Niche partitioning in small mammals: interspecific and biome-level analyses using stable isotopes

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Small mammal assemblages from South America provide a unique opportunity to measure coexistence and niche partitioning between marsupials and placentals. We tested how these two major clades partition environmental resources by comparing stable isotopic ratios of similar sized Didelphidae and Sigmodontinae in four Brazilian biomes: Pampas grassland, Pantanal wetland, Cerrado woodland savanna, and Atlantic Forest. Generally, didelphid isotopic niche follows a scaling law, because we found an association between $\delta^{15}N$ enrichment and body mass. Sigmodontines that primarily partition the environment via forest strata showed a greater intake of C_4 or/and crassulacean acid metabolism (CAM) plants than didelphids, as reflected by their wider trophic niche. Values of $\delta^{13}C$ were highest in savannas and grasslands (Cerrado and Pampas biomes), and values of $\delta^{15}N$ were highest in the Atlantic Forest (in sigmodontines) and Pampas (in didelphids). While assessing patterns between the two major Brazilian biomes (Atlantic Forest and Cerrado), we found evidence of a broader trophic niche for both clades in the Cerrado. In the Atlantic Forest, niche occupation by Didelphidae was completely enclosed within the Sigmodontinae trophic niche. Both clades showed less overlap in the Cerrado, a less productive environment. Our results highlight the importance of a comparative framework and the use of stable isotopes for testing ecological questions related to how small mammalian communities partition their niche.

Key words: coexistence, Didelphidae, diet, food resource, forest strata use, phylogenetic approach, Sigmodontinae

Na América do Sul, as assembleias de pequenos mamíferos proporcionam uma oportunidade única de analisar a coexistência e partição de nicho entre marsupiais e placentários. Neste estudo, testamos como estes dois clados particionam os recursos do ambiente através da comparação das razões de isótopos estáveis em Didelphidae e Sigmodontinae. O nicho isotópico de didelfídeos segue a regra de escala, uma vez que encontramos associação entre o enriquecimento de $\delta^{15}N$ e massa corporal. Sigmodontíneos, que particionam o ambiente primariamente através do estrato vertical, apresentam maior consumo de plantas C_4 ou/e CAM que didelfídeos, refletindo no seu maior nicho trófico. Os valores de $\delta^{13}C$ são maiores no Cerrado e Pampa, enquanto os valores de $\delta^{15}N$ são maiores na Floresta Atlântica (em sigmodontíneos) e no Pampa (em didelfídeos). Ao verificar estes padrões comparativamente entre dois grandes biomas brasileiros (Floresta Atlântica e Cerrado), encontramos evidências

de um nicho ecológico mais amplo para os dois clados no Cerrado. Na Floresta Atlântica a ocupação de nicho de Didelphidae está completamente anexada dentro do nicho de Sigmodontinae. Ambos os clados possuem menor sobreposição de nicho no Cerrado, que é um ambiente menos produtivo. Nossos resultados destacam a importância de estudos comparativos e do uso de isótopos estáveis para entender como comunidades de pequenos mamíferos particionam seus nichos.

South America hosts a large diversity of nonvolant small mammals, made up of community assemblages of two evolutionarily distinct clades: Marsupialia and Placentalia. Studies of South American small marsupials, mostly represented by the diverse Didelphidae clade, have shown that diversification rates of these animals are lower than expected compared with other mammal clades (Jansa et al. 2014). In contrast, morphological evidence showed rapid-diversification rates in Sigmodontinae rodents, the most diverse South American clade of placentals (Maestri et al. 2016a). The evolutionary history of these two groups was influenced by different and well-known biogeographical events: the Splendid Isolation in which South American marsupials remained isolated over most of the Cenozoic (Simpson 1980), and the Great American Interchange (GABI) when most placental extant groups dispersed from North to South America, facilitated by the formation of the Isthmus of Panama (hypothesized ca. 2.8 Ma—O'Dea et al. 2016). Didelphids and sigmodontines often share the same environments and, to some extent, have morphological similarities relative to locomotion (Bubadué et al. 2019).

In Brazil, didelphids and sigmodontines overlap across all six biomes recognized by the Instituto Brasileiro de Geografia e Estatística (IBGE 2019): Atlantic Forest, Amazon Rainforest, Pantanal wetland, Caatinga scrubland, Cerrado woodland savanna, and Pampas grassland (Paglia et al. 2012). To cope with coexistence across the wide range of the vegetational domains found in Brazil, small mammals can partition their environment using food resources as well as spatial and temporal differences (Vieira and Monteiro-Filho 2003; Novillo et al. 2017; Ribeiro et al. 2019), none of which are exclusive strategies to avoid competition. Because of the wide range of different biomes where these mammals successfully coexist, we highlight the importance of estimating how they potentially can use these strategies across different biomes.

Didelphids and sigmodontines include a wide range of species to some extent displaying similar feeding habits (Vieira and de Moraes 2003; Arregoitia and D'Elía 2020; Bubadué et al. 2021). Previous dietary studies showed marsupials to be more generalist than sigmodontine rodents because species have a larger variety of food items depending on seasonal and/or environmental availability (Cáceres 2002, 2004; Vieira and de Moraes 2003), even when specialized for the consumption of specific food items in their core diet (Vieira and de Moraes 2003). On the other hand, sigmodontines are characterized by broad dietary niches (Arregoitia and D'Elía 2020), larger species diversity and dietary specializations than marsupials (Maestri et al. 2017; Arregoitia and D'Elía 2020), and often presenting more specialized phenotypes (Maestri et al. 2016b;

Arregoitia et al. 2017; Missagia et al. 2021). When studying small mammal communities, however, we can encounter particular difficulties relative to species food preferences, because detailed and confident information on species diet is scarce for both clades (Vieira and de Moraes 2003; Arregoitia and D'Elía 2020), often requiring researchers to work with extrapolated and overly simplified data (e.g., Maestri et al. 2017; Chemisquy et al. 2021). As a potential remedy, stable isotope analyses can provide novel information on species use of resources (Ben-David and Flaherty 2012; Missagia et al. 2019). Such studies shed light on the coexistence patterns between rodents and marsupials through quantification of the trophic niche and feeding ecology (Mauffrey and Catzeflis 2003; Galetti et al. 2016; Missagia et al. 2019). Studies on sympatric rodents (Bovendorp et al. 2017a) and marsupials (Kuhnen et al. 2017) support partial feeding overlap between species that might exhibit wide or narrower isotopic niches relative to different degrees of omnivory. In Atlantic Forest communities, Galetti et al. (2016) identified broader isotopic niche space for rodents than marsupials. They also found species locomotory habits to influence isotopic composition in different taxa. Ribeiro et al. (2019) demonstrated that isotopic niches of small mammals from the Brazilian Cerrado biome can vary according to food availability, species dietary preferences, and habitat complexity, while Missagia et al. (2019) recently demonstrated, using a phylogenetic approach in akodontine rodents, that isotopic trophic diversity varies more within than between clades.

Stable isotope analysis is a useful tool to study mammalian ecology (Crawford et al. 2008), but several factors can affect correct interpretation of its results. In general, $\delta^{15}N$ values increase with trophic level, and $\delta^{13}C$ differences between C_3 and C_4 plants are reflected in $\delta^{13}C$ values of plants that herbivores eat and, subsequently, in their predators (Ben-David and Flaherty 2012). In addition, if carefully interpreted, isotopes can be used to investigate the contribution of particular food sources in diverse communities (e.g., Whitney et al. 2018) and for individual preferences within a species (e.g., Voigt and Kelm 2006). Mixed models have been applied to estimate the proportional contributions of food sources to the isotopic composition of the consumer tissues at the local scale (Phillips 2012). Although this approach can be difficult to implement on a broader geographical scale, published data provide a good overview on the isotopic range of small mammals in different areas of the Neotropics and how to interpret them as to their potential dietary sources. For example, higher $\delta^{15}N$ values (> 3‰) in small mammals from Atlantic Forest most likely are associated with higher degree of faunivory, particularly consumption of arthropods, but

also fungi, whereas low $\delta^{15}N$ levels are associated with preference for plant items such as fruits or leaves (Galetti et al. 2016; Bovendorp et al. 2017a). High $\delta^{13}C$ values (> −20‰) suggest consumption of C_4 and/or crassulacean acid metabolism (CAM) plants by small mammals in the Atlantic Forest (Galetti et al. 2016). Results and interpretations are similar for Cerrado, but $\delta^{15}N$ values seem to vary more than in the Atlantic Forest (Galetti et al. 2016 compared with Ribeiro et al. 2019). To our knowledge, no isotopic study on small mammal communities has incorporated other Neotropical biomes, and no comparative studies have been carried out among biomes, including forest, savannah, wetland, and grassland ecotypes.

We combined isotopic and comparative approaches to test how the trophic niche of small mammals varied interspecifically and across four of the six Brazilian biomes: Pampas grassland, Pantanal wetland, Atlantic Forest, and Cerrado woodland savanna. At the interspecific level, we aimed to compare the trophic niche between marsupials and rodents using a comparative/phylogenetic approach. We were interested in the level of phylogenetic structure and amount of isotopic variation within each clade, Didelphidae and Sigmodontinae, and the level of overlap between them. As rodents and marsupials share and partition the environment, particularly based on use of distinct forest strata (Vieira and Monteiro-Filho 2003; Vieira and Camargo 2012) and body mass (see spatial scaling law of Ritchie and Olff 1999), we evaluated the relationship of species average body mass, diet, and locomotor categories, with $\delta^{13}C$ and $\delta^{15}N$ values.

Considering the variation across biomes, we tested for the impact of local climate on stable isotopes of the sampled small mammals because isotopes can vary depending on environmental conditions of each site (Handley et al. 1999). We also compared the level of overlap between didelphids and sigmodontines within and between the two largest biomes within our sample, Atlantic Forest and Cerrado woodland savanna. Finally, by quantifying trajectories of changes in isotopic values between clades from the Cerrado to the Atlantic Forest, we aimed to identify patterns of trophic shift toward similar environments using the method proposed by Turner et al. (2010). Based on results from previous research (Atlantic Forest—Galetti et al. 2016; Cerrado—Ribeiro et al. 2019), we predicted that Cerrado species would show higher $\delta^{13}C$ and $\delta^{15}N$ values than for both clades in the Atlantic Forest. This is because the Cerrado biome has fewer stable environments where arthropod availability remains constant while fruit availability does not (Ribeiro et al. 2019), and it is also richer in C_4 plants compared with other Brazilian forests. Eventually, this would increase variation in the Cerrado biome, and therefore we predicted the trophic niche to be wider for both clades in this biome than in the Atlantic Forest. Despite obvious evolutionary differences, studies on small marsupials and placental mammals suggest similar ecological strategies of opportunistic behavior (Vieira and Monteiro-Filho 2003; Vieira and Camargo 2012; Bubadué et al. 2019). Nevertheless, we expected rodents and marsupials not to overlap completely in each biome

and the trophic niche of marsupials to be smaller than that of Sigmodontinae, independently of biome.

MATERIALS AND METHODS

Sampling.—We selected 164 adult specimens of small mammals deposited in the mammal collection of the Universidade Federal de Santa Maria (UFSM–Brazil). These specimens were collected during previous mammal trapping surveys undertaken between 2002 and 2010 in the Brazilian states of Goiás, Mato Grosso, Mato Grosso do Sul, São Paulo, Paraná, and Rio Grande do Sul (Cáceres et al. 2007, 2008, 2010, 2011, 2014; Melo et al. 2011, 2013; Sponchiado et al. 2012). Adults were selected based on the associated skull morphology (closed sutures and all permanent teeth erupted). We chose to work only with adults because ontogeny can alter isotopic ratios in mammals due to lactation (Ben-David and Flaherty 2012). The specimens belonged to 45 species: 15 Didelphidae and 30 Sigmodontinae. Specimens originally were collected in 44 different localities distributed within four Brazilian biomes (Fig. 1; Table 1). Field studies have reported an average of 8.2 species captured per site in the Atlantic Forest (Bovendorp et al. 2017b) and 5.8 species in the Cerrado (Mendonça et al. 2018). Sponchiado et al. (2012) reported a total of nine species captured in an area within the Pampas biome, while 19 species were reported in an area of Pantanal by Cáceres et al. (2011). We report isotopic data from 9 (Pampas grassland) to 27 (Atlantic Forest) species per biome.

For most specimens, we recorded body mass before death, which we used to estimate mean body mass per species. We also gathered information on locomotion (Astúa 2009; Paglia et al. 2012; Brandão and Nascimento 2015; Smith and Owen 2016; Bubadué et al. 2019) and diet (Paglia et al. 2012; Arregoitia and D'Elía 2020; Bubadué et al. 2021) from the literature for every species included in this study (Supplementary Data SD1).

Stable isotope analysis.—We collected at least 0.5 g of hair for each specimen from which we measured $\delta^{13}C$ and $\delta^{15}N$. Each sample was submerged in a 2:1 chloroform:methanol mixture (Meier-Augenstein et al. 2011) for 1 h and then left to air-dry in fume hood to clean the samples of body oils and other adhered contaminants. Subsamples of 0.7 mg of the clean hair were weighed into 5×3 mm tin capsules and combusted in a Pyrocube elemental analyzer (Elementar, Hanau, Germany). Sample gases were transferred via helium carrier gas to a Thermo Delta XP Plus isotope ratio mass spectrometer (Thermo, Bremen, Germany). Sample data were reported in standard delta per mil notation (δ ‰) relative to V-PDB ($\delta^{13}C$) and AIR ($\delta^{15}N$) international standards. Laboratory reference materials were interspersed within the measurement run to correct for linearity and drift. Analytical precision (*SD*) of GEL (Gelatin) was $\delta^{13}C = 0.06‰$ and $\delta^{15}N = 0.09‰$ (full isotopic data in Supplementary Data SD2).

Interspecific variation.—For comparative analyses, we built a majority-rule consensus tree from Upham et al. (2019) for sigmodontine and didelphid species included in this study. Isotopic values were averaged by species to identify the presence of phylogenetic signal in the data (Blomberg and Garland
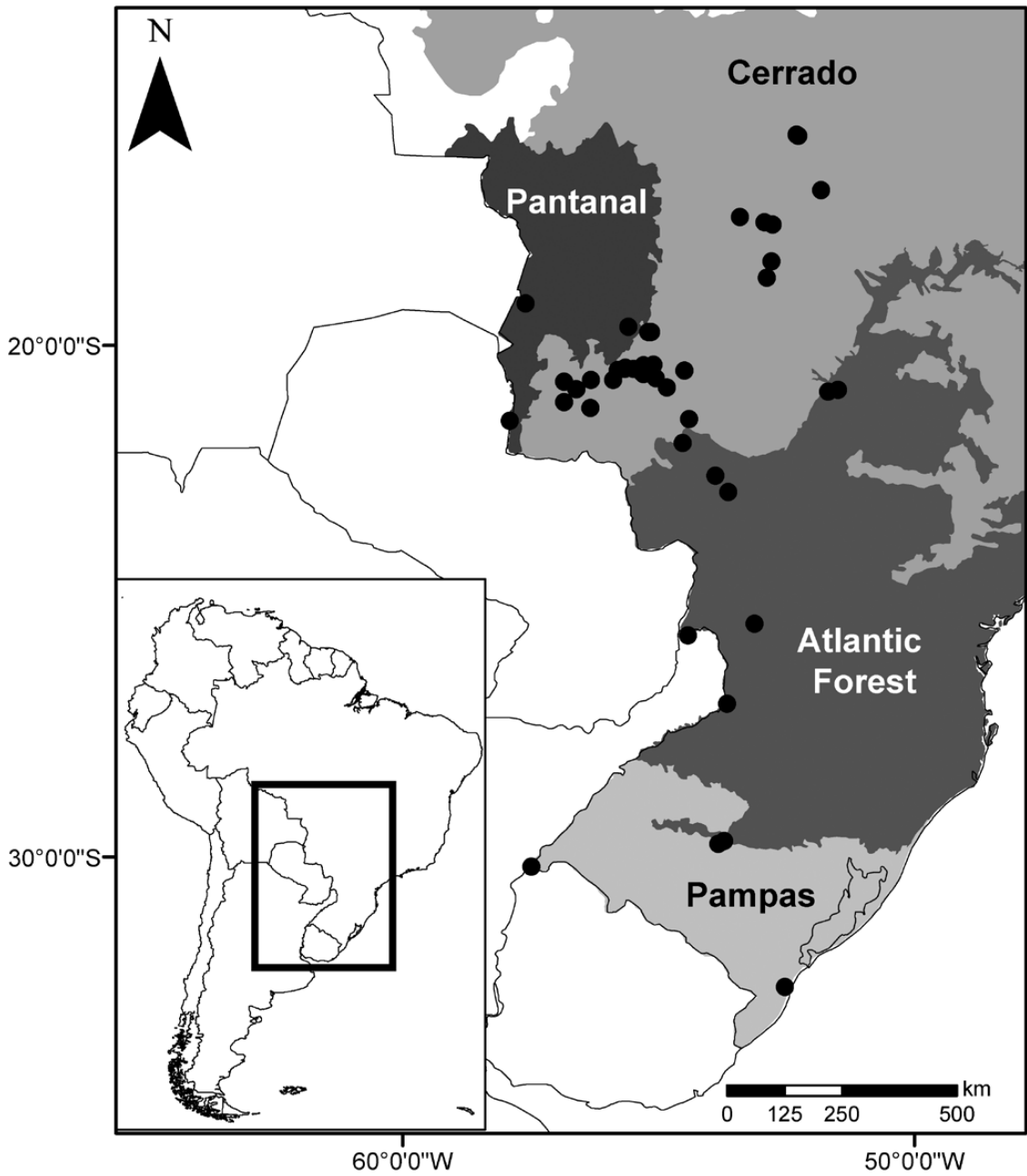
Fig. 1.—Map of South America, separating biomes and with collection localities of our data set.

Table 1.—Number of specimens and species separated by clade and biome. In the Atlantic Forest, number of species in parentheses corresponds to the number after isotopic values in Galetti et al. (2016) were added.

Biome	Didelphidae		Sigmodontinae	
	Specimens	Species	Specimens	Species
Atlantic Forest	5 (16)	4 (12)	27 (34)	11 (15)
Cerrado	38	12	54	14
Pantanal	6	4	21	8
Pampas	4	2	9	7

2002). We used the function "phylosig" to measure the phylogenetic signal (*K*-statistic), available in the package "phytools" (Revell 2012). We expected closely related species to exhibit similar ecology and behavior, hence similar isotopic data (e.g., Bubadué et al. 2019). To determine if comparative models such as phylogenetic generalized least squares (PGLS) were necessary to be implemented for our models of interspecific variation, we also estimated the phylogenetic signal (*K*-statistic) in the residual deviations of the predicted variable for the model testing association between isotopes and averaged body mass between species (Revell 2010).

We used linear model evaluation with randomized residuals in a 9,999 permutations procedure (function lm.rrpp of the package RRPP—Collyer and Adams 2018) to asses if $\delta^{13}C$ and $\delta^{15}N$ values differed between Didelphidae and Sigmodontinae. We also used this procedure to test if isotopic ratios differed among diet, log body mass, and species locomotion categories. These analyses were repeated for Didelphidae and Sigmodontinae separately.

PGLS was not implemented in these models due to the lack of phylogenetic signal in the residual model values.

To measure the level of overlap between clades and test the hypothesis that didelphids' ellipses area would be smaller than in Sigmodontinae (Galetti et al. 2016), we used the R package SIBER (Jackson et al. 2011) to compute and delimit stable isotope Bayesian ellipses, correcting ellipse areas (SEA$_B$) for sample size in each group.

Biome comparisons.—We extracted bioclimatic variables with a resolution of 10 min from the WorldClim raster database (Hijmans et al. 2005) for each locality of small mammal collection. Using averaged values by species and site, we implemented a correlation table to test the association between stable isotopes and climatic condition. We also considered the correlation between bioclimatic variables to select or not select them following a Variance Inflation Criterion (VIF). In the case of multicollinearity, we prioritized the variable with the strongest correlation with our data. Only annual mean precipitation was selected in this procedure.

Biplots of $\delta^{13}C$ and $\delta^{15}N$ were used to visualize the dispersion of isotopic values between marsupials and rodents in our data within the four biomes (Atlantic Forest, Cerrado, Pantanal, and Pampas). The Layman et al. (2007) community-wide measures of trophic structure required at least five species per group to be compared in each community (in our case, biomes). Thus, we selected the largest biomes for which we had enough data to undertake comparative analyses: Atlantic Forest (12 Didelphidae spp., 15 Sigmodontinae spp.) and Cerrado (11 Didelphidae spp., 16 Sigmodontinae spp.). For Atlantic Forest, we added the isotope ratios of hair published for small mammals by Galetti et al. (2016), whose values were similar to those in our data for the repeated species in the same biome, to meet the sampling criteria for that area. We averaged our data per species and biome (Layman et al. 2007), and used the R package SIBER (Jackson et al. 2011) to compute the Bayesian estimates of the following metrics for the Atlantic Forest and Cerrado: $\delta^{15}N$ range as a measure of trophic length (NR), $\delta^{13}C$ range as an estimate of diversity of basal resources (CR), and mean distance to centroid as a measure of trophic diversity taking the degree of species spacing into account (CD).

We delimited stable isotope Bayesian ellipses in SIBER (Jackson et al. 2011) correcting ellipse areas (SEA$_B$) for sample size for each clade, and we separated data from the Atlantic Forest and Cerrado samples. Standard ellipse core isotopic niche areas (SEA$_C$) allowed comparisons of groups by disregarding outliers. We also calculated the total convex hull area (TA) as an indicator of the whole niche width for each clade within each biome. A similar approach was used and described in detail by Missagia et al. (2019).

We measured the probability of the trophic niche (= SEA) in didelphids to be smaller than that of sigmodontines in each biome. Within each clade, we measured the probability of trophic niche to be smaller in the Atlantic Forest than in the Cerrado. We also measured and compared trophic niche overlap between Didelphidae within Sigmodontinae and vice versa for each biome. To make sure our data were not biased because of the different composition of species between biomes, we selected a subsample containing only the species that we had in common for each biome and repeated the overlapping estimations for comparing both biomes (*Didelphis albiventris*, *Gracilinanus agilis*, *Akodon montensis*, *Cerradomys maracajuensis*, *Necromys lasiurus*, *Oecomys bicolor*). In this last procedure, we did not separate clades because we did not have enough samples for each clade.

Turner et al. (2010) provided an R script used to adapt phenotypic trajectory analysis for isotopes. This final analysis allowed us to evaluate the magnitude and direction of change of stable isotope ratios from Cerrado to the Atlantic Forest between the clades. For an empirical *P*-value, the ranked percentile of observed differences between clades were used. This was computed using 9,999 random permutations of residuals from reduced linear models generated by a residual permutation procedure (Turner et al. 2010; Collyer and Adams 2018).

RESULTS

Interspecific variation.—In both clades, we did not find a phylogenetic signal for $\delta^{13}C$ values (Didelphidae $K = 0.416$, $P = 0.324$; Sigmodontinae $K = 0.268$, $P = 0.938$) or $\delta^{15}N$ values (Didelphidae $K = 0.112$, $P = 0.826$; Sigmodontinae $K = 0.353$, $P = 0.795$). The probability of the didelphid trophic niche (SEA = 8.721) being smaller than that of sigmodontines (SEA = 17.632) was 98.5%. No difference in stable isotopes was detectable for $\delta^{13}C$ values with respect to clades, diet, locomotor categories, and body mass ($P > 0.05$; Table 2). Relative to $\delta^{15}N$ values, we found differences between clades ($R^2 = 0.079$, $F = 5.230$, $P = 0.027$), with the highest values for sigmodontines, and among locomotor categories ($R^2 = 0.283$, $F = 3.942$, $P = 0.010$; Table 2). Significant interaction between clades and diet was also detectable for $\delta^{15}N$ ($R^2 = 0.098$, $F = 4.757$, $P = 0.036$; Table 2).

Table 2.—Linear model evaluation with randomized residuals in a 9,999 permutation procedure using clades (didelphid and sigmodontines), diet, body mass (BM), and locomotor categories (LC) as predictors of isotopic signatures in the full sample. Significant or marginally significant results are in bold.

	d.f.	SS	R^2	F	P
Y = $\delta^{13}C$					
Clades	1, 43	2.260	0.007	0.309	0.618
Diet	3, 41	5.830	0.018	0.256	0.837
BM	1, 43	2.010	0.006	0.274	0.607
LC	4, 40	45.970	0.145	1.693	0.157
Clades: Diet	1, 39	8.020	0.036	1.496	0.230
Clades: BM	1, 41	20.33	0.064	2.837	0.102
Clades: LC	3, 36	4.270	0.013	0.192	0.882
Y = $\delta^{15}N$					
Clades	1, 43	10.597	0.079	5.230	**0.027**
Diet	3, 41	3.863	0.029	0.403	0.745
BM	1, 43	4.477	0.033	0.728	0.234
LC	4, 40	38.103	0.283	3.942	**0.010**
Clades: Diet	1, 39	13.216	0.098	4.757	**0.036**
Clades: BM	1, 41	6.889	0.051	2.442	0.137
Clades: LC	3, 36	4.647	0.035	0.765	0.524

The plot of $\delta^{13}C$ versus $\delta^{15}N$ showed greater variation within Sigmodontinae (extreme values are within Sigmodontinae for both isotopes) than within Didelphidae, particularly for $\delta^{13}C$ (#16 *Akodon azarae* and #20 *A. reigi* with the greatest $\delta^{13}C$ values), although considerable overlap occurred between clades (overlap area = 6.965; Fig. 2A). Insectivorous species showed a wide range of isotopic variation, and overlapping values occurred among all dietary categories (Fig. 2A). When samples are labeled based on locomotor categories, we detected high interspecific variation of isotopic values within the terrestrial category followed by the arboreal category (Fig. 2B). Analyzing the clades separately, we found no association within either clade between $\delta^{13}C$ and diet, mean body mass, or locomotion categories. For $\delta^{15}N$, we identified a positive and significant association with body mass for didelphids (Fig. 3) and with locomotion categories for sigmodontines (Table 3). Diet was significantly associated with $\delta^{15}N$ in didelphids, but this factor lost its significance when incorporated within an interaction model with body mass (Table 3). Locomotor category differences among sigmodontines are the same as described in Fig. 2B for all species.

Biome comparisons.—Annual precipitation was negatively correlated with $\delta^{13}C$ values (Spearman's $R = -0.232$, $P = 0.018$) and positively correlated with $\delta^{15}N$ values (Spearman's $R = 0.239$, $P = 0.015$). High $\delta^{13}C$ values were present in open and dry areas (Cerrado and Pampas biomes), especially for Sigmodontinae. Didelphidae $\delta^{15}N$ values were highest in the Pampas and the Cerrado and lowest in the Pantanal and Atlantic Forest biomes. Sigmodontinae $\delta^{15}N$ values were highest in Atlantic Forest and Cerrado and lowest in the Pampas and Pantanal (Fig. 4).

Small mammals CR was larger in the Atlantic Forest (0.904) than in the Cerrado (0.882), while the opposite trend was encountered for NR (Cerrado = 1.386, Atlantic Forest = 0.584). Centroid distance was higher in Cerrado (0.821) than in Atlantic Forest (0.538). SEA, SEA$_C$, and TA were smaller in Didelphidae than in Sigmodontinae for both biomes. Didelphidae from the Atlantic Forest showed a smaller niche than in the Cerrado, while the opposite trend occurred in Sigmodontinae (Table 4; Fig. 5). The probability of SEA$_B$ being smaller in didelphids than sigmodontines was 100% in the Atlantic Forest and 85% in the Cerrado. The probability of didelphids SEA$_B$ in the Atlantic Forest being smaller than in Cerrado was 100%. Within sigmodontines, the probability of SEA$_B$ being smaller in the Atlantic Forest than in the Cerrado was 13%. SEA overlap between clades in the Atlantic Forest was 3.48 (Didelphidae AF area: 3.48; Sigmodontinae AF area: 21.94) and 2.66 in the Cerrado (Didelphidae CER area: 9.66; Sigmodontinae CER area: 14.02). SEA overlapping area among biomes was 1.359 for didelphids and 7.086 for sigmodontines. A biplot generated adding data from Galetti et al. (2016) visually showed these trends (Fig. 5A). When adding only the common species shared between biomes in the overlapping estimations, we found that the ellipse area of Cerrado was larger (29.545) than in the Atlantic Forest (11.914) and that 89.59%

of the Atlantic Forest isotopic niche was within the Cerrado isotopic niche.

Isotopic trajectories validated a shared tendency between clades of decreasing $\delta^{13}C$ from the Cerrado to the Atlantic Forest and increasing $\delta^{15}N$ in the same direction. The magnitude (trajectory size difference = 0.22; $P > 0.05$) and direction (angle between vectors = 22.22; $P > 0.05$) of isotopic trends from Cerrado to the Atlantic Forest were the same for both clades (Fig. 5B).

DISCUSSION

Our results showed that variation of $\delta^{15}N$ in our sampled small mammals can be predicted by locomotion categories (explaining 33% of $\delta^{15}N$ variation). Highest values of $\delta^{15}N$ were reported for the semifossorial insectivores *Oxymycterus quaestor* and *Brucepattersonius iheringi* and for the semiaquatic carnivorous *Chironectes minimus*, while terrestrial species (such as the insectivores *Akodon reigi* and *Deltamys kempi*), omnivorous *C. maracajuensis*, and the arboreal insectivore *Oecomys roberti* had the smallest measures. The locomotory abilities of small mammals and their associated morphological adaptations can determine how species forage and move within the vertical strata (Bubadué et al. 2019). Vertical stratification has been consistently pointed out as one of the main resource partitioning strategies used by small mammals in their natural environment (Vieira and Monteiro-Filho 2003; Vieira and Camargo 2012; Camargo et al. 2018). In comparison, and although our general comparative models were not controlled by site, our results were congruent with the findings of Galetti et al. (2016), who found that locomotion predicted trophic niche segregation of small mammals in Atlantic Forest sites. Galetti et al. (2016) also reported high levels of $\delta^{15}N$ in semifossorial and the smallest levels in arboreal and terrestrial small mammal species (their data were not included in our interspecific analysis, so the shared results are independent and comparable).

We found that our attempt to categorize small mammal diets was not useful in explaining variation in $\delta^{15}N$ or $\delta^{13}C$ isotopic ratios. This can be an effect of the lack of knowledge about these species' biology resulting in a failure to accurately categorize their diet (Paglia et al. 2012; Arregoitia and D'Elía 2020; Bubadué et al. 2021). This categorization problem was previously noted by Missagia et al. (2019) for Akodontini rodents. Another issue when analyzing stable isotopes is the fact that factors other than diet can influence ratios in animal tissues (see Ben-David and Flaherty 2012 for a review on mammals), such as environmental particularities (Handley et al. 1999; Newton 2010), species differences in metabolic rates (MacAvoy et al. 2006), or both.

Averaging our data per site and species, we found that, to some extent, stable isotope variation indeed is impacted by climatic conditions, because our isotopic data correlated with annual precipitation. Studies on foliar and soil $\delta^{15}N$ showed that water availability, associated with temperature, and latitudinal variation can increase local $\delta^{15}N$ ratios
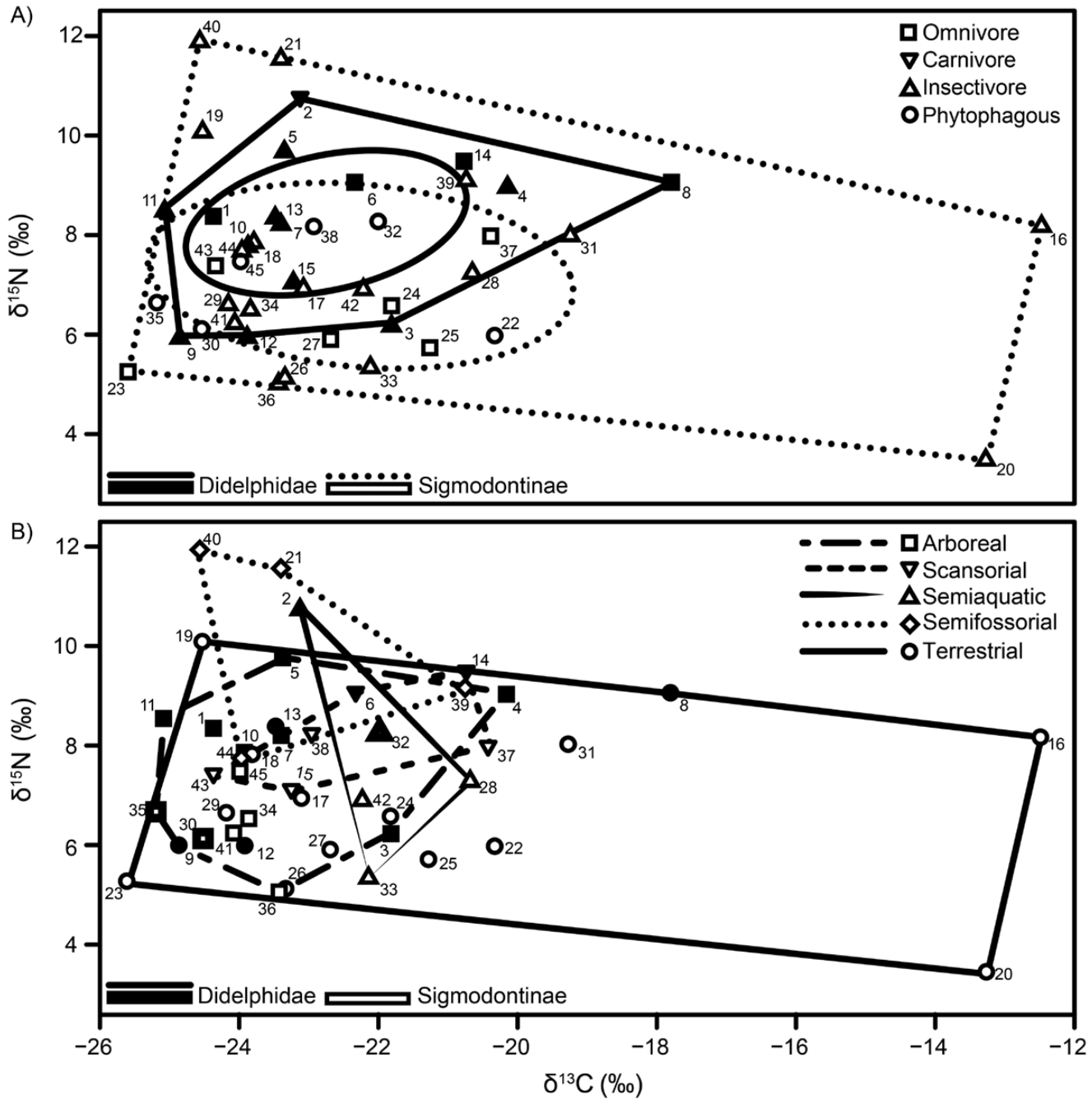
Fig. 2.—Averaged per species scatter plot of δ¹³C (‰) versus δ¹⁵N (‰) stable isotopes. Polygons were used to calculate total niche area, and standard ellipses areas were used to compare trophic niche between groups. Species were grouped according to (A) clades and diet and (B) locomotor categories (legends embedded). Didelphidae: 1. *Caluromys philander*, 2. *Chironectes minimus*, 3. *Cryptonanus agricolai*, 4. *Cryptonanus chacoensis*, 5. *Cryptonanus guahybae*, 6. *Didelphis albiventris*, 7. *Gracilinanus agilis*, 8. *Lutreolina crassicaudata*, 9. *Marmosa budini*, 10. *Marmosa murina*, 11. *Marmosa paraguayana*, 12. *Monodelphis domestica*, 13. *Monodelphis kunsi*, 14. *Philander canus*, 15. *Thylamys macrurus*. Sigmodontinae: 16. *Akodon azarae*, 17. *Akodon lindberghi*, 18. *Akodon montensis*, 19. *Akodon paranaensis*, 20. *Akodon reigi*, 21. *Brucepattersonius iheringi*, 22. *Calomys callosus*, 23. *Cerradomys maracajuensis*, 24. *Cerradomys marinhus*, 25. *Cerradomys scotti*, 26. *Deltamys kempi*, 27. *Euryoryzomys nitidus*, 28. *Holochilus chacarius*, 29. *Hylaeamys megacephalus*, 30. *Juliomys pictipes*, 31. *Necromys lasiurus*, 32. *Nectomys rattus*, 33. *Nectomys squamipes*, 34. *Oecomys bicolor*, 35. *Oecomys mamorae*, 36. *Oecomys roberti*, 37. *Oligoryzomys chacoensis*, 38. *Oligoryzomys nigripes*, 39. *Oxymycterus nasutus*, 40. *Oxymycterus quaestor*, 41. *Rhipidomys macrurus*, 42. *Scapteromys tumidus*, 43. *Sooretamys angouya*, 44. *Thaptomys nigrita*, 45. *Wilfredomys oenax*.

(Handley et al. 1999). Our results for small mammals also showed an increase of δ¹⁵N in areas with higher annual precipitation. Morphological studies on cranial shape variation associated with a climatic gradient in rodents and marsupials also support these results, which are interpreted by some authors as an effect of resource availability (Cáceres et al. 2016;
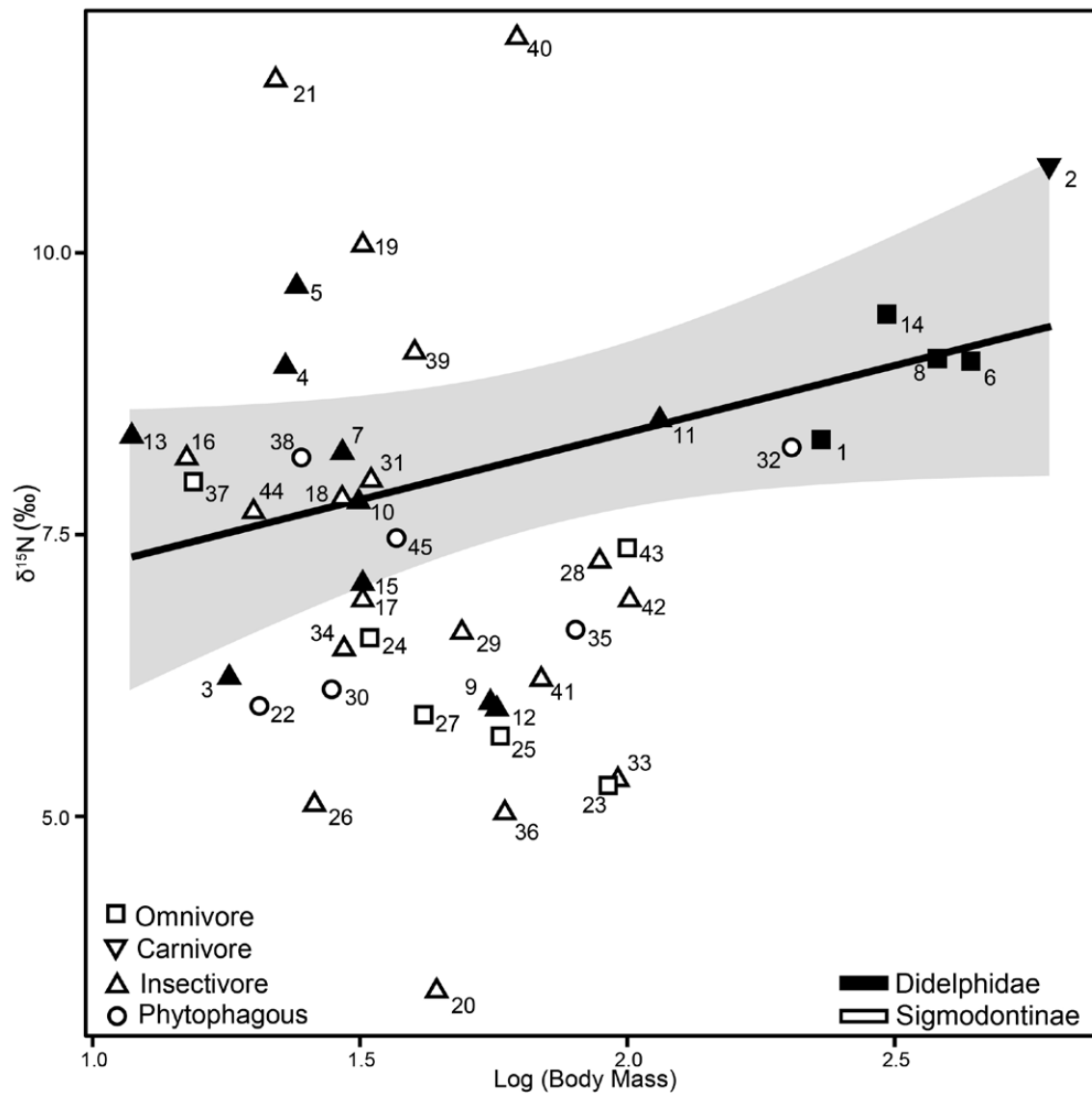
Fig. 3.—Regression plot between δ¹⁵N (‰) and log (body mass). Regression line and the 95% confidence interval (shaded area) are only plotted for Didelphidae's significant relation between variables. Dietary categories are plotted with different symbols in accordance to legend. Sigmodontinae plotted for comparison (legend embedded). Didelphidae: 1. *Caluromys philander*, 2. *Chironectes minimus*, 3. *Cryptonanus agricolai*, 4. *Cryptonanus chacoensis*, 5. *Cryptonanus guahybae*, 6. *Didelphis albiventris*, 7. *Gracilinanus agilis*, 8. *Lutreolina crassicaudata*, 9. *Marmosa budini*, 10. *Marmosa murina*, 11. *Marmosa paraguayana*, 12. *Monodelphis domestica*, 13. *Monodelphis kunsi*, 14. *Philander canus*, 15. *Thylamys macrurus*. Sigmodontinae: 16. *Akodon azarae*, 17. *Akodon lindberghi*, 18. *Akodon montensis*, 19. *Akodon paranaensis*, 20. *Akodon reigi*, 21. *Brucepattersonius iheringi*, 22. *Calomys callosus*, 23. *Cerradomys maracajuensis*, 24. *Cerradomys marinhus*, 25. *Cerradomys scotti*, 26. *Deltamys kempi*, 27. *Euryoryzomys nitidus*, 28. *Holochilus chacarius*, 29. *Hylaeamys megacephalus*, 30. *Juliomys pictipes*, 31. *Necromys lasiurus*, 32. *Nectomys rattus*, 33. *Nectomys squamipes*, 34. *Oecomys bicolor*, 35. *Oecomys mamorae*, 36. *Oecomys roberti*, 37. *Oligoryzomys chacoensis*, 38. *Oligoryzomys nigripes*, 39. *Oxymycterus nasutus*, 40. *Oxymycterus quaestor*, 41. *Rhipidomys macrurus*, 42. *Scapteromys tumidus*, 43. *Sooretamys angouya*, 44. *Thaptomys nigrita*, 45. *Wilfredomys oenax*.

Magnus et al. 2017, 2018; see also Resource Rule description of McNab 2010).

In contrast, drier environments present higher levels of δ¹³C, suggesting the presence of C₄ vegetation in the diet of small mammals when these resources are available. C₄ plants occur at higher percentages in grassland and savanna regions, which tend to have lower precipitation throughout the year (Still et al. 2003; Powell and Still 2008), which might have a direct impact on the increase of trophic niche diversity within our data.

Thus, we argue that δ¹³C values, at least in our study model, can be related to whether the environment presents C₄ or CAM plants or not, rather than species-specific preferences to include them or not in their diet. To give some specific examples, C₄ or CAM plants (δ¹³C > −20‰) only are implied in the diet of the terrestrial didelphid *Lutreolina crassicaudata* (−17.8‰) and the akodontines *N. lasiurus* (−19.2‰), *A. reigi* (−13.2‰), and *A. azarae* (−12.5‰—Bubadué et al. 2019; Missagia et al. 2019). These high δ¹³C values only were detectable in

Table 3.—Linear model evaluation with randomized residuals in a 9,999 permutation procedure using body mass (BM), and locomotor categories (LC) as predictors of isotopic signatures separating between clades.

Didelphidae	d.f.	SS	R^2	F	P
Simple models					
$\delta^{13}C \sim BM$	1, 13	2.928	0.055	0.763	0.408
$\delta^{13}C \sim Diet$	2, 12	11.485	0.217	1.667	0.178
$\delta^{13}C \sim LC$	3, 11	7.542	0.143	0.611	0.598
$\delta^{15}N \sim BM$	1, 13	9.060	0.328	6.342	**0.027**
$\delta^{15}N \sim Diet$	2, 12	11.253	0.408	4.122	**0.035**
$\delta^{15}N \sim LC$	3, 11	7.533	0.273	1.374	0.310
Diet * BM model					
$\delta^{15}N \sim BM$	2, 10	11.253	0.407	3.662	0.051
$\delta^{15}N \sim Diet$	1, 10	0.599	0.022	0.390	0.554
$\delta^{15}N \sim Diet * BM$	1, 10	0.416	0.015	0.271	0.629
Sigmodontinae					
$\delta^{13}C \sim BM$	1, 28	18.501	0.070	2.123	0.156
$\delta^{13}C \sim Diet$	3, 26	10.505	0.040	0.361	0.741
$\delta^{13}C \sim LC$	4, 25	40.628	0.158	1.145	0.329
$\delta^{15}N \sim BM$	1, 28	2.042	0.021	0.605	0.444
$\delta^{15}N \sim Diet$	3, 26	7.065	0.073	0.684	0.555
$\delta^{15}N \sim LC$	4, 25	43.691	0.453	5.168	**0.005**

terrestrial species that were typical of open habitats, where C_4 plants are available commonly (Still et al. 2003; Powell and Still 2008). Our visual empirical data of carbon ratios support this because they are the highest for South American savanna and grassland (Cerrado and Pampas biomes; Fig. 4). A mixture of C_3 and C_4 plants are available commonly in these biomes (Wagner et al. 2018; Ribeiro et al. 2019), although we highlight that high values of $\delta^{13}C$ also were present in specimens from the Atlantic Forest biome, as reported by Galetti et al. (2016).

Within clades, Sigmodontinae showed the same pattern as the overall small mammal model (discussed previously), in which locomotory category was the main predictor of $\delta^{15}N$ ratios. Sigmodontines showed greater separation among locomotory categories than didelphids with respect to $\delta^{15}N$ ratios, with the highest trophic level being secured by semifossorial insectivores and a terrestrial insectivore (*A. paranaensis*) and the lowest either to arboreal, semiaquatic, and other terrestrial phytophagous or insectivorous species. Didelphidae, on the other hand, supported resource partitioning following a scaling law. The scaling law was described by Ritchie and Olff (1999) to predict how organisms of different body sizes find and partition food resources within the same community. By way of summary, smaller and larger animals differ significantly in how they find and forage for different food sources, as well in their capability to incorporate larger prey into their diet more frequently (Bubadué et al. 2021). We potentially identified this trend in didelphids because they vary more in size than sigmodontines within our sample. Didelphids' body size variation ranges from 11 to 620 g in our sample, while sigmodontines range from 15 to 202 g. Moreover, some of the largest marsupials we sampled have preferences for animal food sources, as reflected by their high $\delta^{15}N$. These species are, in order of increasing mass, *Philander canus*, *L. crassicaudata*, *D. albiventris* (well known to strategically

include more animal food items in its diet when fruits are scarce—Cáceres 2002), and *C. minimus*. All these species are considered the most carnivorous South American marsupials, particularly *L. crassicaudata* and *C. minimus*, although they generally are categorized as omnivorous (Cáceres 2002, 2004; Santori and Moraes 2012).

In comparison, the overall trophic niche of Didelphidae we sampled is smaller than in Sigmodontinae, and it completely overlaps the rodent isotopic space, supporting the idea of a narrower diversity of niches in marsupials. This can be explained by niche conservatism in Didelphidae (Chemisquy et al. 2021) compared to Sigmodontinae, which presents broader overall species richness, phylogenetic diversity, and possibly functional diversity in the Neotropics (Maestri and Patterson 2016; Maestri et al. 2016a). Nevertheless, we sampled fewer didelphid species than sigmodontines, and therefore the smaller trophic niche in didelphids could be related to a simple effect of sample size. Within biome comparisons and with a comparable number of species between clades, we always identified the same trend: trophic niche is smaller in didelphids than sigmodontines (Galetti et al. 2016). On the other hand, between biomes, sigmodontines and didelphids show some similarities, suggesting that, despite their differences, these animals' diets depend primarily on resource availability.

Didelphids and rodents show the largest SEA in the Cerrado (Neotropical savanna) compared with their own clades' SEA in the Atlantic Forest. This is not an effect of species composition differences between biomes because our SEA measurements in Cerrado and Atlantic Forest that only focused on the common species subsample showed similar results. Moreover, environmental differences between Cerrado and Atlantic Forest shift the trajectories of sigmodontines' and didelphids' isotope ratios in the same direction (increase of $\delta^{15}N$ and decrease of $\delta^{13}C$ toward the forest biome). These environmental shifts are congruent with the previously discussed correlations of our isotopic data with precipitation—where annual precipitation was positively correlated with $\delta^{15}N$ and negatively with $\delta^{13}C$—because the Cerrado is a dryer and less stable environment than the Atlantic Forest (IBGE 2019).

Because of these environmental particularities, the comparison between trophic niches within Atlantic Forest and Cerrado biomes show that the two clades partition the environment very differently in these biomes. The Atlantic Forest supports 100% of didelphids' trophic niche within sigmodontines. Still, only a portion of the trophic niche of didelphids is shared within the wide range of sigmodontines. Community studies in the Atlantic Forest have shown that small mammals partition environmental resources based on vertical strata (Grelle 2003; Vieira and Monteiro-Filho 2003; Melo et al. 2011) and that spatial heterogeneity is not as important for species composition in a forest biome as it is in the savanna (Melo et al. 2011; Camargo et al. 2018). Conversely, and while didelphid SEA still is smaller than that of sigmodontines, the trophic niche overlap area in the Cerrado is considerably smaller than in the forest, suggesting a more direct partition of food resources in
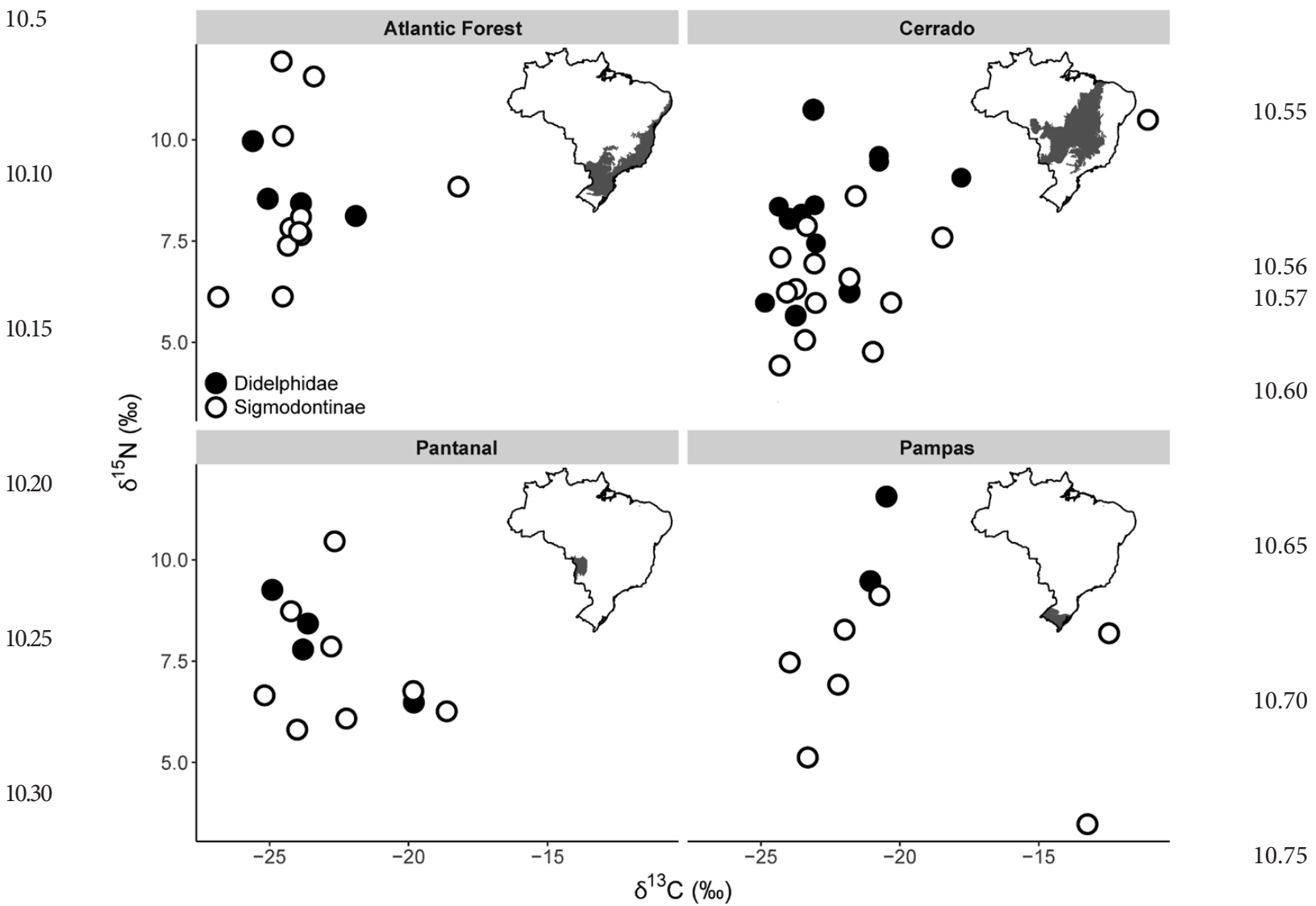
**Fig. 4.**—Scatter plots of δ¹³C (‰) versus δ¹⁵N (‰) separated by biomes and clades. Inset maps show location of biomes in Brazil.

Table 4.—Values of standard ellipse area (SEA), standard core ellipse area (SEA$_C$), and total area calculated for each clade in each biome: AF = Atlantic Forest, CER = Cerrado, D = Didelphidae, S = Sigmodontinae.

	SEA	SEA$_C$	TA
AF D	3.167	3.484	8.123
AF S	20.645	21.935	44.495
CER D	8.778	9.655	19.416
CER S	12.943	14.021	31.274

the savanna than in the forest biome (Fig. 5). Considering that the Atlantic Forest is more productive than the Cerrado (Raich et al. 1991), it is possible that food availability and stability in the Atlantic Forest would support greater overlap between clades. This would explain why resource partitioning in the Cerrado is much more obvious between clades. Compared with our results, Camargo (2016) found that marsupials tend to decrease their isotopic niche in gallery forest compared with

woodland savanna forests, while the opposite occurs for rodent species. He argued that in environments where resource availability is greater, marsupials are able to shift their diet. Our results also support this because didelphids have smaller isotopic niche in the Atlantic Forest (more productive) than in the Cerrado (less productive), while sigmodontines have the opposite trend.

In summary, our results are in agreement with the common notion of opportunistic feeding characteristics in Neotropical small mammals' ecology, along with their niche plasticity, which probably is the primary factor that allowed their successful coexistence in a number of different environments. Our study, in addition to previous isotopic (Galetii et al. 2016; Ribeiro et al. 2019), morphological (Bubadué et al. 2019, 2021), and field research (Grelle 2003; Vieira and Monteiro-Filho 2003; Melo et al. 2011; Vieira and Camargo 2012; Camargo et al. 2018), supports the idea that both clades, most likely because of their different evolutionary and biogeographical backgrounds, cope with coexistence by using two main
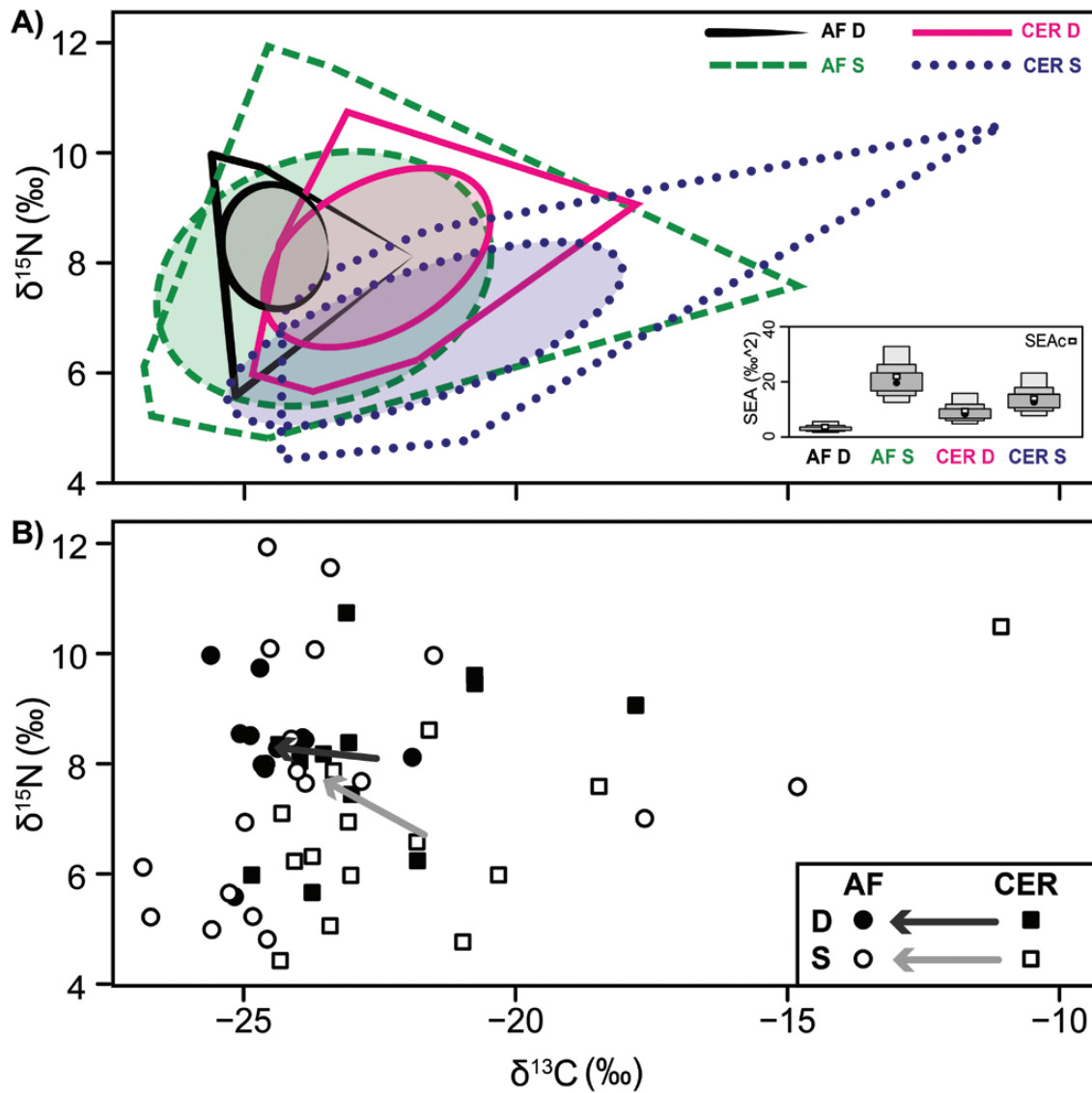
Fig. 5.—Plots of $\delta^{13}C$ (‰) versus $\delta^{15}N$ (‰) comparing Didelphidae and Sigmodontinae from Atlantic Forest and Cerrado. (A) Standard ellipses isotopic niche area and convex hulls are plotted for each group. A smaller plot is available showing the range of the Bayesian ellipses generated, the standard Bayesian ellipse average and standard core ellipse area (SEA_C) in white. Each group is labeled as legend embedded. AF D = Atlantic Forest Didelphidae; AF S = Atlantic Forest Sigmodontinae; CER D = Cerrado Didelphidae; CER S = Cerrado Sigmodontinae. (B) Scatter plot with all sampled species in each biome and phenotypic trajectories showing the changing path tendencies between Cerrado (squares) and Atlantic Forest (circles). D = Didelphidae (in black); S = Sigmodontinae (in white).

partitioning strategies: scaling law (didelphids) and vertical partitioning of resources (particularly sigmodontines). When dealing with different environments (e.g., Atlantic Forest versus Cerrado biomes), marsupials and rodents either can decrease their trophic niche, most likely based on food abundance of preferable food items throughout the year (habitat homogeneity), or increase niche partitioning, responding to habitat productivity and seasonality (Camargo 2016; Ribeiro et al. 2019). Eventually, our approach using stable isotopes can be used as a guideline to study trophic variation and coexistence patterns in different clades.

SUPPLEMENTARY DATA

Supplemental data are available at the *Journal of Mammalogy* online.

Supplementary Data SD1.—Stable isotope data for each species included in this study with information on taxonomy, locomotory categories, diet categories, and mass (common logarithm).

Supplementary Data SD2.—Stable isotope data for each specimen included in this study with information on taxonomy, municipality, biome, geographical coordinates, sex, and mass.

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