (Aslan and Behrensmeyer, 1996). In PCA (Fig. 4A), we observed different sorting conditions in taphonomic settings A and B, with a predominance of easily-transported bones (FTI> 75) and relatively difficult-to-transport bioclast (FTI 50–75), respectively. Hard-to-transport bones (e.g. tibia, femur, teeth and skull bones) predominate in the tank assemblages of taphonomic setting B. This is due to the deceleration of the flow when reaching the depressions where the deposits were formed, accumulating the denser elements and keeping the lighter ones in transport. Araújo-Júnior et al. (2015) explain that tank assemblages of taphonomic setting A originate from flash-flood events, but the predominance of less dense (e.g. vertebrae, ribs and osteoderms) indicates a long distance between the places of death and preservation. Therefore, considering the fossil deposits here ana-
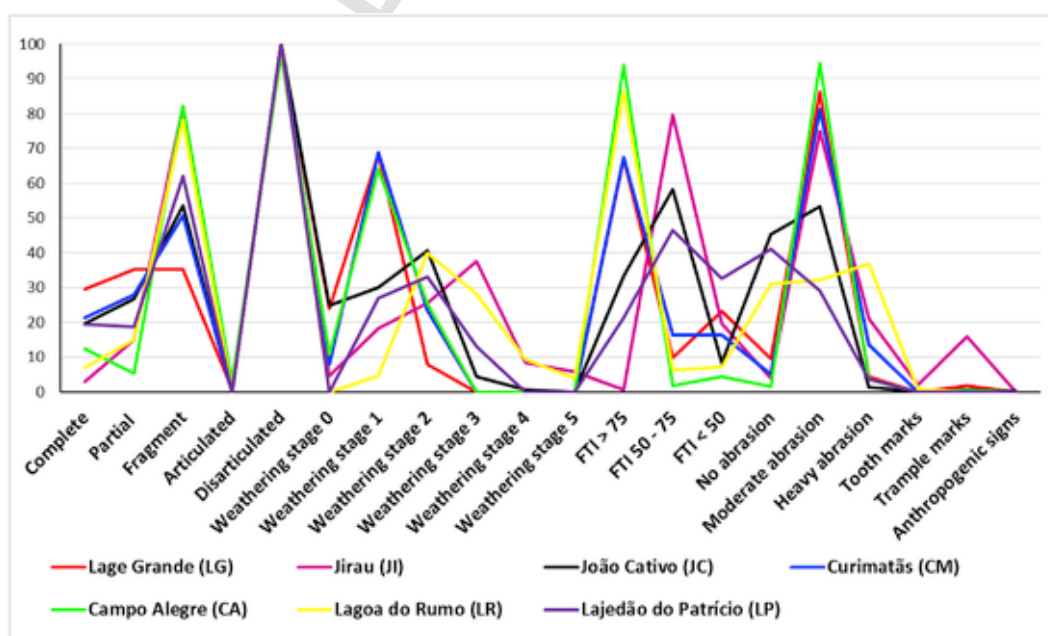

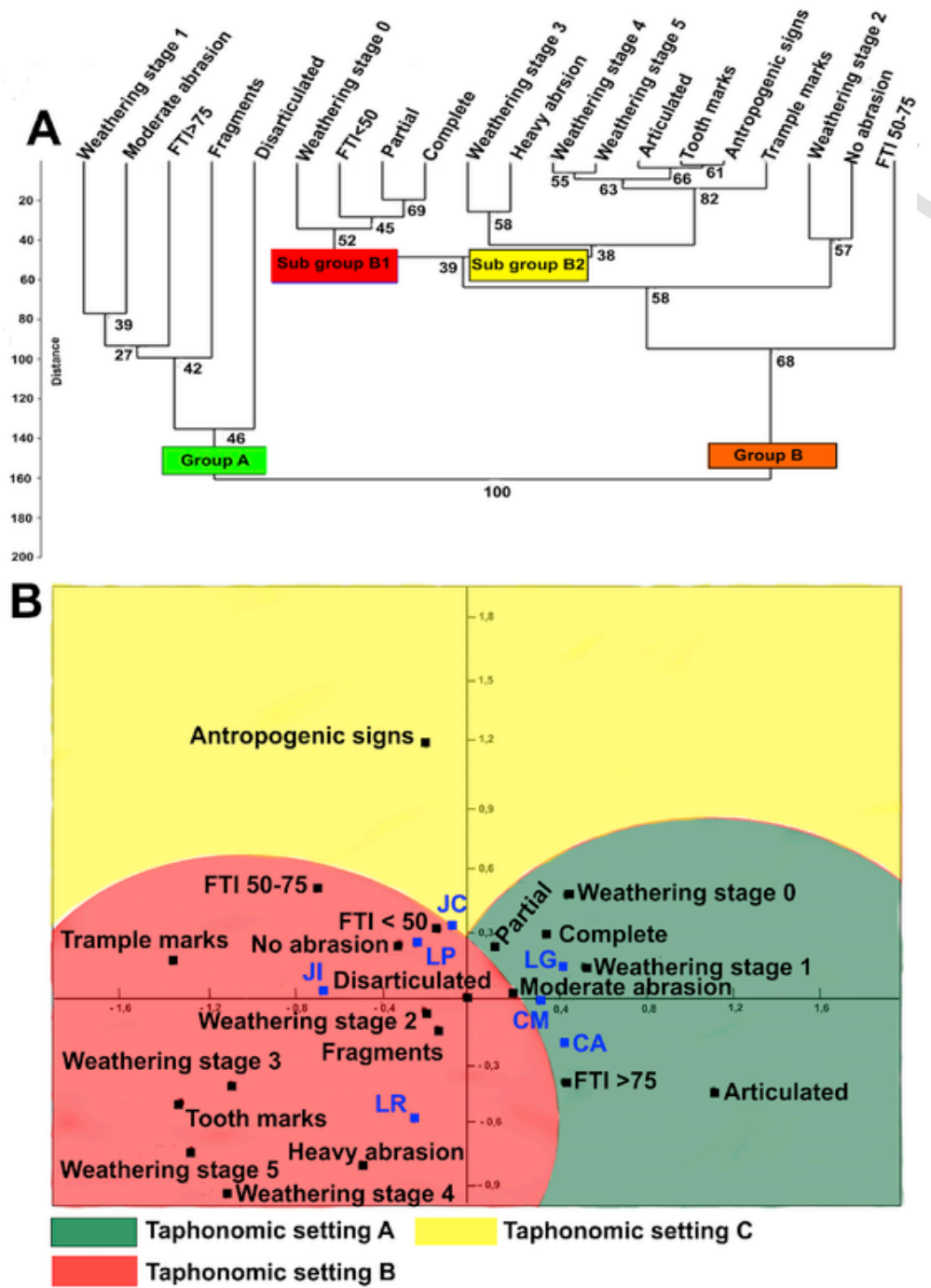**Fig. 2.** Taphonomic categories and their percentages in each fossiliferous deposit.

Fig. 3. Results of multivariate analyses for tank assemblages; A. Dendrogram with the grouping of taphonomic signatures (R-mode); B. Plotting of categories of taphonomic features and tank deposits in the correspondence analysis.

lyzed, the first hypothesis is more plausible for the Group A deposits, however, the second hypothesis better explains the moderate abrasion for the Group B deposits.

In Group B and taphonomic settings B and C, we observed bones with very rare taphonomic attributes: biogenic traces (trampling marks, anthropogenic signs and tooth marks), specimens with weathering stage 3–5, and skeletal remains with no abrasion and intense abrasion (Fig. 3A). These taphonomic features are distributed into two subgroups (B1 and B2) within Group B (Fig. 3A). Tooth marks were identified in a few bones caused by mid-sized canids by scavenging (Araújo-Júnior et al., 2011). Wiest et al. (2016) identified bone modifications similar to those mentioned above, explaining that

such alterations (e.g. tooth marks)were caused after soft tissue decay. Therefore, indicating that the bones were accessed after prolonged sub-aerial exposure.

Anthropogenic signs in skeletal remains are rare in the Quaternary fossil record of Brazil (Dantas et al., 2012; Mothé et al., 2014). In this analysis, this type of alteration was only observed in a specimen of camelid *Paleolama major* (Araújo-Júnior et al., 2017). In Fig. 3B, this alteration was plotted in taphonomic setting C, similarly to the observed by Araújo-Júnior et al. (2017). Therefore, due to the rarity of anthropogenic signs in tank deposits, we consider this alteration as extrinsic and does not represent a characteristic process of formation of the tank assemblages.
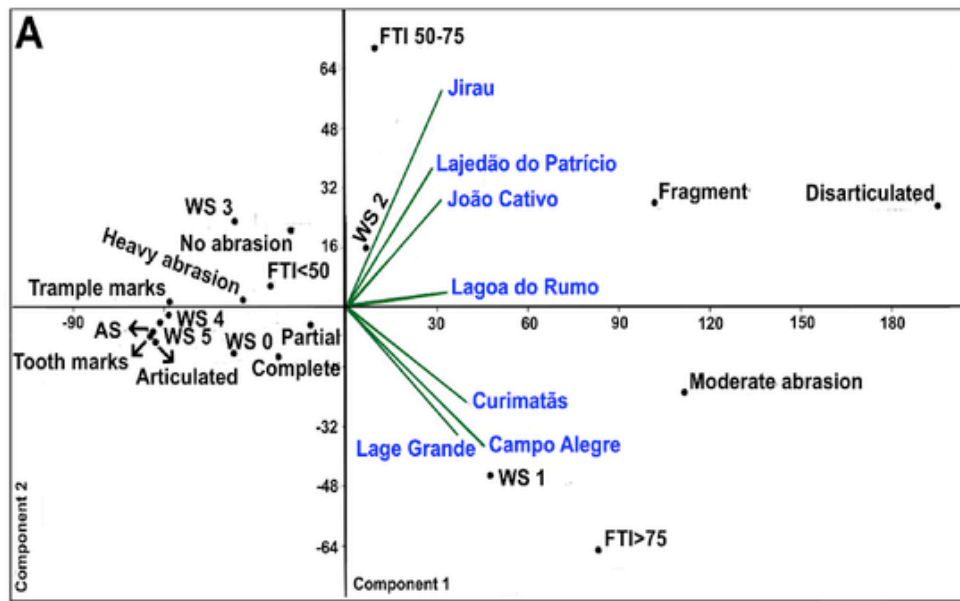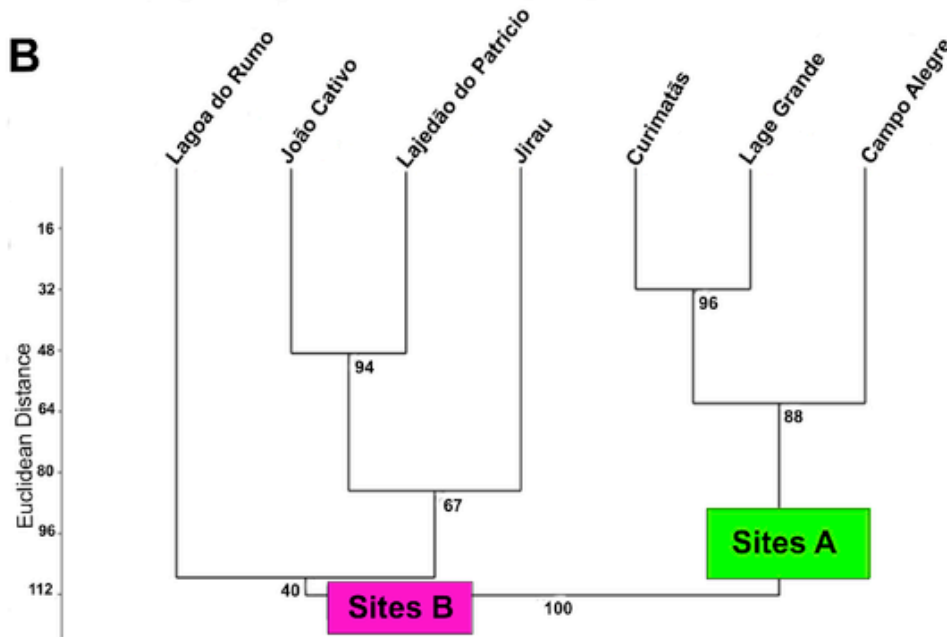
Fig. 4. Results of multivariate analyses for tank assemblages; A. Plotting of taphonomic signatures and tank deposits in the Principal Component Analysis (PCA); B. Dendrogram with the grouping of paleontological sites (Q-mode).

Based on the clustering of CA, CM and LG (Fig. 4B) composing Group A and taphonomic setting A, these assemblages present the most common features for tank deposits. These features indicate an environmental scenario where after death, carcasses underwent necrolysis followed by disarticulation and fragmentation within a few years (Behrensmeyer and Miller, 2012), suggesting seasonality in the input of skeletal elements in thanatocoenoses and lower reworking rates. The fossiliferous deposits of JI, LR, LP, and JC represent Group B and taphonomic setting B, with weathering stages (stage 2–5) that indicate a longer period of exposure of bones to taphonomic agents with higher rates of reworking. Under these conditions, the bones were disarticulated and modified by physical and biotic agents such as trampling, scavenging and eventually butchering. Thus, Group B and taphonomic setting B consist in more complex fossil assemblages than those of taphonomic setting A and Group A.

4. Geochronology

All fossil deposits with more than one age display time-averaging in the order of 10^3–10^4 kyr (Fig. 5). Time-averaging is caused by a physical (low rate of sedimentation and reworking) and biotic (bioturbation) processes, mixing non-contemporary skeletal remains in the same fossil record (Patzkowsky and Holland, 2012). In the case of tank deposits, Araújo-Júnior et al. (2017) have attributed this phenomenon to a low clastic sedimentation rate and reworking. The degree of time-averaging identified is very similar to that identified by Behrensmeyer (1982) in fluvial and alluvial deposits.

As shown in Fig. 5B, these fossil deposits represent a combined time interval of 70 kyr–9 kyr, comprising the time interval Late Pleistocene-Early Holocene. Furthermore, we can observe that time-averaging is a common process in tank deposits, with fossil concentra-
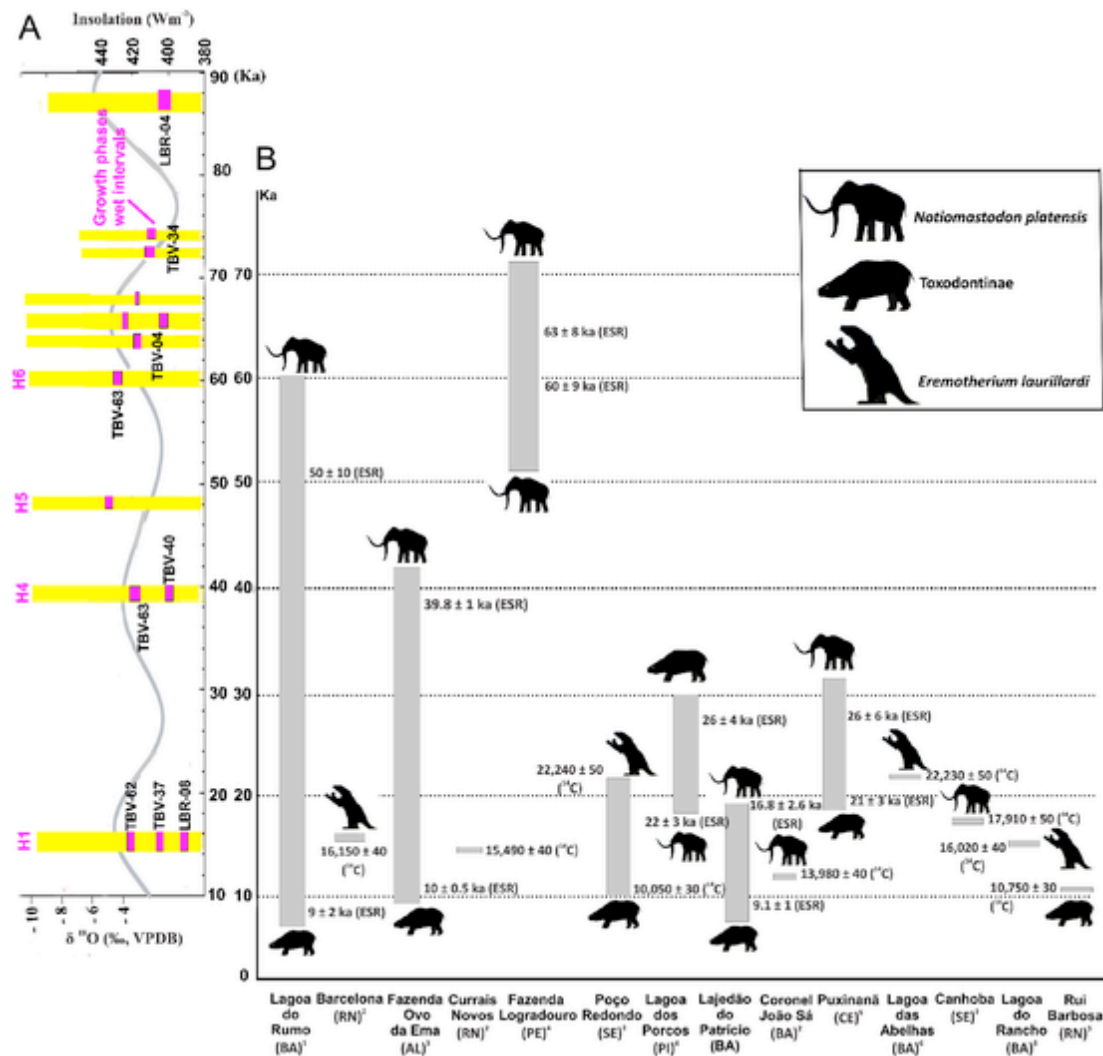
Fig. 5. A. Speleothem growth pattern of northeastern Brazil (BA). Pink dots indicate speleothem growth stages, while yellow bars correlate with Heinrich events (extracted from Wang et al., 2004); B. Time-averaging and chronological dispersion of northeast Brazil megafauna dated by ESR and ^{14}C. The symbols represent the taxa dated in their relative position. BA, Bahia State; PE, Pernambuco State; RN, Rio Grande do Norte State; AL, Alagoas State; CE, Ceará State; SE, Sergipe State; PI, Piauí State; VPDB, Viena PeeDee Belemnite; TBV, Toca da Boa Vista Cave; LBR, Lapa dos Brejões Cave [1]Ribeiro et al. (2013); [2]Dantas et al. (2013); [3]Oliveira et al. (2010); [4]Kinoshita et al. (2005); [5]Kinoshita et al. (2008); [6]Scherer et al. (2017). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

tions presenting different degrees of time-averaging, the most significant being Lagoa do Rumo. Therefore, it is likely that time-averaging is recurrent phenomenon identified in tank fossil deposits, being a regional-scale phenomenon for this typo of fossil accumulation.

Among the taxa dated in northeastern Brazil, *Notiomastodon platensis* has the highest number of available ages. The time range covered by this taxon (Fig. 5) indicates its presence during the Late Pleistocene, from 63 ± 8 kyr at Fazenda Logradouro (Pernambuco; Kinoshita et al., 2005) to about 10 ± 0.5 kyr at Fazenda Ovo da Ema (Alagoas; Oliveira et al., 2010). Toxodontinae has the second largest number of ages available, with a time range extending between 39.8 ± 1 and 9 ± 2 kyr at Lagoa do Rumo (Bahia; Ribeiro et al., 2013), indicating the presence of this taxon during the Late Pleistocene-Early Holocene (Fig. 5). *Eremotherium laurillardi* is the taxon most identified in fossil deposits in northeast Brazil, but it has few available ages, being restricted to the Late Pleistocene (Fig. 5; Dantas et al., 2013; Scherer et al., 2017). This can be attributed to the difficulty of dating its skeletal remains, due to the absence of enamel in its teeth, being possible to date them only when collagen is preserved in the bones.

When comparing our results to the paleoclimatic curve of Wang et al. (2004), produced using samples from the Chapada Diamantina (Bahia State), we observed that the region has gone through 14 cli-

matic intervals in this lapse, 7 dry and 7 wet (Fig. 5). Wang et al. (2004) propose that the short wet intervals identified for the region are punctual, only 8% of the last 210 kyr. Thus, we can assum that the climatic pattern of northeastern Brazil was arid/semi-arid intercalated with very short wet periods during the Late Pleistocene-Early Holocene.

In Fig. 5, ages between 25.9 and 25 kyr and 17.3 and 15.1 kyr overlap with Heinrich 2 and 1 millennial-scale events. Ages between 40 kyr and 42 kyr, 49.5 and 48 kyr, and 60.5 and 59.5 kyr overlap with events Heinrich 4 and 6. According to Wang et al. (2004) and Cruz et al. (2009), these millennial-scale events are characterized by abrupt climate changes, where rainfall conditions are established, due to the displacement of the Intertropical Convergence Zone further south. In the period between 15.1 and 13.2 kyr, it was identified an extremely dry period detected by the depositional gap in cave speleothems of Rio Grande do Norte State (Cruz et al., 2009). Only one age coincided during this period, indicating that this event may have affected the bioclast accumulation and preservation. Cruz et al. (2009) detected a slight increase in humidity between 13.2 and 8 Kyr characterized by abrupt alternations of dry and wet climates. This period overlaps with the last records of mega-mammals in northeastern Brazil, indicating that such environmental and climatic changes may have been decisive in the extinction of this fauna. According to

Cione et al. (2003), these climate forces affected the mega-mammal communities through the disappearance of habitats, impacting negatively the reproductive and nutritional dynamics of this fauna. The ages shown in Fig. 5 are distributed among dry and short wet periods, so we postulate that seasonality between rainy and dry periods in arid or wet climatic conditions is the determining factor for accumulation and preservation of skeletal remains in tank deposits. Therefore, the genesis of fossil concentrations of tank deposits were subject to different climatic and environmental conditions.

5. Taphonomic biases: paleoenvironmental and paleoecological inferences

As interpreted earlier, the climate in RIB was arid/semi-arid during the late Quaternary, characterized by seasonality between long dry and short rainy periods. This climatic pattern generated an environment scenario of low supply of clastic sediments, allowing bones to be exposed to subaerial surfaces during drought periods. In the rainy season, the skeletal remains of thanatocoenoses were transported by flash-floods and debris-flow generated by events of intense precipitation. Thus, the taphonomic biases described below responsible for the genesis of tank deposits were conditioned the climate.

The first taphonomic bias observed in tank deposits is the loss of species diversity. Many studies have shown that the taxonomic composition of tank fossil deposits has a large domain of large-sized mammals and mega-mammals compared to small and mid-sized vertebrates (Santos et al., 2002; Alves et al., 2007; Silva, 2008; Araújo-Júnior et al., 2013, 2015; Faria et al., 2013 Asakura et al., 2016; Faria and Carvalho, 2019). This sorting fits with the expected in conditions of arid climate and low supply of clastic sediments by cyclic resedimentation events and reworking by flash-floods. In this environmental scenario, the loss of taxonomic diversity is related to ecological and anatomical factors intrinsic to large-sized mammals and mega-mammals: (1) bone resistance to destructive processes; (2) gregarious behavior, which generates a high probability of preservation. Therefore, the loss of taxonomic diversity between biocoenosis and taphocoenosis is due to the attributes described above causing the destruction of bones of small and mid-sized vertebrates due to their lower resistance to destructive processes.

The scarcity and rarity of skeletal elements of young individuals is attributed to two factors: (i) long journey of herds and animals in search of water in intense dry periods, where on this journey the younger animals perished due to predation and starvation; and (ii) small resistance of your bones to destructive processes similar to that of small and mid-sized vertebrates. Loveridge et al. (2006) and Wiest et al. (2016) postulated an environmental scenario similar, when herds of existing elephants travel to distant water sources during extreme droughts, calves are often lost or separated and subject to predation.

The second bias is related to physical integrity, due to the almost exclusive presence of fragmented and disarticulated bones in the compared deposits. The main agent of fragmentation and disarticulation of the skeletal remains inside and outside the tanks are the successive events of transport by flash-floods/debris-flows, causing the resedimentation and reworking of bones in environmental conditions of the low contribution of clastic sediments. During periods of drought, the tanks attracted a large number of animals in search of water and food. Their death nearby the tanks may have generated minor fragmentation and disarticulation of bones and carcasses by biogenic agents. The low frequency of biological modification (tooth marks) in tank deposits can be associated with two hypotheses: (1) absence of predators and scavengers; and (2) in environments with high environmental stress (water deficit) overloads scavengers and predators causing an underutilization of carcasses and, consequently, scarcity or absence of tooth marks in bioclasts. Thus, it is likely that the low frequency of biological changes is linked to hypothesis 1 and 2. Wiest et al. (2016) also attributed the low frequency of skeletal changes by carnivores/scavengers to condi-

tions of environmental stress as postulated in hypothesis 2 described above.

The third bias is related to the spatial resolution of the deposits tank of BIR. Compared fossil assemblages present local spatial resolution indicating that the thanathocoenosis that served as the source of skeletal material was close to their final burial place. This indicates that during times of environmental stress, the fauna clustered around the water sources where the deposits were formed. Therefore, when we relate preservation and spatial resolution biases with the type of transport, we attribute that the low frequency of breaks and biological alterations were obliterated by the resedimentation and reworking processes.

The fourth bias is the presence of time-averaging in the order of 10^3 and 10^4, indicating that the analyzed fossil deposits are the result of multiple bioclast input, transport and reworking events. When we compare the time interval of tank deposits with the sedimentary characteristics of the layers where the fossils are found, we identified a regime of low clastic sedimentation for the region during the Late Pleistocene and Early Holocene. Thus, this scenario of low input of clastic sediments coupled with high energy transport corroborates the hypothesis of fragmentation, disarticulation and loss of species diversity, directly favoring the accumulation of more resistant skeletal elements such as those of megafauna.

6. Conclusion

In the comparison among taphonomic, sedimentary and taxonomic diversity of fossiliferous tank deposits, we identified that fossil deposits are formed in alluvial and fluvial depositional environments. The species diversity represented in these deposits was conditioned by environmental conditions of water scarcity, low input of clastic sediments and cyclic resedimentation and reworking by events of flash-floods and debris-flows. This processes generated multi-dominant paucitaxic and multitaxic fossil concentrations, with disarticulated bones and predominance of fragmented specimens, and the accumulation and preservation of the majority of large-sized mammals and mega mammals.

"Group A" fossil concentrations are formed in the environmental context of lower resedimentation and reworking. On the other hand, "Group B″ fossil concentrations incorporated higher taphonomic biases attributed to higher resedimentation and reworking during the period of accumulation. Thus, despite the differences identified between "Groups A and B", the arrangements of taphonomic processes seem to have been very similar between the tank deposits compared, varying only in intensity.

During the period of formation of the fossil tank deposits (70 kyr–9 kyr), the BIR experienced 14 climatic intervals (7 dry and 7 wets), with the ages evenly distributed during this period. The seasonality between periods of aridity and humidity identified between 70 kyr and 9 kyr for the Brazilian Intertropical Region, is the main factor controlling the accumulation and deposition processes of skeletal remains preserved in the fossiliferous tank deposits.The time-averaging identified for tank deposits is approximately of 10^3–10^4 years, indicating that the cyclicity between erosive and depositional processes generated attritional fossil concentrations. Therefore, bones were exposed for thousands of years in the Taphonomically Active Zone (TAZ), which led to the destruction of bones of small and medium vertebrates and consequent lower representativeness in the compared taphocoenoses.

Therefore, during the long dry periods the fauna that formed the biocoenosis clustered nearside the tanks, in searching for water and food, where many animals died near the tanks due to hunger, thirst, disease, and predation athough there are few direct signs of it. After death, their carcasses were incorporated into the thanatocoenoses, undergoing necrolysis and bone modifications in arid/semi-arid conditions. In the rainy season the fluvial and alluvial plains, experienced flash floods, carrying and accumulating peripheral specimens (fragmented or complete), along with in-situ elements, and reworking previously buried bioclasts. The cyclicity of these death events attributed to dry periods plus transport, sorting and accumulation in flash

floods events gave rise to time-averaging fossil concentrations. The seasonality of the process of accumulation and burial of bioclasts is directly linked to the alternation between drought and short rainy periods.

Uncited references

Faria et al., in press; Guerra and Guerra, 2008; Dantas et al., 2011.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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