

Human-modified landscapes alter mammal resource and habitat use and trophic structure

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The broad negative consequences of habitat degradation on biodiversity have been studied, but the complex effects of natural–agricultural landscape matrices remain poorly understood. Here we used stable carbon and nitrogen isotopes to detect changes in mammal resource and habitat use and trophic structure between preserved areas and human-modified landscapes (HMLs) in a biodiversity hot spot in South America. We classified mammals into trophic guilds and compared resource use (in terms of C_3 - and C_4 -derived carbon), isotopic niches, and trophic structure across the 2 systems. In HMLs, approximately one-third of individuals fed exclusively on items from the agricultural matrix (C_4), while in preserved areas, ~68% depended on forest remnant resources (C_3). Herbivores, omnivores, and carnivores were the guilds that most incorporated C_4 carbon in HMLs. Frugivores maintained the same resource use between systems (C_3 resources), while insectivores showed no significant difference. All guilds in HMLs except insectivores presented larger isotopic niches than those in preserved areas. We observed a complex trophic structure in preserved areas, with increasing $\delta^{15}N$ values from herbivores to insectivores and carnivores, differing from that in HMLs. This difference is partially explained by species loss and turnover and mainly by the behavioral plasticity of resilient species that use nitrogen-enriched food items. We concluded that the landscape cannot be seen as a habitat/nonhabitat dichotomy because the agricultural landscape matrix in HMLs provides mammal habitat and opportunities for food acquisition. Thus, favorable management of the agricultural matrix and slowing the conversion of forests to agriculture are important for conservation in this region.

stable isotope analysis | landscape matrix | agriculture | diet | noninvasive sampling

Agriculture is one of the main drivers of habitat loss and fragmentation (1), especially in tropical forests (2). Landscape conversion can cause drastic changes in landscape composition, which have selective effects on species, particularly those that are forest dependent (3), and have reduced species richness and diversity worldwide (4). Species with high body mass, large home ranges, and sensitivity to habitat loss and fragmentation are the first to vanish from human-modified landscapes (HMLs) (5, 6). Nonetheless, some species, including various mammals, persist and use the agricultural landscape matrix (landscape matrix hereafter) (7). The landscape matrix has the potential to offer food resources to animals (8, 9), especially where agricultural fields are present. Use of such resources might be harder to detect, particularly among elusive species, such as mammals in tropical forests.

Studies on feeding ecology can contribute to our understanding of these changes. However, despite providing essential knowledge, the use of traditional methods (e.g., direct observation, fecal

analysis, and stomach content analysis) can be time consuming and expensive, especially if the aim is to determine resource origin and assess temporal variation in the diet. As an alternative and complementary method, stable isotope analysis (SIA) has gained prominence in recent decades in applied animal ecology (10), becoming a reliable tool to unravel individual-level ecological processes and complex community interactions (11).

In comparison to traditional methods, SIA presents many advantages, including potential for noninvasive sample collection and assessing several temporal windows with a single sampling event while also generating information on elusive species (11–13). Stable carbon (^{12}C and ^{13}C) and nitrogen (^{14}N and ^{15}N) isotopes are commonly used in studies of feeding ecology, species movement, and trophic processes (11, 13, 14). Specifically, stable carbon isotopes allow the evaluation of changes in species resource use according to the differences in the isotopic values of plants exhibiting the C_3 and C_4 photosynthetic cycles, which are reflected in animal tissues along the trophic chain (15). Stable nitrogen isotopes are used to obtain information on feeding ecology that is complementary to that obtained from stable carbon isotope analysis but

Significance

Knowledge of resource and habitat use by wildlife is essential to support conservation actions. Stable isotope analysis (SIA) is a useful method for the acquisition of this type of information. Samples for SIA can be obtained through indirect and non-invasive methods, which is favorable for studies of threatened species. We used SIA to compare the resource and habitat use and trophic structure of mammals between preserved areas and human-modified landscapes in a tropical rainforest. Our study shows that mammals in human-modified landscapes present an altered trophic structure and use food items from the agricultural matrix, while they depend on forest resources in preserved areas. Our findings stress the need for favorable management of the agricultural matrix to support wildlife survival.

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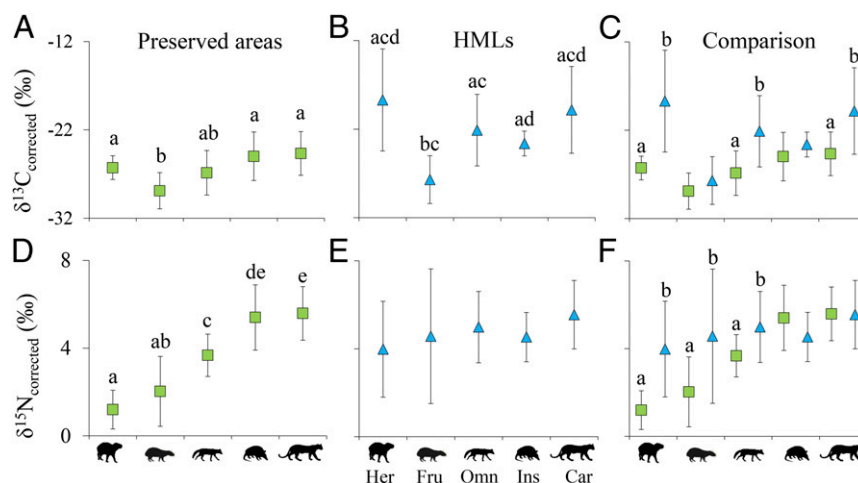


Fig. 2. Comparison of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among mammal trophic guilds in the Atlantic Forest, state of São Paulo, Brazil. Mean $\delta^{13}\text{C}_{\text{corrected}}$ and $\delta^{15}\text{N}_{\text{corrected}}$ values $\pm$ SD for mammal trophic guilds in (A and D) preserved areas, (B and E) HMLs, and (C and F) both systems together. Lowercase letters indicate relationships with significant differences ($P < 0.01$, $P < 0.05$). Her, herbivores; Fru, frugivores; Omn, omnivores; Ins, insectivores; Car, carnivores.

including only species that were common between systems ($n = 16$; *SI Appendix, Fig. S1*), showing that our results for trophic guilds were not influenced by interspecific differences in resource use.

Resource Use. The frugivores in both systems had the lowest $\delta^{13}\text{C}_{\text{corrected}}$ values (Fig. 2 A and B), indicating that this guild is the most dependent on resources from forest remnants (*SI Appendix, Table S2*). The herbivores and carnivores in the HMLs showed relatively wide ranges of $\delta^{13}\text{C}_{\text{corrected}}$ values, while the herbivores in preserved areas and insectivores in the HMLs presented the smallest ranges (SI Appendix, Table S2). Overall, the $\delta^{13}\text{C}_{\text{corrected}}$ values and ranges were smaller in the preserved areas than in the HMLs (except in the case of insectivores), with significant differences among herbivores [ANOVA; $F_{(1,32)} = 16.75$; $P = 0.0003$], omnivores [$F_{(1,52)} = 10.25$; $P = 0.0023$], and carnivores [$F_{(1,140)} = 30.59$; $P < 0.0001$] (Fig. 2C).

We observed a significant difference in mean $\delta^{15}\text{N}_{\text{corrected}}$ values between the C_3 and mixed groups in preserved areas [ANOVA; $F_{(1,124)} = 134.83$; $P < 0.0001$] and among the C_3 , mixed, and C_4 groups in HMLs [$F_{(2,191)} = 12.2$; $P < 0.0001$] (*SI Appendix, Fig. S2*). In both systems, individuals that incorporated C_4 carbon into their body structures presented the highest $\delta^{15}\text{N}_{\text{corrected}}$ values, as observed for all trophic guilds except insectivores (*SI Appendix, Table S3*), suggesting their consumption

of nitrogen-enriched food items from the agricultural matrix (e.g., sugarcane).

We observed a distinct difference in resource use by mammals between systems (Fig. 3), supporting our hypothesis. In the preserved areas, most species predominantly fed on C_3 resources (Fig. 3A), showing dependency on the forest remnants and a low contribution of C_4 resources. Conversely, in HMLs, ~34.5% of individuals fed exclusively on C_4 resources, indicating the intense use of items from the agricultural matrix and few individuals feeding only on C_3 resources (Fig. 3B). Most species in HMLs used a mixture of C_3/C_4 resources, indicating the use of both the remnants and the matrix as feeding areas.

In both systems, frugivores depended on C_3 resources, and insectivores presented small variation, using a mixture of C_3/C_4 resources. We observed drastic differences for 3 guilds between the 2 systems: herbivores switched from C_3 to C_4 resources, omnivores changed from predominantly C_3 consumers to showing mixed use, and a relatively high proportion of carnivores consumed only C_4 resources. No species in preserved areas presented $\delta^{13}\text{C}_{\text{corrected}}$ values corresponding to the C_4 group.

Isotopic Niches. Isotopic niches in preserved areas were smaller than in HMLs in all cases except for insectivores (Fig. 4). The pattern presented by insectivores was reversed in comparison to those shown by the other trophic guilds, with a niche almost 3

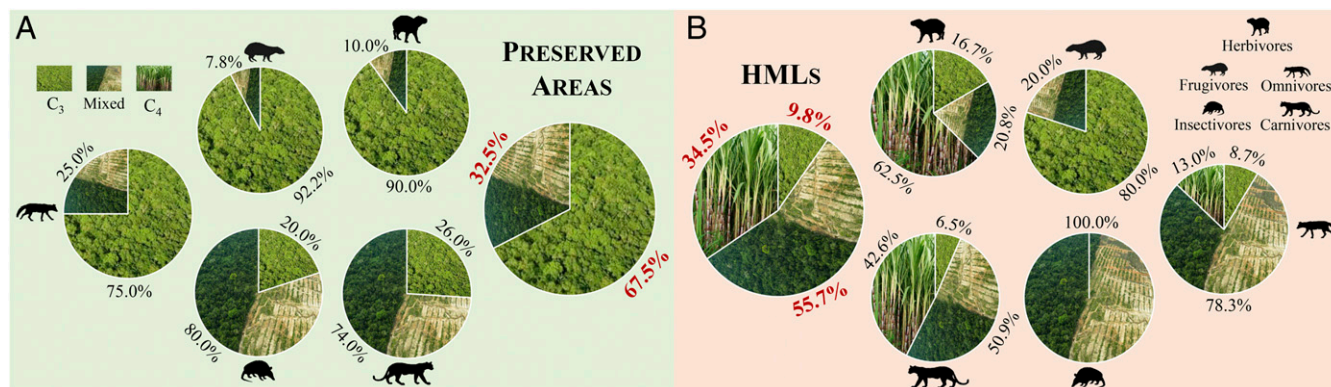


Fig. 3. Resource use of mammals in the Atlantic Forest, state of São Paulo, Brazil. Percentages of individuals with C_3 , mixed, or C_4 diets in trophic guilds (as indicated) in (A) preserved areas and (B) HMLs.

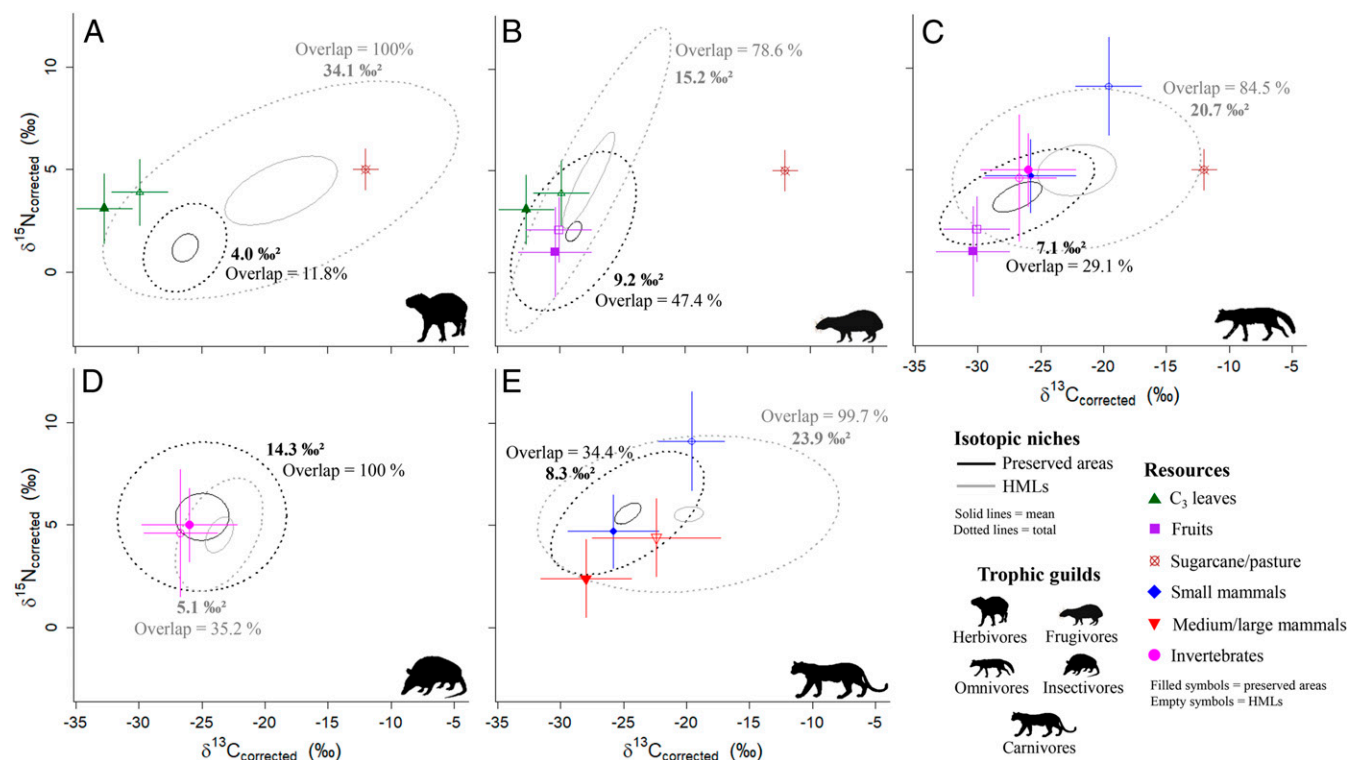


Fig. 4. Mammal isotopic niches in the Atlantic Forest, state of São Paulo, Brazil. Corrected standard ellipse area (SEAc in ‰²; dotted lines), mean resource use (solid lines), and the percentage overlap of the different mammal trophic guilds in preserved areas (black) and HMLs (gray). (A) Herbivores, (B) frugivores, (C) omnivores, (D) insectivores, and (E) carnivores. Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values $\pm$ SD of the main resources consumed by each guild are included in the panels (filled forms indicate preserved areas; empty forms indicate HMLs).

times larger in preserved areas. The largest difference in niche size was observed among herbivores, with an isotopic niche more than 8 times larger in HMLs than in preserved areas. The isotopic niches of all guilds in HMLs overlapped most of the niches in preserved areas, except in the case of insectivores, which showed the reverse pattern, highlighting the high diversity of prey consumed in preserved areas (Fig. 4).

Trophic Structure. We observed a distinct difference in the trophic structure of mammals between the 2 systems (Fig. 2), supporting our hypothesis. In preserved areas, there were significant differences in mean $\delta^{15}\text{N}_{\text{corrected}}$ values among trophic guilds [ANOVA; $F_{(4,121)} = 25.99$; $P < 0.0001$] (Fig. 2D), while the differences were not significant for HMLs [$F_{(4,189)} = 1.16$; $P = 0.16$] (Fig. 2E). Comparing systems, we observed significant differences for herbivores [ANOVA; $F_{(1,32)} = 15.23$; $P = 0.0005$], frugivores [$F_{(1,67)} = 9.93$; $P = 0.0024$], and omnivores [$F_{(1,52)} = 4.92$; $P = 0.0309$] (Fig. 2F) in addition to a wider range of values for all guilds in HMLs except for insectivores (SI Appendix, Table S2). These results indicate that mammals in HMLs that consume primary resources (e.g., fruits and leaves) present elevated $\delta^{15}\text{N}_{\text{corrected}}$ values.

Discussion

Resource Use. Differences in landscape composition (i.e., the availability of C₃/C₄ resources) explain the changes in resource use by mammals between systems. In HMLs, more than one-third of the mammals exclusively used C₄ resources, while the preserved areas were the closest representations of pristine Atlantic Forest remnants. Overall, there was a transition in the resource use of mammals between systems, from C₃ to C₄, demonstrating the impact of land use changes on species diets and habitat use. The size of the isotopic niches strengthens our

findings, reflecting the plasticity of mammals in terms of their use of C₄ resources from the matrix in HMLs (large niches) and the greater constraint in preserved areas (smaller niches).

These changes were most evident for herbivores, omnivores, and carnivores, which incorporated high proportions of C₄ carbon in the HMLs. Grazing species, such as *Hydrochoerus hydrochaeris*, benefit from changes in landscape composition, presenting C₄-dominated diets, and the high availability of C₄ resources (e.g., sugarcane and corn) may stimulate the population growth of this species (22). Even arboreal browsers, such as *Coendou spinosus*, had individuals with C₄-dominated diets, which contrasts with observations in the preserved areas. Moreover, the high $\delta^{15}\text{N}$ values for herbivores in HMLs corroborate the consumption of items from the agricultural matrix, which have elevated $\delta^{15}\text{N}$ values due to the use of organic fertilizers and cultivation methods (12, 14, 16, 23).

Omnivores presented C₃-dominated diets in preserved areas, which is explained by the high availability of fruits (24, 25), an abundant C₃ resource in these areas. Fruits are less available in HMLs; thus, omnivores may increase their consumption of small vertebrates (e.g., rodents, birds, and reptiles) and invertebrates, prey that feed on items from the agricultural matrix (7) and C₄ crops (e.g., sugarcane and corn). These animals thus change to having a mixed diet, such as observed in species in the genus *Didelphis*. The elevated $\delta^{15}\text{N}$ values of omnivores in HMLs are a consequence of this high intake of animal matter and nitrogen-enriched items. HMLs favor the presence of omnivores such as *Didelphis albiventris* and *Chrysocyon brachyurus*, which are tolerant to open habitats and absent from preserved areas, and support the augmentation of the populations of others, such as *Cerdocyon thous* (26), and the presence of these species contributes to the increased $\delta^{15}\text{N}$ values of this guild.

Carnivores were the second guild that most consumed C_4 resources in HMLs. This incorporation of C_4 carbon is a reflection of the prey base, which includes several species with C_4 -dominant diets. Similar to the results obtained for pumas (*Puma concolor*) between landscapes with different levels of forest cover (7), other carnivore species in HMLs also increased the intake of C_4 carbon in comparison to those in preserved areas. For example, small felids (genus *Leopardus* and *Puma yagouaroundi*) feed mainly on small mammals, which present higher $\delta^{13}C$ values in HMLs (7) than in preserved areas (27). Even species considered to be sensitive to habitat loss, such as *Leopardus pardalis* and *Leopardus wiedii* (28), contained individuals with C_4 -dominant diets, indicating their plasticity and resilience to survive in HMLs. Nonetheless, most felids are threatened in Brazil, and trends indicate declines in their populations in response to anthropogenic pressure (28).

The resource use of frugivores and insectivores was less affected by land use changes; in the HMLs, frugivores were the only guild to preferentially use C_3 resources. This feeding preference shows that even small, low-quality forest remnants are essential for providing food and habitat. Although they feed mainly on C_3 resources in preserved areas, even threatened frugivores, such as *Tapirus terrestris* and *Tayassu pecari* (28), had individuals incorporating C_4 carbon into their body structures. *T. terrestris* is known to feed in orchards and cultivated areas (29), while *T. pecari* herds raid crops and plantations (30), corroborating our results. Individuals of these species also present high $\delta^{15}N$ values, similar to individuals of the genus *Mazama* and *Cuniculus paca* in HMLs, indicating the consumption of nitrogen-enriched food items (e.g., fruits in orchards).

Comparing systems, mammal insectivores showed small variation in resource use, reflecting the feeding specialization of armadillos (*Dasypus novemcinctus* and *Cabassous tatouay*) and anteaters (*Myrmecophaga tridactyla* and *Tamandua tetradactyla*), which feed mainly on termites and ants (20, 21). Termite $\delta^{13}C$ values vary with the foraging substrate, which affects whether they have C_3 - or C_4 -dominant diets or mixed diets (31, 32), while ants have lower $\delta^{13}C$ values (33, 34) depending on the C_3 resources available. In both systems, insectivores presented mixed diets, but a few individuals in preserved areas fed exclusively on C_3 prey. This variation is explained by the higher diversity of prey in preserved areas (35, 36); such diversity is lower in HMLs, but there is a higher abundance of generalist prey, increasing diet specificity. Insectivores in preserved areas presented a wider range of $\delta^{13}C$ and $\delta^{15}N$ values than those in HMLs, resulting in an isotopic niche that was 3 times larger, which is a reversed pattern compared to that found in the other guilds.

Trophic Structure. In preserved areas, mammals showed an ordered trophic structure with increasing $\delta^{15}N$ values, indicating ^{15}N bioaccumulation from herbivores to carnivores. This scaling of ^{15}N enrichment is expected for longer trophic chains (37), which commonly occur as an ecosystem increases in size (38). Our results for preserved areas point toward a structure similar to that in the Eltonian pyramid, which has also been observed among other terrestrial organisms, such as birds (39) and ants (40), and more commonly among aquatic organisms, such as fish (41), supporting our hypothesis.

Conversely, the mean $\delta^{15}N$ values for different guilds in the HMLs were similar, especially considering the high $\delta^{15}N$ values for primary consumers. Animals in HMLs are expected to have higher $\delta^{13}C$ and $\delta^{15}N$ values than those in preserved areas (23). In particular, mammals with mixed or C_4 -dominant diets presented higher $\delta^{15}N$ values, as also noted in other studies (7, 16). Changes in trophic structure, similar to those reported here, were also recorded for other taxa in response to environmental disturbance (40–42). The results for carnivores were very similar between systems despite some individuals in HMLs having

higher $\delta^{15}N$ values than those in preserved areas. Nonetheless, HMLs also presented carnivorous individuals with the lowest $\delta^{15}N$ values for this guild, resulting in similar mean values between systems. These findings show that human activities cause impacts beyond the loss of species richness and diversity, also changing species diets, habitat use, and trophic structure.

We considered 2 explanations for the distinct difference in trophic structure between the 2 systems. The first is based on species plasticity in terms of thriving in modified habitats, as we observed for most species in the HMLs, which consumed nitrogen-enriched items from the agricultural matrix. A second explanation for the difference between the 2 systems is related to species turnover, as most sensitive species disappear from HMLs, being replaced by generalist species and those tolerant to open habitats, an effect already detected in the Atlantic Forest (43).

Conclusions. The scenario we assessed is similar to those in other biomes and ecosystems worldwide, particularly tropical areas dominated by agriculture. The agricultural landscape matrix, despite negatively affecting the richness, diversity and abundance of mammals (44–46), acts as a complementary or predominant feeding area and habitat for several species, showing that the habitat/nonhabitat dichotomy (44) is not the most adequate classification. Matrix management aimed at wildlife conservation has been recently discussed (9, 44–46) but is still an incipient matter. The replacement of natural ecosystems with agriculture has created conflict between production and conservation, and an understanding between these areas is necessary for biodiversity maintenance (47, 48). Based on the diets of mammal species, our study provides a first step in determining which species have the highest likelihood of surviving in HMLs. Future studies should address knowledge gaps regarding how items originating from the agricultural matrix may affect species diet quality and the long-term effects on population growth and species survival. Even if such effects are not hugely negative, continuous and large habitat remnants represent the last refuges for wildlife, are the most similar habitats to pristine areas, and are irreplaceable for the persistence of sensitive species (49). These habitats support assemblages with a more complex trophic structure than those in HMLs, acting as source areas for the maintenance of biodiversity in HMLs.

Materials and Methods

Study Areas. We selected 2 systems in the Atlantic Forest biome for sampling: preserved areas and HMLs. We considered preserved areas to be those in a better conservation state with high forest cover. We selected 2 landscapes with similar structural and floristic compositions within the largest area of continuous forest in the Atlantic Forest (>1 Mha), state of São Paulo, Brazil (*SI Appendix, Fig. S3 and Table S4*). For the second system, we selected 2 HMLs with similar structural, floristic, and compositional characteristics, with low forest cover, and dominated by anthropogenic matrices in the state of São Paulo, Brazil (*SI Appendix, Fig. S4 and Table S5*).

Samples for SIA. We used mammal hair for the SIA. For the preserved areas, we used hair originating from carnivore fecal samples, hair traps, and opportunistic collection from the field. For the HMLs, we used hair samples collected by the authors and collaborators who conducted other studies (e.g., refs. 7 and 50), including carnivore fecal samples and opportunistically collected samples; the methods used for sample collection and identification for the HMLs are described in detail in the aforementioned studies. Descriptions of the sampling procedures used in the preserved areas, fecal sample screening, hair identification, and preparation of samples for SIA are provided in *SI Appendix*.

SIA. The prepared material was submitted to combustion in a CHN-1110 elemental analyzer (Carlo Erba), and the resultant gases were separated in a chromatographic column. Later, the gases were inserted into a coupled continuous flow isotope ratio mass spectrometer (Delta Plus; Thermo Scientific) to evaluate the isotopic composition of the samples. The isotopic

values of carbon and nitrogen were expressed in delta notation ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) in per mil (‰) relative to the V-PDB (Vienna Pee Dee Belemnite) and atmospheric N_2 standards, respectively. The delta values were calculated based on the standards using the following equation: $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1]$ multiplied by 1,000, where X represents the stable carbon or nitrogen isotopes (^{13}C or ^{15}N), and R represents the isotope ratio ($^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$).

We performed the replication of the same individual material for only 10% of the samples, but the precision of the analytical method for 22 replicates of an internal standard in all batches was estimated to be 0.09‰ for carbon and nitrogen. The samples were compared to international standards by the use of international reference materials: NBS-19 and NBS-22 for carbon and IAEA-N1 and IAEA-N2 for nitrogen.

Data Analysis. Considering the difference in mammal assemblage composition between systems, we grouped species into trophic guilds following Paglia et al. (21) and Magioli et al. (50): herbivores, frugivores, omnivores, insectivores, and carnivores (SI Appendix, Table S6).

Resource Use. We adapted the analytical approach used by Magioli et al. (7). The analysis consists of using a simple mixing model that interpolates the stable carbon isotopic values of the samples, accounting for specific fractionation factors, with the mean values of the different vegetation types (C_3 and C_4 plant photosynthetic cycles), also considering the minimum and maximum values obtained for all animal samples analyzed. To estimate fractionation factors ($\Delta^{13}\text{C}$ and $\Delta^{15}\text{N}$) for most species without existing values, we used the SIDER package (51) available in R 3.4.3 (52), which estimates species-specific fractionation factors from phylogenetic regression models according to a database of fractionation values available for several species. We generated fractionation factors using the script available in Healy et al. (51) (SI Appendix, Table S6).

To determine the origin of food items consumed by mammals (i.e., forest remnants, C_3 , or agricultural matrix, C_4), we calculated the C_3 and C_4 carbon content in each sample ($\delta^{13}\text{C}$ values corrected by $\Delta^{13}\text{C}$ values). After calculating the proportions of C_3/C_4 -derived carbon, we classified the samples into 3 groups: 1) C_3 group, species that consumed only items from forest remnants (>70% C_3 carbon; $\delta^{13}\text{C} = -32$ to -26 ‰); 2) mixed group, species that fed on items from both remnants and agricultural matrix (30 to 70% C_3 carbon; $\delta^{13}\text{C} = -25.9$ to -18.1 ‰); and 3) C_4 group, species that only

consumed items from the agricultural matrix (<30% C_3 carbon; $\delta^{13}\text{C} = -18$ to -12 ‰). Details of the calculation of the C_3 and C_4 carbon content are provided in SI Appendix.

We also compared the $\delta^{15}\text{N}$ values within and between the groups in both systems. To do this, we corrected the $\delta^{15}\text{N}$ values using the fractionation factors ($\Delta^{15}\text{N}$) generated by the SIDER package (SI Appendix, Table S6). We compared the percentages of individuals belonging to each group among trophic guilds and considering all samples analyzed in each system. We determined the significance of the differences in mean $\delta^{13}\text{C}_{\text{corrected}}$ and $\delta^{15}\text{N}_{\text{corrected}}$ values between guilds and systems using 1-way ANOVA and Tukey post hoc tests.

Isotopic Niche Analysis. To assess the difference in resource use between trophic guilds, we analyzed the size of the isotopic niches using the SIBER package (53) in R 3.4.3. To account for the sample size, we used the SEA corrected (SEAc). To compare the isotopic niches between guilds, we calculated the Bayesian estimate of the SEA (SEAb). The ellipses were calculated and compared between guilds in the different systems, and their overlap was evaluated (details are provided in SI Appendix).

Trophic Structure. To assess the differences in the trophic structure of the 2 systems, we used the mean $\delta^{15}\text{N}_{\text{corrected}}$ values. We identified significant differences in the trophic guilds within and between systems using 1-way ANOVA and Tukey post hoc tests.

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