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1 **Isotopic paleoecology ($\delta^{13}\text{C}$, $\delta^{18}\text{O}$) of late Quaternary herbivorous mammal** 2 **assemblages from southwestern Amazon**

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32

33 **Abstract**

34 We report the first ¹⁴C AMS datings and carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) stable isotopes
35 data to reconstruct the paleoecology of medium to large herbivorous mammals from late
36 Quaternary of southwestern Amazon (Acre and Rondônia states, Brazil). AMS ¹⁴C
37 datings for *Neochoeus* sp. (29,072 - 27,713 Cal yr BP), *Notiomastodon platensis* (25,454
38 - 24,884 Cal yr BP) and *Eremotherium laurillardi* (11,320 - 11,131 Cal yr BP) supports
39 the Lujanian ages. All fossils have low $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ isotopic values that suggest
40 heterogenous forest habitats, agreeing with paleovegetation reconstitution. Most species
41 were browsers ($p_i\text{C}_3 = 100\%$; Niche breadth, $B_A = 0$), where the key species with the
42 largest body mass, *N. platensis* (~6,300 kg) and *E. laurillardi* (~3,500 kg), possibly had
43 a more generalized browser diet in closed-canopies to woodlands. Their diet distinguished
44 from the C_3/C_4 generalist *Trigodonops lopesi* (~1,900 kg), which foraged in wooded
45 savannas ($p_i\text{C}_3 = 70\%$; $B_A = 0.72$), similarly with its relative *Toxodon platensis* (~1,800
46 kg) that had a browse-dominated mixed feeder diet ($p_i\text{C}_3 \geq 84\%$, $B_A \leq 0.38$) in other
47 localities of Amazonia. *Palaeolama major* (~280 kg) was possibly a strictly folivorous
48 within subcanopies, whereas *Tapirus* sp. (~250 kg) and *Mazama* sp. (~40 kg) were
49 browsers in subcanopies to woodlands. *Holmesina rondoniensis* (~120 kg) was a browser
50 but not restricted, where could also feed on herbaceous from understories in woodlands,

and *Neochoerus* sp. (~ 200 kg) feeding predominantly herbaceous plants in wooded savannas ($\delta^{13}C_3 = \sim 69\%$; $B_A = 0.75$). We estimate that the interspecific competition could have been avoided by different feeding strategies, although more investigations are still needed to better understand their ecological interactions in the habitats of the southwestern Amazon during the late Quaternary.

Keywords

Pleistocene, Amazon, megafauna, paleodiet, stable isotopes, AMS ^{14}C dating

1. Introduction

An emblematic Pleistocene fauna of herbivorous mammals is recognized in southwestern Amazon (Simpson and Paula Couto, 1981; Paula Couto, 1982, 1983a, 1983b; Ranzi, 2000; Nascimento, 2008; Ranzi, 2008). The native notoungulates, cingulates, pilosans, caviids and also the Holarctic immigrants, such as proboscideans, cetartiodactyls and perissodactyls are the most significant Quaternary members in this region (Ranzi, 2000; Góis et al., 2004; Porto et al., 2004; Holanda and Cozzuol, 2006; Nascimento, 2008; Ranzi, 2008; Holanda et al., 2011).

The first fossil occurrences have been reported at the beginning of the 20th century from alluvial Quaternary deposits outcropping along the banks of the Juruá River, affluent of the Amazon River in the states of Acre and Amazonas, Brazil (Simpson and Paula Couto, 1981; Ranzi, 2000, 2008). However, the knowledge about the Pleistocene mammal fossils from Rondônia state began in the 1980s, after the beginning of intense gold mining activity in the alluvial deposits of the Madeira River, also tributary of the Amazon River (Nascimento, 2008; Holanda et al., 2011).

75 Despite the great faunistic diversity, there are few inferences regarding the
76 paleoecology of these assemblages. Ranzi (2000) assessed the ecological importance of
77 the Pleistocene fauna from Juruá River in a comparative study with modern species,
78 although no specific method for paleoecological fauna reconstruction has been performed.

79 The most traditional studies for paleoecological reconstructions use morphological
80 inferences through analyses of dental hypsodonty, enamel microwear and mesowear,
81 cranial shape adaptations, among others (e.g., Fortelius and Solounias, 2000; Solounias
82 and Semprebon, 2002; Bargo et al., 2006; Naples and McAfee, 2012). Other studies
83 retrieve direct evidence of the food content ingested through analysis of plant microfossils
84 extracted from dental calculi and coprolites (e.g. Marcolino, 2012; Asevedo et al., 2012;
85 2020). Nevertheless, increasing number of studies are employing isotopic analysis of
86 fossilized mammalian mineralized tissues, proving to be an excellent tool (e.g., Sánchez
87 et al., 2004; Macfadden, 2005; Domingo et al., 2012; Lopes et al., 2013; França et al.,
88 2014; Dantas et al., 2013; 2017; Pansani et al., 2019).

89 The analysis of stable isotopes in paleoecology is based on the natural variation of
90 stable isotope composition in animals (Fricke, 2007; Koch, 2007; Higgins, 2018).
91 Ingestion of water and food along with the physiological processes of each animal leave
92 a geochemical impression on the inorganic (bioapatite) and organic (collagen)
93 components of its bones and teeth (Koch, 2007). Stable isotopes of carbon in mineralized
94 mammal tissues are derived from their food, and are closely related to the photosynthetic
95 pathways used by the plants consumed (Fricke, 2007; Koch, 2007; Marshall et al., 2007).
96 On the other hand, the stable isotope of oxygen is mainly derived from the water ingested
97 by drinking and food, and accordingly brings important inferences related to climatic
98 factors (e.g., precipitation and temperature) of the species habitats (Sponheimer and Lee-
99 Thorp, 1999; Fricke, 2007; Koch, 2007). Therefore, the analysis of carbon and oxygen

isotopes is important to identify feeding preferences and paleoenvironment of extinct mammals, as isotopic compositions vary with diet, location and ecosystem (Fricke, 2007; Koch, 2007; Higgins, 2018).

The present study provides a reconstruction of the paleoecology of medium to large herbivorous mammal assemblages from late Quaternary of southwestern Amazon through stable carbon and oxygen isotope analyses, and also supplying: (i) ^{14}C datings by accelerator mass spectrometry (AMS) to contextualize the fossil assemblages, (ii) inferences about the paleoenvironment, and (iii) ancient diet and niche partitioning.

2. Material and methods

2.1. Samples

Eighteen bulk samples of enamel, dentin and bones were collected from species of Pilosa (Megatheriidae: *Eremotherium laurillardi* Lund, 1842), Cingulata (Pampatheriidae: *Holmesina rondoniensis* Góis et al., 2012), Proboscidea (Gomphotheriidae: *Notiomastodon platensis* Ameghino, 1888), Notoungulata (Toxodontidae: *Trigodonops lopesi* Roxo, 1921), Perissodactyla (Tapiridae: *Tapirus* sp. Brisson, 1762), Cetartiodactyla (Camelidae: *Palaeolama major* Liai, 1872 and Cervidae: *Mazama* sp. Rafinesque, 1817) and Rodentia (Caviidae: *Nechoerus* sp. Hay, 1926) (Supplementary Table 1). These samples were analyzed to obtain stable carbon and oxygen isotope composition from carbonate component of the bioapatite. AMS ^{14}C datings were performed for *E. laurillardi*, *N. platensis* and *Nechoerus* sp. samples, and were calibrated into calendar ages before present using CALIB 7.1 program (Reimer et al., 2013). Both analyses were performed at the Center for Applied Isotope Studies (CAIS) of the University of Georgia, United States.

The fossil specimens came from Quaternary alluvial deposits in several localities in the southwestern Amazon of the Upper Juruá (8°47'S - 9°49'S, 72°41'W - 72°49'W; Fig 1, locality 1, a-d) and Chandless rivers (9°49'50"S, 70°08'31"W, Fig. 1, locality 2) in Acre state, as also in Araras locality, Madeira River (10°03'01"S, 65°19'31"W; Fig. 1, locality 3), Rondônia state, Brazil. The specimens are deposited in the paleontological collections of the Laboratório de Pesquisas Paleontológicas of Universidade Federal do Acre (LPP/UFAC), Rio Branco, Acre and the Museu da Memória Rondoniense (MERO), Porto Velho, Rondônia, Brazil.

Previous data of stable carbon and oxygen isotopes of the Toxodontidae *Toxodon platensis* Owen, 1840 from southwestern Amazon in Peru (8°24'S - 12°38'S, 71°18'W - 74°17'W) and Bolivia localities (11°00'S - 14°01'S, 65°06'W - 69°00'W; Fig. 1, localities 4 - 9; Supplementary Table 1) by Macfadden (2005) were integrated into analysis in order to compare with the sympatric toxodontid *T. lopesi*, and also the other fossil taxa from Brazilian Amazonian localities.

2.2. Material processing

The stable isotope and AMS ¹⁴C datings analyses followed the methodological steps of Cherkinsky (2009). Two cleaning steps were initially performed on the bone and tooth samples: first, a mechanical wash using an ultrasonic bath and wire brush to remove external material (i.e., dirt, secondary materials, etc), and second, a chemical cleaning to remove diagenetic carbon compounds. The materials were soaked overnight in 1N acetic acid, then washed free of acetic acid by repeated decantation. Loose or extraneous material was discarded and the samples were dried at approximately 70°C. After drying, samples were crushed into small fragments and again reacted with 1N acetic acid in a 250-mL Erlenmeyer flask. The flask was 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 was performed at ~20-minute intervals until no substantial release of fine, foamy gas bubbles occurs, and it was repeated at least 4-5 times. Once the evolution of fine gas bubbles has ceased, it can be assumed that all secondary or surface-exchanged carbonates have been removed.

The completely cleaned bone samples were washed free of acetic acid by repeated soaking and decantation with demineralized water and then vacuum-dried with 100% phosphoric acid to dissolve the bone/tooth mineral and release carbon dioxide from hydroxyapatite. The resulting carbon dioxide was cryogenically purified from other reaction products and catalytically converted to graphite. The sample ratios were measured separately using a stable isotope ratio mass spectrometer.

All results are reported using delta notation, $\delta = [(R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000]$ (Coplen, 1994). The reference for carbon isotope values ($R = {}^{13}\text{C}/{}^{12}\text{C}$) is Vienna Pee Dee Belemnite (VPDB) and oxygen isotope ($R = {}^{18}\text{O}/{}^{16}\text{O}$) is ~~the~~ Vienna Standard Mean Ocean Water (VSMOW).

2.3. Interpretation of $\delta^{13}\text{C}$ data

The interpretation of carbon isotope values found in tooth/bones of medium-to large-bodied herbivorous mammals are based on fractionated values of the plant photosynthetic pathway consumed (Fricke, 2007; Koch, 2007; Higgins, 2018). Plants have two main photosynthetic pathways, C_3 and C_4 (Ehleringer and Cerling, 2002). C_3 plants, which fix carbon using the Calvin Cycle, comprise ~85% of terrestrial plant biomass, encompassing most trees, shrubs, and grasses from high-elevation, high latitude, and cool-growing seasons. The $\delta^{13}\text{C}$ values range from -35‰ to -22‰ with mean value

of -27‰ (Koch, 2007; Marshall et al., 2007). Values of $\delta^{13}\text{C}$ below -30‰ reflect C_3 plants from closed-canopy forest environments, whereas values close to the limit of C_3 plants may be associated with C_3 grasslands (e.g., -23 to -22‰ ; Kohn, 2010). C_4 plants, in turn, fix carbon using the Hatch-Slack cycle and comprise about 5-10% of the terrestrial plant biomass, including predominantly grasses, herbs and eudicotyledons adapted to arid and high luminosity index environments (Ehleringer and Cerling, 2002). The $\delta^{13}\text{C}$ values range from -17‰ to -9‰ and the mean value is -13‰ (Koch, 2007; Marshall et al., 2007).

Consumers are enriched in ^{13}C compared to the plants. Previous studies demonstrated that medium-to large-bodied herbivorous mammals had an enrichment of around 14‰ (δ^* bioapatite-diet; Cerling and Harris, 1999). However, recently, Tejada-Lara et al. (2018) suggested that the body mass (bm) influences the physiological carbon enrichment values, and their determination should be calculated based on an equation: $\delta^* = 2.4 + 0.034 (\text{bm})$.

In spite of the body mass estimates for extinct species that do not have living relatives are approximations and vary in literature, it was considered the most recent published data to integrate in the analysis (i.e., Ghizzoni, 2014; Dantas, 2019; Dantas et al., 2020; Table 1). For the fossils of extant taxa, *Tapirus* sp. and *Mazama* sp., we followed the body mass data of the most common species of the respective genera in the Amazon region, *Tapirus terrestris* Linnaeus, 1758 (i.e., Padilla and Dowler, 1994) and *Mazama americana* Erxleben, 1777 (i.e., Duarte and Jorge, 1996; Table 1). Through these data, it was calculated an enrichment of 12‰ for taxon with body mass less than 75 kg, 13‰ for those species between 75 kg to 600 kg, 14‰ between 600 kg to 3,500 kg, and 15‰ for species as from 3,500 kg.

Accordingly, diet categories based on the digestive physiology of herbivores can be discerned between browsers, grazers and mixed feeders. Browser mammals consume larger proportions of fruit and foliage from C₃ shrub and tree plants (Fricke, 2007; Koch, 2007; Higgins, 2018), and based on the different enrichments in bioapatite (i.e., 15‰ to 12‰), they have average $\delta^{13}\text{C}$ values of – 12‰ to – 15‰, respectively. Grazing mammals are consumers of herbs and grasses (Fricke, 2007; Koch, 2007; Higgins, 2018). C₃ grazers may have $\delta^{13}\text{C}$ values approximately between – 8‰ to – 7‰ and – 11‰ to – 10‰, although it is still difficult to distinguish the diet between C₃ grasses and wood resources, due to the overlap in $\delta^{13}\text{C}$ values for certain phytophysiognomies (e.g., C₃ grassland and wooded savanna). On the other hand, C₄ grazers have specific average $\delta^{13}\text{C}$ values of 2‰ to –1‰. Mixed feeder species that consume both browse and grass (C₃-C₄), have intermediate values between the average of browsers and C₄ grazers (– 12‰ to – 15‰ and 2‰ to –1‰).

In order to identify the landscape characteristics of mammalian fossil habitats, we used the interpretation of the $\delta^{13}\text{C}$ ranges from Domingo et al. (2012) following the specific enrichment values. Therefore, species from (i) closed-canopy forest habitats [i.e., higher density areas of trees forming canopy] have values from – 20‰ and – 15‰ to – 23‰ and – 18‰; (ii) mesic woodland habitats [i.e., low-density forest with sparse understory plants] have values from – 15‰ and – 10‰ to – 18‰ and – 13‰; (iii) wooded C₃ grassland [i.e., arboreal savannas] have values from – 10‰ and – 7‰ to – 13‰ and – 10‰; (iv) mixed C₃ and C₄ habitats [i.e., arboreal savannas] have values from – 7‰ and – 2‰ to – 10‰ and – 5‰; and (iv) open C₄ grassland habitats [i.e., open savannas] have values from – 2‰ and 6‰ to – 5‰ and 3‰.

Comparisons between carbon isotope values of the fossil taxa and the living related species from the literature were performed taking into account the enrichment addition of

2‰ to the extant species, because of the $\delta^{13}\text{C}$ decay of atmospheric CO_2 in current ecosystems (Suess effect), as a consequence of the large burning of fossil fuels since the beginning of the Industrial Revolution in the 18th century (Keeling, 1979). Previous data of stable carbon isotopes analyzed in collagen samples from current species were converted to bioapatite values. Herbivorous mammal collagen is known to be 5‰ enriched in relation to the food (Koch, 2007). Thus, following Tejada-Lara (2018), from the $\delta^{13}\text{C}$ value of the resource found ($\delta^{13}\text{C}_{\text{collagen}} - 5\text{‰}$) was added the specific enrichment values for bioapatite according to the body mass of the species.

2.3.1. Diet proportions and ecological niches estimates

In order to refine the diet interpretations, the $\delta^{13}\text{C}$ data and respective enrichment values considered for each taxon were used to calculate the proportion of C_3 and C_4 diet for the species, using the following equation presented by Phillips (2012):

$$(1) \quad \delta^{13}\text{C}_{\text{mix}} = \delta^{13}\text{C}_1 f_1 + \delta^{13}\text{C}_2 f_2$$

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

Where, C represents the mean $\delta^{13}\text{C}$ values of C_3 ($\text{C}_1 = -12\text{‰}$ to -15‰) and C_4 ($\text{C}_2 = 2\text{‰}$ to -1‰) plant consumers. f_1 and f_2 are the proportion of C_3 and C_4 resources, respectively.

Through the values obtained from the proportion of resources it was possible to calculate the ecological niche breadth according to the following Pianka (1973) equation:

$$B = 1 / \sum p_i^2$$

Where, B is the niche breadth and p_i the proportion of resources consumed. This measure was then standardized from 0 to 1 following the equation of Levins (1968):

$$B_A = B - 1/n - 1$$

Where, B_A is standardized niche width, B is the niche breadth, and n is the number of resources consumed. The results indicate whether the animal is specialist (0) or generalist (1)

2.4. Interpretation of $\delta^{18}\text{O}$ data

The stable isotope of oxygen in mammalian bioapatite is directly related to their body water. It reflects the oxygen isotope composition that enters in organism through atmospheric O_2 , ingested water and food sources, and exits via respiration, transpiration and excretion. Thereby, resulting in a complex function of climate, diet and physiology (Sponheimer and Lee-Thorp, 1999; Koch, 2007).

Since the $\delta^{18}\text{O}$ values of atmospheric O_2 are relatively constant, large herbivorous mammals that require considerable amount of ingested water from lakes and rivers, have $\delta^{18}\text{O}$ values reflecting the response of meteoric water ($\delta^{18}\text{O}_{\text{mw}}$) to changes in temperature and/or precipitation/humidity (Sponheimer and Lee-Thorp, 1999; Fricke, 2007; Koch, 2007), which can be influenced geographically and temporally by several climatic factors (e.g., continentality, latitude, altitude, amount effect, among others; Sponheimer and Lee-Thorp, 1999; MacFadden and Higgins 2004; Koch, 2007; Higgins, 2018).

Traditionally, in terrestrial ecosystems the more positive $\delta^{18}\text{O}$ values in mammal tissues are indicative of warmer and/or drier habitats/seasons, due to the ^{18}O -enrichment in detriment of the higher ^{16}O -evapotranspiration in ingested waters and plants (Sponheimer and Lee-Thorp, 1999; Fricke, 2007; Koch, 2007). The evapotranspiration effect is larger in C_4 plants that do not close their stomata, and consequently grazer mammals have the most enriched $\delta^{18}\text{O}$ values (Fricke, 2007; Koch, 2007). On the other hand, negative $\delta^{18}\text{O}$ values may reflect a colder and/or wetter habitats/seasons, which contributes to depletion of ^{18}O from water surfaces and plants (Sponheimer and Lee-

Thorp, 1999; Fricke, 2007; Koch, 2007). Specifically, in tropical forested habitats, the reduction of ^{16}O evapotranspiration in C_3 plants adapted to shaded environments, plus the amount effect that cause a depression in the oxygen isotopic curves related to the high precipitation may favors the depletion in $\delta^{18}\text{O}$ values for browser mammals (MacFadden and Higgins 2004; Fricke, 2007; Koch, 2007; Higgins, 2018).

Mammal species inhabiting similar environments can also vary their $\delta^{18}\text{O}$ data in response to different proportion of drinking water surfaces as opposed to plant water consumptions (Sponheimer and Lee-Thorp, 1999; Levin et al., 2006). Some herbivorous mammals get most of their water from plants, and have the $\delta^{18}\text{O}$ values reflecting not only the local precipitation, but also the local environmental relative humidity that control the ^{18}O enrichment in plants (Ayliffe et al., 1992). These taxa are sensitive to changes in $\delta^{18}\text{O}$ values with increased aridity (evaporation-sensitive), differing to those taxa that are obligatory drinkers (evaporation-insensitive; Levin et al., 2006).

2.4.1. Estimation of $\delta^{18}\text{O}$ in ancient environmental waters

The oxygen values in bioapatite of obligatory drinkers can be used as a proxy to past meteoric water $\delta^{18}\text{O}$ estimation. Such relationship is consistent with the relationship between measured phosphate $\delta^{18}\text{O}$ values (^{18}Op) of bones and teeth of modern African (*Loxodonta africana* Blumenbach, 1797) and Asian (*Elephas maximus* Linnaeus, 1758) elephants and estimates of $^{18}\text{O}_{\text{mw}}$ (Ayliffe et al., 1992). Thus, assuming modern elephants are a reasonable analog for the South American proboscidean *N. platensis*, we converted its isotopic values from bioapatite carbonate ($\delta^{18}\text{Oc}$) to phosphate values ($\delta^{18}\text{Op}$) by reducing the $\delta^{18}\text{Oc}$ values to 8.7‰ (Bryant et al., 1996). Posteriorly, it was calculated the $\delta^{18}\text{O}_{\text{mw}}$ of *N. platensis* using the relationship between the oxygen content of the PO_4

component of bioapatite ($\delta^{18}\text{Op}$) and ingested water in modern elephants through the equation of Ayliffe et al. (1992):

$$\delta^{18}\text{Op} = 0.94\delta^{18}\text{O}_{\text{mw}} + 23.3$$

3. Results

The ^{14}C AMS datings indicate that the specimens are biostratigraphically correlated to the Lujanian Stage/Age (SALMA), and include similar ages for *Neochoerus* sp. (29,072 - 27,713 cal yr BP) and *N. platensis* (25,454 - 24,884 cal yr BP) from Madeira and Juruá rivers in Rondônia and Acre states, respectively. Furthermore, a more recent age was obtained for *E. laurillardi* (11,320 - 11,131 cal yr BP) from the Chandless River, Acre state (Supplementary Table 1).

The low $\delta^{13}\text{C}$ values obtained from bioapatite in mammals from the southwestern Amazon Pleistocene mammals (-17.47‰ to -8.83‰ ; Supplementary Table 1), indicate a tendency toward a C_3 specialist diet ($p\text{C}_3 = 100\%$; $B_A = 0$) from closed-canopy forest to wooded C_3 grasslands (Table 1; Fig. 2).

The largest bodied species *N. platensis* (bm: $\sim 6,300$ kg) and *E. laurillardi* (bm: $\sim 3,500$ kg) have $\delta^{13}\text{C}$ values below the average of -12‰ for C_3 diet, which indicate browsing diet in more closed physiognomies (Fig. 2A). *E. laurillardi* possibly inhabited closed-canopy forests in Acre (Juruá River: $-17.04 \pm 0.20\text{‰}$; Chandlers River: -15.37‰) and mesic woodlands in Rondônia (-14.23‰ ; Table 1). *N. platensis*, in turn, has a slightly broad range of $\delta^{13}\text{C}$ values and inhabited closed-canopy forests and mesic woodlands in both localities of Acre ($-14.11 \pm 2.4\text{‰}$) and Rondônia ($-15.09 \pm 1.16\text{‰}$; Table 1; Fig. 2A).

Among the species with the highest body mass, the notoungulate *T. lopesi* (bm: $\sim 1,900$ kg) of Rondônia has a $\delta^{13}\text{C}$ value significantly more positive (-8.83‰ ; Table 1),

indicative of mixed feeder ($B_A = 0.72$) in wooded savanna-like habitats with dominant C_3 plants ($p_iC_3 = 70\%$; Table 1; Fig. 2B). For the sympatric toxodontid *T. platensis* (bm: ~ 1,800 kg) from southwestern Amazon localities in Bolivia ($-13.9 \pm 1.6\text{‰}$; $p_iC_3 \geq 86\%$, $B_A \leq 0.32$) and Peru ($-13.2 \pm 1.4\text{‰}$; $p_iC_3 \geq 84\%$, $B_A \leq 0.38$) by Macfadden (2005), the $\delta^{13}C$ values indicate browse-dominated mixed feeder habits in mesic woodlands to wooded C_3 grasslands (Table 1; Fig. 2B).

For the mammal species with lower body mass, a more positive $\delta^{13}C$ value was observed for the large capybara *Neochoerus* sp. (bm: ~ 200 kg) from Rondônia (-9.66‰) close to the value found in the toxodont for the same region (Fig. 2). The species probably had a more generalist diet between C_3 and C_4 resources ($B_A = 0.75$), accessing more open landscapes dominated by C_3 plants ($p_iC_3 = 69\%$; Table 1; Fig. 2C).

The other mammal species have $\delta^{13}C$ values below the average of -14‰ and -15‰ ($\epsilon^* = 13$ and 12‰ , respectively), and also pointed to specialist browser diet such as the ground sloth and the proboscidean (Fig. 2C). *Tapirus* sp. (bm: ~ 250 kg) probably was a browser in closed-canopy forests in Juruá River (-17.33‰) and mesic woodlands in Rondônia (-14.77‰ ; Table 1; Fig. 2C). The camelid *P. major* (bm: ~ 280 kg) was a browser in closed-canopy forest in Juruá River (-17.47‰), and the pampatheriid *H. rondoniensis* (bm: ~ 120 kg) and the cervid *Mazama* sp. (bm: ~ 40kg) were browsers in solely-mesic woodlands habitats in Rondônia (-14.89‰ and -15.47‰ , respectively; Table 1; Fig. 2C).

The $\delta^{18}O$ values are constantly low for all the species (19.90 to 25.80 ‰; Table 1; Supplementary Table 1; Fig. 2), indicating similar conditions in precipitation amount and degree of rainfall/transpiration for both forest and wooded savanna landscapes in localities of Acre and Rondônia states. The slightly $\delta^{18}O$ variations may have been influenced by monsoonal climates (wet and dry seasons) affecting the $\delta^{18}O$ values of

ingested water ($\delta^{18}\text{O}_{\text{mw}}$). The $\delta^{18}\text{O}_{\text{mw}}$ results for *N. platensis* point more ^{18}O -depleted water sources around the Madeira River in Rondônia (mean = $-9.50\text{‰} \pm 0.9\text{‰}$) compared to the localities of Juruá River in Acre (mean = $-7.51\text{‰} \pm 0.5\text{‰}$; Table 2). It corroborates with the lowest $\delta^{18}\text{O}$ values founded for the generalists *T. lopesi* and *Nechoerus* sp. also from Rondônia (20.29 ‰ and 19.90 ‰; Table 1; Fig. 2B and C). Their oxygen results plus the enriched $\delta^{13}\text{C}$ values can indicate a more open habitats close to riverine resources. By contrast, the browser *P. major* from Acre, showed the highest $\delta^{18}\text{O}$ value (25.80 ‰; Table 1; Fig. 2C), probably related to the consumption of more ^{18}O -enriched water sources. Although, the more depleted $\delta^{13}\text{C}$ values found in this camelid may also indicate a significant diet of foliage, and would explain the more positive oxygen value, because leaf water is more ^{18}O -enriched.

4. Discussion

4.1. Radiocarbon dating of mammal assemblages from southwestern Amazon

The AMS ^{14}C datings of the fossils indicate that the mammal assemblages from southwestern Amazon in Acre and Rondônia states are biostratigraphically correlated to the Lujanian Stage/Age SALMA. Late Pleistocene ages were obtained for Juruá and Madeira river records, which is in agreement to the chronological and biostratigraphy of fossiliferous deposits for both rivers (~ 43 to 29 ka BP and $\sim > 46$ to 27 Ka BP, respectively; Latrubesse and Rancy, 1998; Rizzotto and Oliveira, 2005), whereas an early Holocene age was obtained for the new record in Chandless River, Acre.

The Pleistocene assemblages are also chronologically correlated to the fossil records of other river basins of western Amazonia, including the Ucayali River, Peru (40 to 32 ka BP), Madre de Dios River, Peru (38 to 36 ka BP), and Caquetá River, Colombia (55 to 30 Ka BP; Latrubesse and Rancy, 1998).

372

373 4.2. *The habitat landscapes from late Quaternary of southwestern Amazon*

374 The isotopic carbon and oxygen signature of the late Quaternary mammals from
375 Acre and Rondônia states, support that the paleocommunity would have inhabited C₃-
376 dominated environments, with species occurring from closed-canopies, mesic woodlands
377 to wooded savannas (Fig. 3A-C). The suggested environmental heterogeneity also
378 characterizes the modern landscapes of the southwestern Amazon, consisting of non-
379 flooded "Terra Firme" and periodically flooded Várzea forests. The dominant regional
380 physiognomy is composed of spaced trees with few dense shrubby strata (open
381 ombrophilous forest), with floristic formations also composed of palm trees (e.g., *Attalea*
382 *speciosa*), bamboos (e.g., *Guadua superba*) and sororocas (e.g., *Phenakospermum*
383 *guianensis*). Closed canopy forests (dense ombrophilous forests) to open ones
384 conditioned by climate seasonality (semideciduous seasonal forests), mixed forest and
385 grassy-woody vegetation (campinaranas), and forested savannas also configure the
386 current physioecological zones of this rich Amazon region (IBGE, 2012).

387 The paleoenvironmental interpretation of the late Quaternary in Amazonia is an
388 issue still debated. Many paleoenvironmental reconstructions suggest that the distribution
389 of the Amazonian rainforest has changed mainly due to climatic fluctuations during
390 glacial/interglacial events. As consequence, it was proposed alternating periods of forest
391 contraction forming refuge regions followed by its expansion during distinct dry and wet
392 conditions (Haffer, 1969; Liu and Colinvaux, 1985; Bush et al., 1990; Colinvaux et al.,
393 1996; Ledru, 2002; Ledru et al., 2006), savanna corridors during Last Glaciation (van der
394 Hammen and Hooghiemstra, 2000), as well as retractions of equatorial rain forests
395 associate to expansion of tropical ones (similar to Atlantic forest; Arruda et al., 2017).
396 Nevertheless, some studies do not support these changes in landscapes, and suggest a

paleoclimatic scenario relatively undisturbed for Amazonian rainforest during the last 50 ka BP (Colinvaux et al., 1996, 2000, 2001; Bush et al., 2004; Irion et al., 2006; Mayle and Power, 2008).

The isotopic results of the mammalian fossils do not correspond with abrupt changes in the C₃ landscapes. The carbon and oxygen isotope values persist constantly low for all the specimens analyzed, including fossils of the glacial periods around ~ 30 to 25 ka BP (¹⁴C results of *Neochoeerus* sp and *N. platensis*, respectively), and of the beginning in interglacial period around ~11 ka BP (¹⁴C dating of *E. laurillard*). These data are in concordance with the isotope data of *T. platensis* specimens from Amazonian localities in Peru and Bolivia with ages ranging from ~ 38 ka to 15 ka BP evaluated by Macfadden (2005).

These results corroborate with the humid climate conditions during the late glacial - early Holocene estimated for the southwestern Amazon. Specifically, in Rondônia state, palynological analysis indicate that forests were dominant in Katira creek around 55 ka to 26 ka BP (van der Hammen and Absy, 1994) and in Madeira Formation during 46 to 27 ka BP (Rizzotto and Oliveira, 2005). Through isotopic, sedimentological and geomorphological analyses performed in a marginal area of Madeira river, Rossetti et al. (2017) also confirmed that the climate was wet and cold from 40 ka BP up to the Last Glaciation Maximum (LGM). Pollen data indicates the presence of cold-adapted plants (e.g., *Alnus*, *Hedyosmum*, *Weinmannia* and *Podocarpus*), which became absent in the Holocene, in association with herbs and tree taxa similar to modern ones (Cohen et al. 2014).

During the LGM, the humidity was reduced and the temperature was between 2° and 6°C below modern values (van der Hammen and Absy 1994; van der Hammen and Hooghiemstra 2000; Cohen et al. 2014). Thus, an intensified aridity toward the end of the

late Pleistocene was estimated in Madeira river region (Rossetti et al., 2017), whereas savanna expansion was proposed for Katira site related to a dry climatic phase between 26 to 13 ka BP (van der Hammen and Absy, 1994). On the other hand, in localities of Amazonas and Rondônia border, the carbon isotopes of soil organic matter suggest that these regions were still covered by forest vegetation between 17 to 9 ka BP (Freitas et al., 2001).

In spite of the carbon isotope results of *T. lopesi* and *Nechoerus* sp. from Rondônia indicating foraging in habitats with low proportion of C₄ plants (~30%), the isotopic signature consistently low for the most of the analyzed specimens do not support dominance of savanna habitats as previously inferred for the same assemblages in other studies (Latrubesse and Rancy, 1998; Ranzi, 2000; Ranzi, 2008). Ground sloths, proboscideans, toxodonts and cingulates were animals able to feeding on grasses, thus if the dry savanna habitats were present in southwestern Amazon, the carbon isotope values characteristic of C₄ plants would have been more significant. On the other hand, our data indicate that some species possibly were inhabiting closed canopy forests and consumed plants with carbon values below – 30‰. These values are seen in plants that are under the influence of the “canopy effect”, which produces ¹³C-depleted and a gradient of leaf δ¹³C values from the ground (most negative values) to the canopy (van der Merwe and Medina, 1991).

Furthermore, an interesting fossil record of *Guadua* sp. in Madre de Dios (Peru), which currently makes up extensive areas of bamboo forests in southwestern Amazonia, suggests that these forests were already present prior to the LGM (~ 3.12 ± 0.02 Ma and ~45 ka BP; Olivier et al., 2009), and that Pleistocene mammals could also have been accessed.

The depleted $\delta^{18}\text{O}_{\text{mw}}$ of *N. platensis* reflects to the "continental and amount effects" that occurs in tropical amazon. Thus, it seems consistent with speleothem and stalagmite oxygen isotope data from western Amazonia. For Cueva Santiago in Amazonian Ecuador the results do not indicate prolonged drying during the last 95 ka ($\delta^{18}\text{O} = -8.05$ to -4.52 ‰), and the climate condition during the LGM (23 ka and 19 ka BP) was wetter (Mosblech et al., 2012). Similarly, in El Condor and Cueva del Diamante caves, both located on the eastern flank of the Andes in northern Peru, indicate a wetter LGM and a drier early-mid Holocene in an opposite pattern to eastern Amazon (Cheng et al., 2013).

Based on oxygen isotopes in fluid inclusions from speleothems from Cueva del Tigre Perdido, in Peruvian Amazon, van Breukelen et al. (2008) proposed that the temperature change was small throughout the last ~13.5 ka BP, but the rainfall amount was reduced by 15–30% below present values. Thus, according to carbon isotopes of soil analysis the warmer and drier conditions could support savanna vegetation in Rondônia only during the early to middle Holocene, whereas during the late Holocene the moisture favored the expansion of the Amazonian rainforest as known today (Pessenda et al., 1998; Freitas et al., 2001). By contrast, any major shift of the forest vegetation toward open savanna was notified for the last 10 ka in the eastern Acre at Severino Calazans (Parssinen et al., in press).

~~4.1.4.3.~~ *Feeding ecology of the late Pleistocene mammals*

In the ancient assemblages of Amazon Quaternary mammals, most species were browsers feeding mostly on leaves and fruits of arboreal/scrub plants. The largest bodied species, *E. laurillardii* and *N. platensis*, probably occupied similar niches in southwestern Amazon, inhabiting from closed-canopy forests to mesic woodlands. The slightly wider range of carbon values for the proboscideans indicates a greater food plasticity (Fig. 4A

and B; Supplementary Table 1). *N. platensis* was an endemic proboscidean from South America, whose generalist diet was probably similar to the extant elephants. Diet followed habitat phytophysiology, and it consisted predominantly of herbaceous plants, foliar and floral branches, fruits and woody parts (Asevedo et al., 2012; 2020; Mothé et al., 2017). According to the carbon isotopes data, this proboscidean could have been a specialist C₃ browser in forest habitats of southwestern Amazon ($\mu\delta^{13}\text{C} = -15.39 \pm 1.63 \text{ ‰}$; median: -15.61; IQR: -2.21; Fig. 4B), but was a browser or mixed feeder in C₃ woodlands/grasslands from Pampean regions of Argentina, Uruguay and Brazil ($\mu\delta^{13}\text{C} = -8.2 \pm 2.1 \text{ ‰}$; median: -8.26; IQR: -1.4; Fig. 4B; Sánchez et al., 2004; Gutiérrez et al., 2005; Domingo et al., 2012; Lopes et al., 2013), a dominant grazing diet in C₄ grasslands in the Brazilian Intertropical Region (BIR; $\mu\delta^{13}\text{C} = -1.08 \pm 2.66 \text{ ‰}$; median: -0.20; IQR: -1.78; Fig. 4B; Sánchez et al., 2004; Viana et al., 2011; Dantas et al., 2013; França et al., 2014; Dantas et al., 2017; Pansani et al., 2019), and a mixed feeding diet in C₃-C₄ woodland/grassland landscapes in Andean regions of Ecuador and Peru ($\mu\delta^{13}\text{C} = -4.7 \pm 3.11 \text{ ‰}$; median: -5.72; IQR: -6.45; Fig. 4B; Sánchez et al., 2004; Domingo et al., 2012), and also in Argentinean Chaco ($\mu\delta^{13}\text{C} = -4.8 \pm 3.27 \text{ ‰}$; median: -4.63; IQR: -5.58; Fig. 4B; Alberdi et al., 2008; Domingo et al., 2012).

With a Pan-American distribution covering the southeastern North America to southern Brazil, the ground sloth *E. laurillardi* has also been estimated as a generalist species (Dantas et al., 2017). The carbon isotope analysis in specimens of the BIR demonstrated a large range that covers pure C₃ (browser), mixed feeders and pure C₄ (grazer) consumers ($\mu\delta^{13}\text{C} = -5.4 \pm 3.92 \text{ ‰}$; median: -5.11; IQR: -4.54; Fig. 4A; Viana et al., 2011; Dantas et al., 2013, 2014; França et al., 2014; Dantas et al., 2017; Pansani et al., 2019), differing from our results for an exclusive C₃ browser pattern in the Brazilian Amazon ($\mu\delta^{13}\text{C} = -15.92 \pm 1.38 \text{ ‰}$; median: -16.14; IQR: -2.60; Fig. 4A).

The reconstruction of the cranial musculature of *E. laurillardi* by Naples and McAfee (2012) suggested a masticatory pattern that could increase in efficiency for each chewing cycle. The high ability of oral processing related to the low digestive efficiency was suggested for the other American giant sloth species, *Megatherium Americanum* (Bargo et al., 2006). This species that had a similar biomechanical apparatus compared to *E. laurillardi*, probably was a generalized selective feeder, capable of consuming a variety of turgid or moderate to soft tough and abrasive food items (Oliveira et al., 2020). *E. laurillardi* would be able to browse on small branches, leaves, and fruits and possibly had a more selective diet in Amazonian localities than *N. platensis*.

On the other hand, the toxodonts, especially *T. lopesi*, have the highest ecological niche breadth among the megamammal species from Amazon, suggesting a more generalist diet between C₃/C₄ resources, tough in C₃ dominant-landscapes. These animals were native ungulates from Pleistocene of South America with very high-crowned teeth (hypsodont), presumably used for grazing abrasive plants (Bond et al., 1997). The isotopic data for *T. platensis*, whose paleoecological interpretations are more complete, have indicated capacity to feed on a variety of vegetation (Macfadden, 2005). *T. platensis* possibly had a predominant diet composed by foliage and fruit of wood plants in southwestern Amazon localities ($\mu\delta^{13}\text{C} = -13.39 \pm 1.49 \text{ ‰}$; median: -13; IQR: -2.35; Fig. 4C; Macfadden, 2005), different than individuals from the BIR that had a wide food spectrum, ranging from browsers to grazers on C₃ plants and mixed C₃-C₄ diets in woodlands and grasslands, and also in open C₄-dominated grasslands habitats ($\mu\delta^{13}\text{C} = -5.08 \pm 5.76 \text{ ‰}$; median: -4.22; IQR: -10.81; Fig. 4C; Macfadden, 2005; Viana et al., 2011; Dantas et al., 2013; França et al., 2014; Dantas et al., 2017; Pansani et al., 2019). *T. platensis* from Argentinean and Brazilian Pampa also had mixed C₃/C₄ diets ($\mu\delta^{13}\text{C} = -6.03 \pm 2.66 \text{ ‰}$; median: -5.15; IQR: -3.28; Fig. 4C; Macfadden, 2005; Lopes et al.,

2013), whereas the individuals from the Bolivian and Argentinean Chaco had a more specialized grazer diet in C₄-dominated open grasslands ($\mu\delta^{13}\text{C} = 0.38 \pm 1.21 \text{ ‰}$; median: -0.40; IQR: -2; Fig. 4C; Macfadden, 2005).

Unfortunately, there are no other paleoecological inferences for *T. lopesi* that would facilitate the understanding of its feeding behavior. This species had an intertropical distribution in northern, northeastern and southeastern Brazil and could have coexisted with *T. platensis*, who was widely distributed in South America (Mendonça, 2012). The less negative value of carbon isotope from *T. lopesi* suggests a more generalist diet compared to *T. platensis*. However, this only result is insufficient to presuppose distinction between their ecological niches, thus more investigations are needed.

Regarding large and medium-sized species, the extinct capybara *Neochoerus* sp. has the highest ecological niche breadth. It presented carbon and oxygen isotope values very similar to the sympatric *T. lopesi* from Rondônia region (Table 1), indicating a more C₃-C₄ generalist diet in wooded savanna habitats closely of ¹⁸O-depleted water sources (Fig. 3C). The current capybara *Hydrochoerus hydrochaeris* Linnaeus, 1766 has semiaquatic habit and are native to wetlands in South America. This rodent are folivores and consumes protein-rich plants near water bodies, particularly grasses and sedges (Corriale and Loponte, 2015). The carbon stable isotopes from dental bioapatite of specimens from Amazonian Peru indicate a C₄ diet ($\mu\delta^{13}\text{C} = -1.6 \pm 3.4 \text{ ‰}$; Tejada-Lara et al., 2020), whereas the species in Corrientes province, Argentina, consume predominantly C₃ grasses and sedges ($\mu\delta^{13}\text{C}_{\text{collagen}} = -15.7 \pm 0.3 \text{ ‰}$; $\delta^{13}\text{C}_{\text{bioapatite}} = \sim -6 \text{ ‰}$; Corriale and Loponte, 2015). Thus, based on feeding behavior of living capybaras we presumed that a significant portion of the Pleistocene capybara diet was also composed of herbaceous plants.

The camelid *P. major* probably had a more selective browser diet for the consumption of dicot foliage plants, due to the very negative $\delta^{13}\text{C}$ values. Leaves are more depleted in ^{13}C than other vegetative structures such as roots, stems and fruits (Badeck et al., 2005). In addition, this specimen presented $\delta^{18}\text{O}$ value more positive than other taxa that could be associated to ingestion of more ^{18}O -enriched water sources, but could also be the reflection of a folivore diet, since leaf water is more ^{18}O -enriched than meteoric water (Sponheimer and Lee-Torp, 1999). The oxygen isotope aridity index for several Pleistocene taxa from southeastern and southwestern United States developed by Yann et al. (2013), discriminates the camelids (i.e., *Palaeolama* and *Hemiauchenia*) with the greatest mean aridity index followed by antilocaprids and cervids. This supports the argument that most $\delta^{18}\text{O}$ values of those taxa comes from the water in food ingested instead the meteoric water, thus corroborating with the folivore diet inference for the camelid from southwestern Amazon.

The identification of leaves and branches of shrub angiosperms fossil remains in *P. major* coprolites from BIR in Bahia state strengthens the inference of a browser diet (Marcolino et al., 2012). Stable isotope data from that region indicates significant consumption of C_3 plants ($\delta^{13}\text{C} = -7.34\text{‰}$; Dantas et al., 2020), therefore in a predominantly open landscape the species probably could inhabit forest edges (Marcolino et al., 2012). Accordingly, browser habits could be a predominant behavior for this camelid.

For the fossils of extant taxa, *Tapirus* sp. and *Mazama* sp., the fruit consumption could be more abundant than for the *P. major* in late Pleistocene. The lowland tapir *Tapirus terrestris* is the largest terrestrial mammal in South America, which occurs from Colombia to northern Argentina in a wide range of ecosystems, including tropical moist forest, xeric Chaco and Cerrado forest, savanna wetlands, and lower montane forest

(Bodmer, 1990b). *T. terrestris* has a primarily browsing diet, and when the fruits are available may consume extensively (Bodmer, 1990b). Thus, the tapir plays a key role in dispersing seeds, especially large ones, for over longer distances, due to their large home range, varying from 220 to 470 ha (Fragoso et al., 2000, 2003). Similar to our results, the isotopic data of carbon of extant *T. terrestris* in localities of Brazil, Colombia, Venezuela, Peru and Bolivia shows low values associated with high proportion of wood plants consumption ($\mu\delta^{13}\text{C} = -13.6 \pm 1.6 \text{ ‰}$; DeSantis, 2011).

The red brocket deer *Mazama americana* is one of the most abundant and widely distributed cervids in Neotropical forests (Redford and Eisenberg, 1992; Eisenberg and Redford, 1999). Its distribution area ranges from Colombia and Venezuela to northern Argentina and southern Brazil, and also occur in a variety of ecosystems such as montane forests, lowland dry forest, rainforests and savannas located near forest edges (Emmons and Feer, 1997). Feeding ecology data from Amazonian populations indicate a fruit and seed-eating diet, whereas leaves, flowers and fungi are also consumed in less quantity (Branan et al., 1985; Bodmer, 1990a, Gayot et al., 2004). A seasonal change in feeding habits was observed by Branan et al. (1985) in Surinam forests, where diet became folivorous due to fruit scarcity during dry season. Geographic differences in the diet can be observed comparing studies made in French Guyana (Gayot et al., 2004) and in the Peruvian Amazon (Bodmer, 1990a), where the proportions of fruit in diet were 56 % and 81 %, respectively.

In the Parque Estadual Chandless (PEC), Acre state, *T. terrestris* and *M. americana* co-occur in a mosaic of heterogeneous forest landscapes, where flood pulses and the presence of open forests subject to the dynamics exerted by the presence of bamboo form a complex of successional gradients (Borges, 2014). *T. terrestris* occurs predominantly in patches of forests near rivers or forest creeks (igarapés) with a predominance of small

branches of pioneer plant species and succulent shoots, sometimes it was observed consuming stems and leaves of young individuals of *Cecropia* sp. and other pioneer species. *M. americana*, in turn, apparently avoided denser forests and opted for more open areas. Bodmer (1990) working with large ungulates in the Ucayali River region, Peru, found that *M. americana* tends to avoid floodplains, although this pattern was not clearly noted in the PEC (Borges, 2014).

The carbon isotope composition of modern *T. terrestris* and *M. americana* from Madre de Dios in Peruvian Amazon ($\mu\delta^{13}\text{C} = -14.6\text{‰} \pm 0.6\text{‰}$ and $-13.1 \pm 1.1\text{‰}$, respectively; Tejada-Lara et al., 2020), and the carbon isotope composition in collagen from Venezuelan Amazon ($\delta^{13}\text{C}_{\text{collagen}} = -23.5\text{‰}$; $\delta^{13}\text{C}_{\text{bioapatite}} = -15.5\text{‰}$ and -21.7‰ ; -14.7‰ , respectively; van der Merwe and Medina, 1991) did not diagnose very significant differences, although the slight difference was attributed to different dietary compositions between leaves and fruits. These values are similar to our data for the late Pleistocene, *T. terrestris* ($\mu\delta^{13}\text{C} = -16.05\text{‰}$) with more negative values associated with a greater preference for more enclosed environments than *Mazama* sp. ($\delta^{13}\text{C} = -15.47\text{‰}$). Thus, we infer that with similar strategies to the present, these ungulates would have different foraging strategies, varying spatially and even seasonally in order to avoid interspecific competitions.

Finally, the isotope value of carbon suggests a browsing diet for the pampatheriid *H. rondoniensis* that inhabited mesic woodlands habitats in the Rondônia region, and contrasts with the dominant grazing habit for the genus suggested by morphological analysis of teeth and mandibular apparatus (Vizcaíno et al., 1998). Despite the efficiency in consuming more abrasive vegetation, the previous inference supports that the taxon was not a strictly grazer. A mixed C₃-C₄ diet of woody and grassy plants was suggested by stable isotope analysis for *H. paulacoutoi* species that inhabited the BIR during the

late Pleistocene ($\delta^{13}\text{C} = -6.05\text{‰}$; Dantas et al., 2020), indicating that these cingulates could also have a more generalist diet. *Holmesina* is associated with wetter and warmer climate environments when compared to the pampatheriid *Pampatherium* from arid and cold environments (Vizcaíno et al., 1998; De Iuliis et al., 2001; Scillato-Yané et al., 2005), and may correspond with the occurrence in more forested landscapes in southwestern Amazonia. It is possible that the analyzed individual of *H. rondoniensis* was foraging on the understory vegetation, feeding predominantly on foliage and fruits of tree/shrub plants, although herbaceous plants were also potentially consumed by these animals.

4.2.4.4. *Niche partitioning strategies and ecological roles from the late Pleistocene mammal assemblages*

In terrestrial ecosystems composed by assemblages of large mammals, the megaherbivores ($\geq 1,000\text{ kg}$) are considered ecological engineers capable of altering vegetation on a landscape scale. With large body size they may disrupt ecosystem structure by directly destroying woody vegetation and consuming large amounts of foliage, and therefore they are generally considered to be limited from the “bottom-up” by food availability, though exert strong “top-down” control on vegetation structure and composition (Owen-Smith, 1992).

The modern elephant *Loxodonta africana* Blumenbach, 1797 is considered a key species structuring savanna ecosystems. It acts in the modeling of the environment, facilitating the access to resources by other middle-sized species, and limiting the abundance of other megamammal species through the competition for resources (Fritz et al., 2002).

With an ecological role similar to extant elephants, we presuppose that the species with the largest body mass, *N. platensis* (6,300 kg) and *E. laurillardii* (3,500 kg), were

probably the key species that ~~which~~ structured mammal assemblages in the southwestern Amazon during the late Pleistocene. Both species were potentially competitors, although the great plasticity and foraging ability of the proboscideans could contribute for a larger home range and possibility to access different resources. The toxodonts *T. lopesi* and *T. platensis* with a lower similar body mass (~ 1,900 kg) could be competitively excluded, thus forced to forage slightly more open environments including the woodlands and arboreal savannas, resulting in a more generalized diet.

Species with larger body mass have a more homogeneous spatial distribution than smaller ones, because their tolerance for lower quality resource consumption (i.e., fibrous foods with low protein content) allows them to use more diverse habitats, alleviating interspecific competition (Owen-Smith, 1992). Thus, the camelid *P. major* (~ 280 kg) that inhabited subcanopies had a possibly strictly folivorous diet, whereas the tapir *Tapirus* sp. (~ 250 kg) had a more diverse diet and the fruits were important dietary items, similar to cervid *Mazama* sp. (~ 40 kg). Although, the tapir possibly foraged more in denser forests and in areas close to water bodies such as igarapés or in floodplain (várzea) forest and rivers compared to the cervid. The pampatheriid *H. rondoniensis* (~ 120 kg) was also a browser in this region, but not restricted and could also feed on herbaceous from understories, and the giant capybara *Nechoerus* sp. (~ 200 kg) with similar diet behavior as the living *Hydrochoerus*, probably fed predominantly C₃ herbaceous and few C₄ grasses near water bodies.

Comparison of our data with several previous studies about the paleoecology of the analyzed specimens, permit to assume that resource partitioning and different behaviors in habitat use were the main mechanisms for reducing interspecific competition and the maintenance of the coexistence of large herbivorous mammal assemblages that inhabited the late Pleistocene of southwestern Amazon. Similarly, Dantas et al. (2017) were also

able to infer the structure of the assemblages, the partitioning and overlapping niches of the Pleistocene megamammals that inhabited the BIR, comparing the results of stable isotopes of carbon and oxygen with the current mammal assemblages of the Africa.

The megamammal species probably could have played important roles in the Amazon forest ecosystem during the late Quaternary, contributing for a greater habitat heterogeneity (i), because the herbivore pressure may vary across the space, resulting in a mosaic landscape (Malhi et al., 2016). Greater variation in floristic composition (ii), due to the large capacity of large fruit seed dispersal for greater distances than large modern ones as the tapirs, thus contributing to increased gene flow between plant populations (Guimarães et al., 2008). The megamammals could also contribute increasing the longevity of mature forest trees and higher forest biomass (iii), due to high pressure by consumption of the understory and subcanopies plants, which can reduce the below-ground competition for nutrients (Terborgh et al., 2015a, b), as well as by accelerating the ecosystem biogeochemical cycling (iv), because nutrients that would be locked for years in leaves and stems are liberated for use through animal consumption, digestion, defecation, and urination, and the nutrients in recalcitrant woody biomass are moved to the decomposition pool through breakage and plant mortality (Malhi et al., 2016).

5. Conclusions

The carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) stable isotope analyses aided in the comprehension of some aspects of feeding ecology and habitats of medium- and mega-herbivores mammals that inhabited the southwestern Amazon during the late Quaternary. The isotopic data together with previous paleoecological interpretations of the studied species, and some information regarding feeding behavior of living species allowed refining the interpretations about the diet and possible ecological interactions. According

to the $\delta^{13}\text{C}_{\text{VPDB}}$ (-17.47‰ to -8.83‰) and $\delta^{18}\text{O}_{\text{VSMOW}}$ (19.90 to 25.80‰) results, the Amazonian late Quaternary mammals inhabited heterogeneous forest habitats, which facilitated the resource partitioning and the use of distinct habitats. The mammal assemblages were composed mostly by browsers, with the only exception being the C_3 and C_4 generalists *Trigodonops lopesi* and *Nechoerus* sp. ($p_i\text{C}_3 = \sim 70\%$; $B_A = \sim 0.75$). The largest bodied species, *Eremotherium laurillardi* and *Notiomastodon platensis*, were probably key species that structured the assemblages through ecosystem modelling, facilitating the access to resources by other large and middle-sized species (e.g., cingulates, tapirs, camelids and cervids), and limiting the abundance of other megamammal species through the competition for resources (e.g., toxodonts). Further paleoecological reconstructions are needed, in order to better understand the paleoenvironmental scenarios and ecological interactions of the mammal species that inhabited the southwestern Amazon during the late Quaternary.

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Figure captions

Fig. 1. Localities of the late Quaternary mammals from southwestern Amazon at along the banks of Juruá (locality 1, a-d) and Chandless rivers (locality 2) in Acre state, as also in Araras locality, Madeira Rriver (locality 3) in Rondônia state, Brazil. The localities of *Toxodon platensis* from Peru and Bolivia (localities 4-9) are from Macfadden (2005).

Fig. 2. Bivariate plot with $\delta^{13}\text{C}_{\text{VPDB}}$ and $\delta^{18}\text{O}_{\text{VSMOW}}$ values from late Quaternary herbivorous mammals of the southwestern Amazonia. The enrichment ranges of $\delta^{13}\text{C}$ values were according to the body mass by Tejada-Lara et al. (2018). A) species with body mass > 3,500 kg ($\epsilon^* = 15 \text{ ‰}$). B) species with body mass between 3,500 to 600 kg ($\epsilon^* = 14 \text{ ‰}$). C) species with body mass between 600 to 75 kg and < 75 kg ($\epsilon^* = 13$ and

12 ‰, respectively). The traces represent the average of $\delta^{13}\text{C}$ values for C_3 and C_4 resources.

Fig. 3. Reconstruction of late Quaternary herbivorous mammals from southwestern Amazon in distinct phytodomains. A) *Tapirus* sp., *Palaeolama major*, *Notiomastodon platensis* and *Eremotherium laurillardi* (from left to right) in closed-canopy forest habitat. B) *Holmesina rondoniensis*, *Toxodon platensis* and *Mazama* sp. (from left to right) in mesic woodland, and C) *Nechoerus* sp. and *Trigodonops lopesi* in arboreal savanna habitat. Artist Beatriz Grigio.

Fig. 4. Box-plot of $\delta^{13}\text{C}_{\text{VPDB}}$ values for the Pleistocene megaherbivores species *Eremotherium laurillardi* (A), *Notiomastodon platensis* (B), *Toxodon platensis* and *Trigodonops lopesi* (C) from southwestern Amazon compared to different ecoregions from South America. Abbreviation: Tri = *Trigodonops lopesi*. Ecoregions: Brazilian Intertropical Region (= BIR; Northeast, Midwest and Southeast of Brazil; Sánchez et al., 2004; Macfadden, 2005; Viana et al., 2011; Dantas et al., 2013, França et al., 2014; Pansani et al., 2019; Dantas et al., 2017), Andean (Ecuador and Peru; Sánchez et al., 2004; Domingo et al., 2012), Chaco (Bolivia and Argentina; Macfadden, 2005; Alberdi et al., 2008; Domingo et al., 2012) and Pampa (Argentina, Uruguay and Brazil; Sánchez et al., 2004; Macfadden, 2005; Gutiérrez et al., 2005; Domingo et al., 2012; Lopes et al., 2013).

Table caption

Table 1. Mean values of $\delta^{13}\text{C}_{\text{VPDB}}$ and $\delta^{18}\text{O}_{\text{VSMOW}}$, proportional contributions of diet sources (pC_3 plants, pC_4 plants) and standardized isotopic niche breadth (B_A) from Quaternary mammal assemblages of southwestern Amazon. A) Araras, Madeira River,

Rondônia state, B) Upper Juruá and Chandless rivers, Acre state, Brazil, C) and D) localities of Bolivia and Peru, respectively from Macfadden (2005). Acronym: BM = Body mass. References: a: Dantas et al. (2020), b: Dantas (2019), c: Padilla and Dowler (1994), d: Ghizzoni (2014), e: Duarte and Jorge (1996).

Table 2. Values of $\delta^{18}\text{O}_{\text{P-VSMOW}}$ and $\delta^{18}\text{O}_{\text{mwVSMOW}}$ obtained from oxygen isotopes in carbonate enamel ($\delta^{18}\text{O}_{\text{C}}$) of *Notiomastodon platensis* from southwestern Amazon.

Supplementary material

Supplementary Table 1. Summary data of $\delta^{13}\text{C}_{\text{VPDB}}$ and $\delta^{18}\text{O}_{\text{VSMOW}}$ values and ^{14}C AMS datings of Quaternary mammal species from southwestern Amazon. Abbreviations: E = enamel, D = dentine and B = bone. Carbon and oxygen isotope data of *Toxodon platensis* from Peru and Bolivia by Macfadden (2005).

Fig. 1

Fig. 2

Fig. 3A

Fig. 3B

Fig. 3C

Fig. 4

Table 1.

Species	BM (~Kg)	n	$\delta^{13}\text{C} \text{ ‰ VPDB}$	$p\text{‰C3}$	$p\text{‰C4}$	B_A	$\delta^{18}\text{O} \text{ ‰ VSMOW}$
A)							
<i>E. laurillardii</i>	3,500 ^a	1	− 14.23	1.00	0.00	0.00	22.72
<i>N. platensis</i>	6,300 ^a	5	− 15.9 ± 1.2	1.00	0.00	0.00	23.07 ± 0.9
<i>T. lopesi</i>	1,900 ^b	1	− 8.83	0.70	0.30	0.72	20.29
<i>Tapirus</i> sp.	250 ^c	1	− 14.77	1.00	0.00	0.00	21.30
<i>H. rondoniensis</i>	120 ^a	1	− 14.89	1.00	0.00	0.00	21.37
<i>Nechoerus</i> sp.	200 ^d	1	− 9.66	0.69	0.31	0.75	19.90
<i>Mazama</i> sp.	40 ^e	1	− 15.47	1.00	0.00	0.00	23.57
B)							
<i>E. laurillardii</i>	3,500 ^a	3	− 16.5 ± 1.0	1.00	0.00	0.00	23.31 ± 1.1
<i>N. platensis</i>	6,300 ^a	2	− 14.1 ± 2.4	1.00	0.00	0.00	24.95 ± 0.5
<i>P. major</i>	280 ^a	1	− 17.47	1.00	0.00	0.00	25.80
<i>Tapirus</i> sp.	250 ^c	1	− 17.33	1.00	0.00	0.00	22.80
C)							
<i>T. platensis</i>	1,800 ^a	5	− 13.9 ± 1.6	≥ 0.86	≤ 0.14	≤ 0.32	25.11 ± 1.6
D)							
<i>T. platensis</i>	1,800 ^a	12	− 13.2 ± 1.4	≥ 0.84	≤ 0.16	≤ 0.38	26.05 ± 1.6

Table 2.

Colection code	Locality	$\delta^{18}\text{Op}\text{‰}$	$\delta^{18}\text{Ow}\text{‰}$
MERO ARQ 016	Madeira River, RO	14.46	-9.40
MERO PV 132 e 136	Madeira River, RO	14.73	-9.12
MERO PV 138	Madeira River, RO	12.96	-10.99
UFAC 1214	Madeira River, RO	14.21	-9.67
UFAC 4408	Madeira River, RO	15.51	-8.29
UFAC 104	Juruá River, AC	15.91	-7.86
UFAC PV 95	Juruá River, AC	16.58	-7.15

Supplementary Table 1.

Species	Collectioncode	Sample	Locality	$\delta^{13}\text{C} \text{ ‰ VPDB}$	$\delta^{18}\text{O} \text{ ‰ VSMOW}$	Calibrated Age (^{14}C)
<i>Notiomastodon platensis</i>	MERO ARQ 016	E	Araras, Madeira River, Nova Mamoré, Rondônia	-16.93	23.16	25,454 - 24,884
	MERO PV 132 e 136	E	Araras, Madeira River, Nova Mamoré, Rondônia	-17.29	23.43	
	MERO PV 138	E	Araras, Madeira River, Nova Mamoré, Rondônia	-15.61	21.66	
	UFAC PV 1214	E	Araras, Madeira River, Nova Mamoré, Rondônia	-14.72	22.91	
	UFAC PV 4408	E	Araras, Madeira River, Nova Mamoré, Rondônia	-14.95	24.21	
	UFAC PV 104	E	Pedra Preta, Juruá River, Acre	-15.83	24.61	
	UFAC PV 95	E	Pedra Preta, Juruá River, Acre	-12.39	25.28	
<i>Eremotherium laurillardi</i>	MERO PV 059	B	Araras, Madeira River, Nova Mamoré, Rondônia	-14.23	22.72	11,320 - 11,131
	UFAC PV 98	B	Arenal, Juruá River, Cruzeiro do Sul, Acre	-16.90	24.09	
	EL 06 s/cod	B	Juruá River, Acre	-17.19	23.77	
	UFAC PV 6450	B	ChandlersRiver, Acre	-15.37	22.07	
<i>Palaeolama major</i>	UFAC PV 061	D	Igarapé São Luis, Juruá River, Acre	-17.47	25.80	
<i>Tapirus</i> sp.	UFAC PV 035	B	Torre da Lua, Juruá River, Cruzeiro do Sul, Acre	-17.33	22.28	
<i>Homelsinarondoniensis</i>	MERO-P-002	B	Araras, Madeira River, Nova Mamoré, Rondônia	-14.89	21.37	
<i>Neochoeerus</i> sp.	MERO (no code)	D	Araras, Madeira River, Nova Mamoré, Rondônia	-9.66	19.90	29,072 - 27,713
<i>Mazama</i> sp.	UFAC PV 4435B	B	Araras, Madeira River, Nova Mamoré, Rondônia	-15.47	23.57	
<i>Trigodonopslopesi</i>	MERO PV 100	D	Araras, Madeira River, Nova Mamoré, Rondônia	-8.83	20.29	

Species	Collectioncode	Sample	Locality	‰VPDB	$\delta^{18}\text{O}$ ‰ <u>VSMOW</u>
<i>Toxodon platensis</i>	U-C1010	E	Beni-Yucuma-Maracas, Bolivia	– 11.00	
	U-C1011	E	Beni-Yucuma-Maracas, Bolivia	– 15.10	
	U-C1019-20	E	Beni-Yucuma-Maracas, Bolivia	– 14.70	
	U-C1012	E	Pando-Cobija, Bolivia	– 14.00	
	U-C1013	E	Pando-Cobija, Bolivia	– 14.50	
	U-C1018	E	Madre de Dios, Peru	– 13.00	
	F-04-001	E	InuyaRiver, Peru	– 12.50	
	F-04-002	E	InuyaRiver, Peru	– 10.70	
	F-04-003	E	InuyaRiver, Peru	– 12.70	
	F-04-004	E	InuyaRiver, Peru	– 11.70	
	F-04-005	E	PisquiRiver, Ucayali, Peru	– 15.30	
	F-04-006	E	Mapuya, Peru	– 12.30	
	F-04-007	E	Mapuya, Peru	– 13.00	
	F-04-008	E	Mapuya, Peru	– 12.80	
	F-04-009	E	Mapuya, Peru	– 15.40	
	F-04-010	E	Mapuya, Peru	– 14.10	
	F-04-011	E	Contamana, Peru	– 14.80	