

RESEARCH ARTICLE

Environmental and human-related gradients shape the community structure of medium and large terrestrial mammals in a central Amazonian white-sand Forest

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Abstract

1. Medium- and large-sized terrestrial mammals play key ecological roles in tropical forests; however, the relative importance of environmental filters and anthropogenic disturbances in structuring their assemblages in Amazonian *campinarana* (white-sand) ecosystems remains poorly understood.
2. In this study, we evaluated the influence of these factors on species composition and habitat use by medium- and large-sized terrestrial mammals, as well as by the frugivore–herbivore guild in Amazonian *campinarana* ecosystems. We used camera traps and structural equation modelling.
3. We recorded 22 species over 4721 camera-trap days, with assemblages dominated by frugivore–herbivores and by dietary and habitat generalists, such as the common opossum (*Didelphis marsupialis*).
4. Habitat use by the overall mammal assemblage was higher in areas with lower vegetation height, whereas terrain elevation relative to the nearest drainage (HAND index) had an indirect effect mediated by vegetation structure. In contrast, frugivore–herbivore species showed more selective responses, with higher habitat-use intensity in areas farther from human influence.
5. Mammal assemblages were predominantly influenced by distance to houses, whereas the composition of the frugivore–herbivore guild was associated with distance to houses and tree height.
6. Our results demonstrate that even low levels of human presence are sufficient to structure mammal assemblages, reinforcing the need for spatially explicit management strategies aimed at conserving the functional integrity of these unique and highly sensitive ecosystems.

KEYWORDS

anthropogenic disturbance, camera trapping, *campinarana*, habitat structure, NMDS, structural equation modelling

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1 | INTRODUCTION

Understanding how species respond to environmental variation is a central topic in ecology, as such responses determine patterns of species distribution, habitat-use intensity and the composition of biological communities (Guisan & Zimmermann, 2000). In this context, environmental heterogeneity emerges as a major driver of community structure, acting as an ecological filter that selects species with different functional strategies and environmental tolerances, particularly in megadiverse regions such as the Amazon Forest (Leal Filho et al., 2025; Oliveira et al., 2021).

The Amazon Forest is characterized by a complex mosaic of natural environments resulting from the interaction between climatic and geomorphological factors, which promotes high habitat diversity and a wide range of ecological processes (Queiroz et al., 2025; Ribas et al., 2025). Among these environments, *terra firme* forests stand out, occupying approximately 82% of the region and characterized by the absence of fluvial flooding, predominantly clayey or clay-sandy soils, and tall forest vegetation (Bredin et al., 2020; Oliveira et al., 2021). Most ecological studies on the Amazon concentrate on *terra firme* forests (Ter Steege et al., 2023).

In addition to *terra firme* forests, the Amazon also harbours white-sand ecosystems. These environments occupy approximately 5% of the region, are patchily distributed across the landscape and are characterized by sandy, highly leached, nutrient-poor and acidic soils (Adeney et al., 2016). White-sand ecosystems range from open areas known as *campinas*, dominated by herbaceous and shrubby vegetation, to forested formations termed *campinaranas*, composed of low-canopy forests when compared to *terra firme* forests (Adeney et al., 2016; Rodrigues et al., 2024). Despite being unique, rare, highly sensitive and supporting ecological communities with high levels of endemism and specialization, these ecosystems remain poorly studied (Adeney et al., 2016; Demarchi et al., 2022).

The knowledge gap around white-sand ecosystems is also evident for mammals, which play key roles in ecosystem functioning by regulating trophic networks, dispersing seeds, cycling nutrients and maintaining forest structure (Batista et al., 2025; Fricke et al., 2025; Mittelman et al., 2021). In addition, mammals are widely used as indicators of environmental quality due to their sensitivity to habitat alteration and have strong socioecological relevance as an important source of subsistence for traditional populations, including those inhabiting protected areas (Lima e Silva et al., 2025; Melo et al., 2015).

Evidence from previous studies in other Amazonian forest ecosystems indicates that vegetation height acts as an environmental filter that shapes assemblage composition by promoting species replacement or exclusion, community simplification and functional losses (Brandão et al., 2025; São Pedro et al., 2025; Tardio & Da Silveira, 2015). In general, environments with taller vegetation tend to support higher diversity of medium- and large-sized terrestrial mammals (Brandão et al., 2025; Feng et al., 2020; Korol et al., 2025; Roll et al., 2015), being more frequently used by carnivores and

large-bodied frugivore–herbivore species, such as tapir (*Tapirus terrestris*), white-lipped peccary (*Tayassu pecari*) and cervids (Tardio & Da Silveira, 2015). For these ungulates, taller vegetation provides shelter from predators and greater availability of fleshy fruits, particularly in oligotrophic environments of the Rio Negro Basin, which are characterized by nutrient-poor soils and limited food resource availability (Tardio & Da Silveira, 2015).

In addition to vegetation height, proximity to water bodies also tends to structure mammal assemblages by promoting species turnover (Brandão et al., 2025). These characteristics influence habitat use by mammals, with felids using areas near water bodies less frequently than frugivore–herbivores (e.g. spotted paca, *Cuniculus paca*, and tapir) or habitat and dietary generalists such as opossums and armadillos (McFarlane et al., 2024; Paredes et al., 2017). Hydrological gradients may influence mammal assemblages both directly and indirectly, although indirect effects mediated by vegetation structure are expected to be particularly important because hydrology strongly determines vegetation stature and forest structure, which in turn modify habitat suitability and resource availability for mammals (Mendonça et al., 2017; Tardio & Da Silveira, 2015).

In contrast, anthropogenic disturbance is expected to influence mammal assemblages primarily through direct ecological filtering. Human pressure, land-use change, logging, fire, deforestation and hunting also strongly alter the structure and composition of mammal assemblages, resulting in species replacement or absence and, under more intense disturbance, defaunation or local extinction (Melo et al., 2015; Quintero et al., 2023; Rosa et al., 2021; Rossi et al., 2025). In this context, large-bodied species that are more sensitive to anthropogenic disturbance or frequently targeted by hunting, such as tapir, white-lipped peccary and jaguar (*Panthera onca*), tend to be rare or absent in areas close to human settlements (McFarlane et al., 2024; Melo et al., 2015; Quintero et al., 2023). In contrast, dietary and habitat generalists with high reproductive rates may benefit from food resources provided by human crops, making them more common in anthropized landscapes, such as nine-banded armadillo (*Dasypus novemcinctus*), common opossum (*Didelphis marsupialis*), spotted paca and cervids. These animals frequently increase their habitat-use intensity in these environments (Ferreira Neto et al., 2023; McFarlane et al., 2024; Rosa et al., 2021; Rossi et al., 2025).

Together, these studies suggest that mammal assemblages are simultaneously shaped by natural environmental gradients and anthropogenic disturbance, acting through both direct and indirect pathways. However, these mechanisms are rarely evaluated within a single analytical framework, particularly in Amazonian white-sand ecosystems. Disentangling these pathways is essential for understanding the processes underlying community assembly and predicting how mammal communities respond to environmental change. Given the ecological importance of mammals and the substantial knowledge gap in white-sand ecosystems, our study provides the first assessment of the direct and indirect effects of hydrological gradients, mediated by vegetation structure, as well as the effect

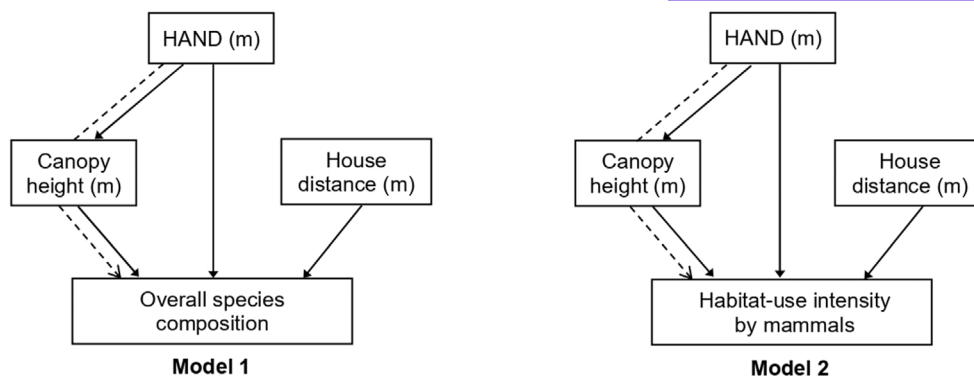


FIGURE 1 Conceptual framework illustrating the predictions tested in this study. The models evaluate the effects of habitat characteristics, including height above nearest drainage (HAND) and vegetation height, as well as human-related variables (distance to houses), on mammal assemblages. Model 1 assesses effects on species composition, and Model 2 on mammal habitat-use intensity, with both models considering the overall assemblage and the frugivore–herbivore guild. Solid arrows indicate direct effects, whereas dashed arrows represent indirect pathways.

of distance to houses, on the structuring of medium- and large-sized terrestrial mammal assemblages in *campinaranas* of Central Amazonia. We predict that vertical distance to the nearest drainage, represented by HAND (Height Above the Nearest Drainage), will influence habitat-use intensity and species composition of mammal assemblages both directly and indirectly (Figure 1). We expect similar direct effects of tree height and distance to houses for both overall mammal assemblages and the frugivore–herbivore guild. Additionally, we expect that environments with taller trees, lower HAND values and shorter distances to houses will be more intensively used by mammals.

2 | MATERIALS AND METHODS

2.1 | Study area

Our study was conducted in the Rio Negro Sustainable Development Reserve (RDS Rio Negro; 60°44'27" W; 3°04'14" S), located on the right bank of the lower Rio Negro, Central Amazonia, Brazil (Figure 2). The RDS Rio Negro encompasses the municipalities of Iranduba, Novo Airão and Manacapuru, in the state of Amazonas (Vasconcelos et al., 2022). The reserve is a protected area designated for the sustainable use of natural resources and is currently inhabited by approximately 800 families distributed across 19 communities and 19 access roads, which are reached via the Rio Negro or unpaved roads branching from highway AM-352. The main activities carried out by resident families include agriculture, timber forest management, fishing, and, to a lesser extent, tourism.

The regional climate is classified as Am (tropical monsoon) according to the Köppen classification, characterized by a mean annual temperature of 25.6°C and mean annual precipitation of approximately 2300 mm (Peel et al., 2007). The dry season occurs from June to November, whereas the rainy season extends from December to May (Marinho & Rivera, 2021).

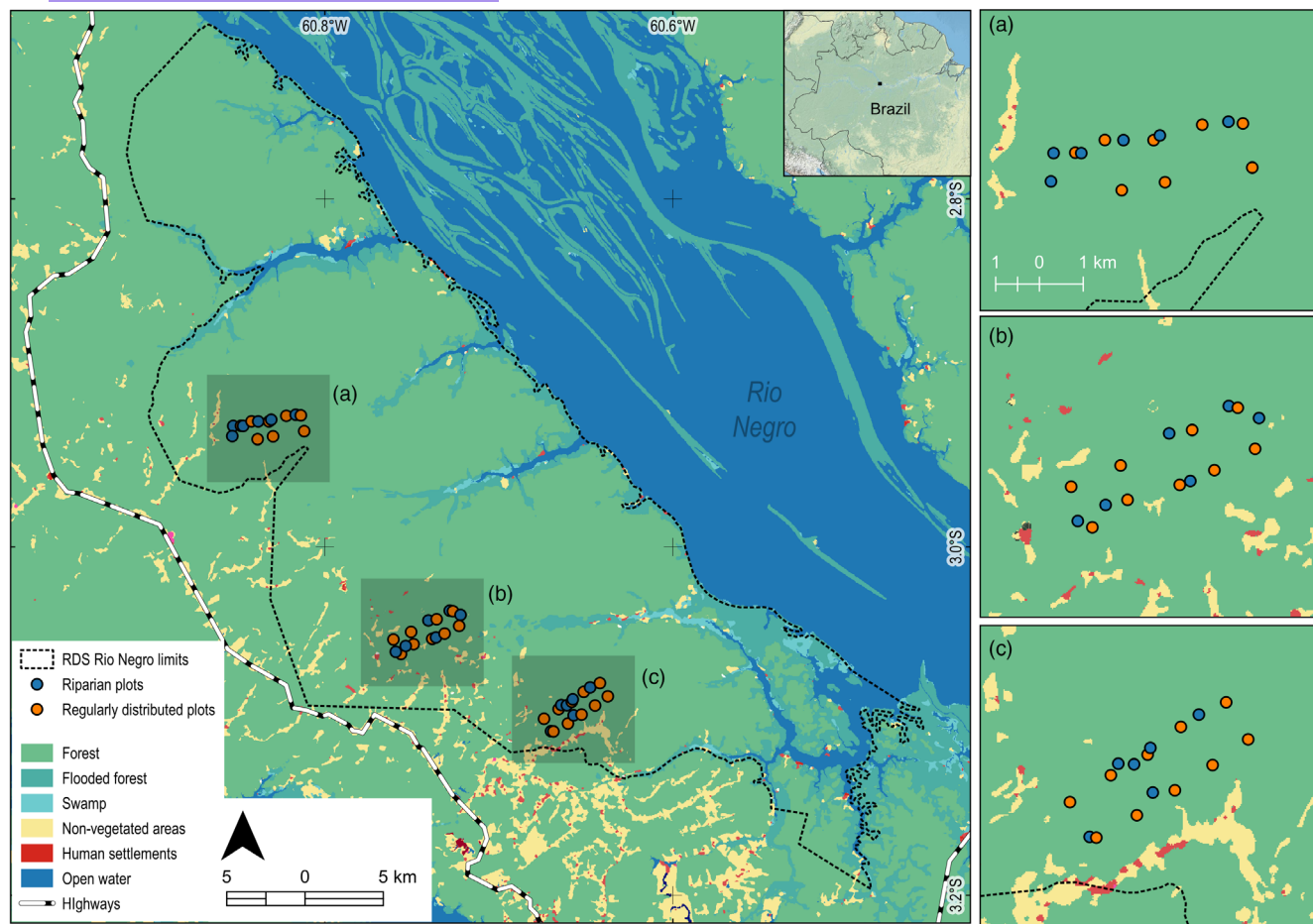
Vegetation in the region is classified as Dense Ombrophilous Forest, with *terra firme* forests predominating. In addition to these formations, patches of *campinas* and *campinaranas* occur, covering approximately 1.8% of the reserve area and occupying sandy, acidic, highly leached and nutrient-poor soils (Magnusson et al., 2023; Pereira et al., 2024). *Campinaranas* may be riparian, occurring along streams, or non-riparian, located farther from water bodies (Mendonça et al., 2017; Pereira et al., 2024).

2.2 | Sampling design

To sample medium- and large-sized mammals, we adopted the RAPELD system, which integrates Rapid Assessment Program (RAP) inventories with Long-Term Ecological Research Projects (PELD) (Magnusson et al., 2005). We sampled three RAPELD modules accessed via unpaved roads branching from kilometres 18, 26 and 50 of highway AM-352. Each module has a rectangular configuration, with two 5-km trails separated by a 1-km access trail (see Pereira et al., 2024).

Each 5-km trail consists of five uniformly distributed plots, spaced 1 km apart, starting at 500 m and extending to 4500 m from the access trail (Figure 2). All plots are located in *campinarana* environments. In addition to the uniformly distributed plots, riparian *campinarana* plots occur along the access trails and between the uniformly distributed plots and are established along small streams, which may experience seasonal variation in water flow and can dry out during certain periods of the year. This design comprises a total of 45 plots, including 30 uniformly distributed plots (10 per module) and 15 riparian plots (five per module) (Figure 2). Plots are 250 m long, starting at the edge of the main trail and following the terrain contour lines (Magnusson et al., 2005).

Ethical approval was not required because the study used a non-invasive camera-trapping method that did not involve the capture, handling or manipulation of animals. Fieldwork was conducted



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FIGURE 2 Location of the study area in the Rio Negro Sustainable Development Reserve (dashed black line), Amazonas, Brazil. The main map shows the three RAPELD sampling modules, and panels (A–C) provide enlarged views of each module to better illustrate the spatial distribution of the sampling plots and nearby human settlements. Riparian plots are represented by blue circles and regularly distributed plots by orange circles. Land-cover classes include forest (green), flooded forest (light green), swamp (cyan), non-vegetated areas (yellow), human settlements (red), open water (blue) and highways (white).

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2.3 | Mammal sampling

We sampled mammals between June 2024 and February 2025, encompassing both the dry and rainy seasons, following the sampling protocol of Rosa et al. (2025). During the dry season, camera traps operated from June to September, and during the rainy season from December to February, totalling approximately 135 sampling days per camera trap.

In each of the 45 plots, we installed one camera trap (Figure 2) equipped with a motion sensor, including 10 Bushnell 24 MP Prime Combo Low Glow® cameras (model 119932CB) and 35 Reconyx HyperFire 2 Professional HP2X® cameras (model HLPXEL10021478). Camera traps were positioned 30–50 cm above the ground, near trails commonly used by animals for movement. Cameras were programmed to take three consecutive photographs followed by a 15-s video, with a 1-min interval between triggers.

Species were identified using field guides (Barros, 2022; Reis et al., 2015) and with assistance from taxonomic specialists. Records were considered independent when separated by at least 1 h. When more than one individual of the same species was recorded in a single event (photograph or video) within this interval, each individual was considered an independent record. Species were classified into trophic guilds according to diet as carnivores, frugivore–herbivores, insectivores or omnivores, following Paglia et al. (2012). Only wild terrestrial medium- to large-bodied mammals were considered in this study. Species included in this category have a body mass greater than 1 kg, following the classification proposed by Brocardo et al. (2023).

2.4 | Environmental and anthropogenic variables

In each plot, we measured the following variables: maximum vegetation height (defined as the 0.995 quantile of recorded heights), vertical distance to the nearest drainage and linear distance to the nearest residence. Vegetation height was obtained using a portable

terrestrial LiDAR (Light Detection and Ranging) device (LD90-3100VHS-FLP, RIEGL Laser Measurement Systems GmbH, Horn, Austria) (Parker et al., 2004), which is a laser-pulse system widely used in forest applications (Giongo et al., 2010). LiDAR sampling was conducted along the entire length of each plot using continuous movement of the equipment. Measurements were taken every 10 m segment, resulting in 25 sampling segments per plot, following the methodology of Torralvo et al. (2019).

Height above nearest drainage (HAND) was derived from a digital elevation model to normalize the relative elevation above the drainage network. This metric therefore also serves as a proxy for local drainage potential and is correlated with groundwater depth and terrain elevation (Nobre et al., 2011; Rennó et al., 2008). The raster layer containing HAND data was obtained from the global model, and HAND values were extracted for each plot using R software, version 4.5.0 (R Core Team, 2025).

To measure the distance from each camera trap to the nearest residence, we imported the geographic coordinates of camera traps into Google Earth Pro (Google LLC, 2024), where the closest individual residence dispersed across the landscape was identified and its location subsequently validated during fieldwork. Distances were determined using the ruler tool, measuring the shortest linear distance (m) between the camera-trap location and the identified residence, following Brocardo et al. (2023).

2.5 | Data analyses

We tested correlations among pairs of explanatory variables (vegetation height, HAND and distance to houses) using Pearson's correlation coefficient ($|r| < 0.7$). All correlations were below 0.5, and variables were therefore treated as uncorrelated. We also assessed multicollinearity among independent variables using the variance inflation factor ($VIF < 5$) implemented in the car package (Fox et al., 2024), with all values below 2.

Response variables included overall mammal species composition, frugivore–herbivore species composition and habitat-use intensity for both groups. Only the frugivore–herbivore guild was analysed separately, as it was the only guild with a sufficient number of records ($N > 250$) to allow robust analyses. To quantify habitat-use intensity, we standardized the data by dividing the number of independent records of each species per plot by the number of camera-trap operating days and multiplying the result by 100, expressing habitat-use intensity as the average number of independent records per 100 camera-trap days, following Mandujano (2024).

Overall species composition and frugivore–herbivore composition were summarized by the first two axes of a non-metric multidimensional scaling (NMDS) ordination using the Bray–Curtis dissimilarity index, calculated from habitat-use intensity data. The NMDS was performed using a three-dimensional solution ($k = 3$) with 500 random starts (trymax = 500). The final solution showed stress

values of 0.124 for the overall mammal community and 0.096 for the frugivore–herbivore guild, with consistent convergence among runs based on Procrustes comparisons.

To evaluate direct and indirect effects of environmental and anthropogenic variables, we used structural equation modelling (SEM) (Kline, 2015). This two-step approach was adopted to preserve the multivariate structure of the community before evaluating the direct and indirect effects of environmental and anthropogenic variables on compositional gradients. We constructed six structural equation models (SEMs) following the conceptual framework shown in Figure 1. Models 1 and 2 assessed the effects of the predictor variables on overall mammal species composition (NMDS1 and NMDS2, respectively), whereas Model 3 evaluated habitat-use intensity for the overall assemblage. Models 4 and 5 assessed the effects of the predictor variables on frugivore–herbivore species composition (NMDS1 and NMDS2, respectively), whereas Model 6 evaluated habitat-use intensity for the frugivore–herbivore guild.

Model fit was assessed using multiple complementary indices, including the chi-square test (χ^2), p -value, comparative fit index (CFI), Tucker–Lewis index (TLI), root mean square error of approximation (RMSEA) and standardized root mean square residual (SRMR). Following Kline (2015), models were considered to have an excellent fit when χ^2 was non-significant ($p > 0.05$), CFI and TLI were ≥ 0.95 , RMSEA < 0.05 and SRMR < 0.08 . Structural equation models were fitted using the lavaan (Rosseel, 2012) and lavaanPlot (Lishinski, 2018) packages, with maximum likelihood estimation and robust standard errors. All analyses were conducted in R software, version 4.5.0 (R Core Team, 2025).

We also evaluated the potential for spatial autocorrelation among sampling locations using Moran's I , implemented in SAM software v4.0 (Rangel et al., 2010). Data were analysed separately for each module, as spatial independence tends to be greater within modules than among them. Because the lavaan package does not provide residuals from structural equation models, we fitted multiple linear regression models including all predictor variables to extract residuals for spatial analyses. Spatial structure analyses used an equal number of pairwise comparisons (28–40, depending on the module), resulting in six distance classes that varied among modules. Significance was tested using 999 permutations. For all response variables analysed (NMDS1, NMDS2 and habitat-use intensity for all mammals and frugivore–herbivores) within each module, we found no significant spatial autocorrelation ($p > 0.05$).

3 | RESULTS

We recorded 22 species of medium- and large-sized terrestrial mammals, distributed across seven orders, 12 families, and 20 genera, totalling 392 independent records over 4721 camera-trap days. The most frequently recorded species were the common opossum

(*Didelphis marsupialis*, $N=67$), spotted paca (*Cuniculus paca*, $N=53$), brown brocket deer (*Passalites nemorivagus*, $N=47$), red brocket deer (*Mazama americana*, $N=41$), collared peccary (*Dicotyles tajacu*, $N=37$) and white-lipped peccary (*Tayassu pecari*, $N=35$), whereas the jaguarundi (*Herpailurus yagouaroundi*) and giant armadillo (*Priodontes maximus*) were recorded only once (Table 1).

Frugivore–herbivores were the most abundant guild (252 records), followed by omnivores ($N=82$), insectivores ($N=32$) and carnivores ($N=26$). Species richness per plot ranged from one to eight species (mean = 3.5; SD = 1.7). Mean maximum vegetation height was 28.3 m (SD = 5.0), mean HAND was 5.6 m (SD = 6.4), and mean distance to the nearest house was 1420 m (SD = 879.9) (Table S1).

Taxon	Common name	Diet	N° rc.
Order Artiodactyla			
Family Cervidae			
<i>Passalites nemorivagus</i>	Brown brocket deer	FRU/HB	47
<i>Mazama americana</i>	Red brocket deer	FRU/HB	41
Family Tayassuidae			
<i>Dicotyles tajacu</i>	Collared peccary	FRU/HB	37
<i>Tayassu pecari</i>	White-lipped peccary	FRU/HB	35
Order Carnivora			
Family Felidae			
<i>Herpailurus yagouaroundi</i>	Jaguarundi	CAR	1
<i>Leopardus pardalis</i>	Ocelot	CAR	7
<i>Leopardus wiedii</i>	Margay	CAR	3
<i>Puma concolor</i>	Puma	CAR	8
<i>Panthera onca</i>	Jaguar	CAR	7
Family Mustelidae			
<i>Eira barbara</i>	Tayra	ONI	6
Family Procyonidae			
<i>Nasua nasua</i>	Coati	ONI	2
Order Cingulata			
Family Dasypodidae			
<i>Cabassous unicinctus</i>	Southern naked-tailed armadillo	INS	3
<i>Dasypus novemcinctus</i>	Nine-banded armadillo	INS	16
Family Chlamyphoridae			
<i>Priodontes maximus</i>	Giant armadillo	INS	1
Order Didelphimorphia			
Family Didelphidae			
<i>Didelphis marsupialis</i>	Opossum	ONI	67
<i>Didelphis imperfecta</i>	White-eared opossum	ONI	7
Order Perissodactyla			
Family Tapiridae			
<i>Tapirus terrestris</i>	Tapir	FRU/HB	8
Order Pilosa			
Family Myrmecophagidae			
<i>Myrmecophaga tridactyla</i>	Giant anteater	INS	5
<i>Tamandua tetradactyla</i>	Southern tamandua	INS	7
Order Rodentia			
Family Cunilidae			
<i>Cuniculus paca</i>	Spotted paca	FRU	53
Family Dasyproctidae			
<i>Dasyprocta fuliginosa</i>	Agouti	FRU/HB	26
<i>Myoprocta pratti</i>	Green acouchi	FRU/HB	5

TABLE 1 Mammal species recorded in the RDS Rio Negro, AM, with taxonomic classification, common name, diet (FRU/HB = frugivore–herbivore, FRU = frugivore, CAR = carnivore, INS = insectivore and ONI = omnivore) and number of records (N° rc.).

3.1 | Structural equation modelling analyses

According to the SEM results, environmental and anthropogenic variables had significant and consistent effects on mammal assemblage structure (Figure 3; Table S2). In all six models, HAND positively influenced vegetation height, indicating that plots located higher and vertically farther from watercourses exhibit taller vegetation.

For overall mammal composition, only NMDS2 was influenced, being structured exclusively by distance to the nearest house (coefficient = -0.48 ; $p < 0.001$). This indicates that mammal assemblage

composition varies along a gradient of human proximity, with compositional changes occurring closer to residences.

Regarding habitat-use intensity by mammals in general, vegetation height had a direct negative effect (coefficient = -0.45 ; $p < 0.001$), indicating higher habitat-use in areas with shorter vegetation. HAND affected habitat-use indirectly, mediated by vegetation structure (coefficient = -0.11 ; $p = 0.004$).

For the frugivore-herbivore guild, species composition was influenced by distance to houses along NMDS1 (coefficient = -0.31 ; $p = 0.046$), indicating compositional changes associated with

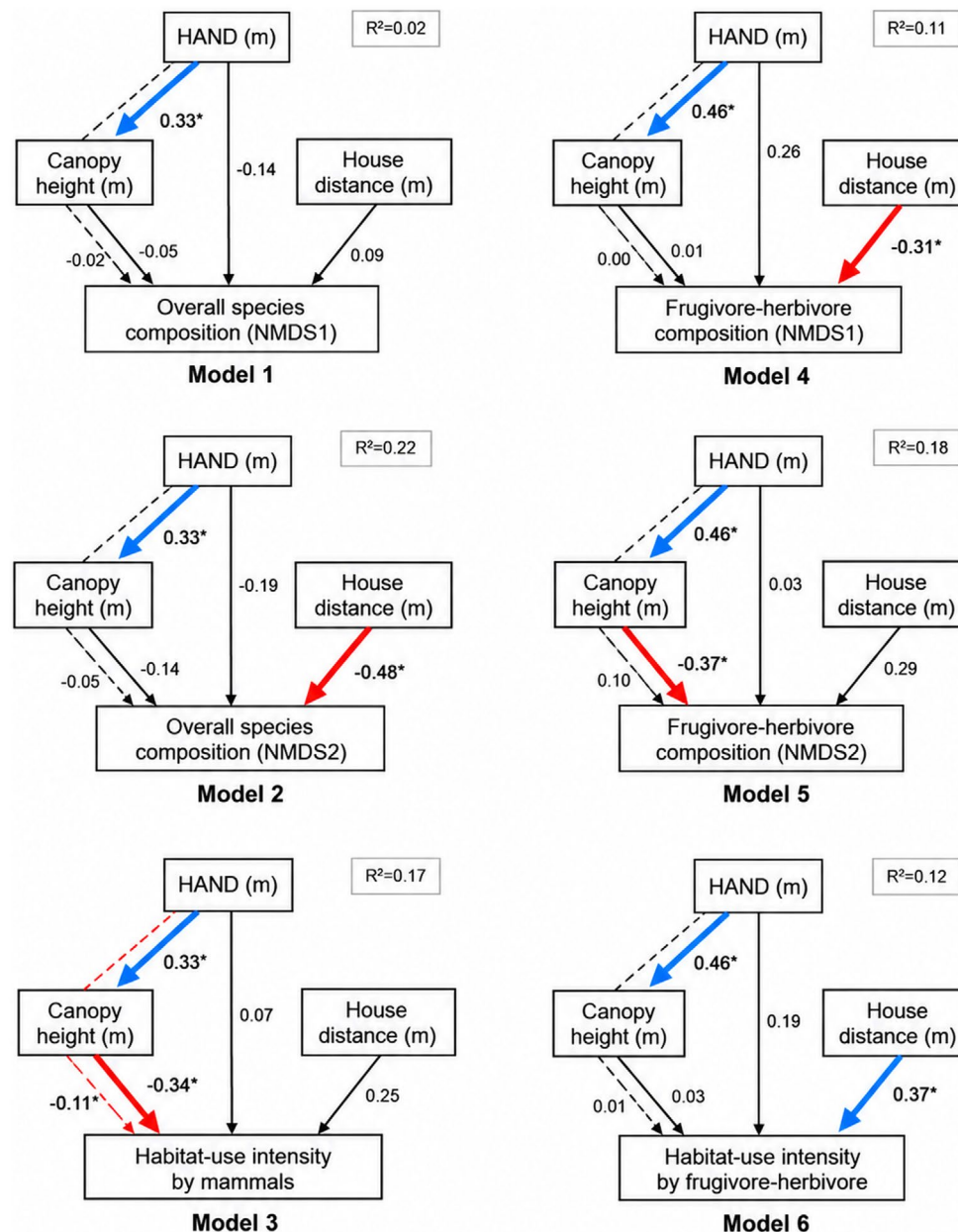


FIGURE 3 Structural equation models (SEM) showing effects of environmental (HAND, vegetation height) and anthropogenic (distance to houses) variables on mammal assemblages. Models 1 (NMDS1) and 2 (NMDS2) evaluate overall species composition, Model 3 evaluates habitat-use intensity by mammals, Models 4 (NMDS1) and 5 (NMDS2) assess frugivore-herbivore species composition, and Model 6 assesses habitat-use intensity for this guild. Solid arrows indicate direct effects, dashed arrows indirect effects, blue = positive, red = negative, black = non-significant. Asterisks (*) denote significant effects ($p < 0.05$). R^2 values indicate proportion of variance explained.

Model	χ^2	p -value >0.05	CFI ≥0.95	TLI ≥0.95	RMSEA <0.05	SRMR <0.08	R^2
Model 1	0.751	0.386	1	1.310	0	0.024	0.02
Model 2	0.751	0.386	1	1.054	0	0.027	0.22
Model 3	0.751	0.386	1	1.067	0	0.026	0.17
Model 4	0.161	0.689	1	1.354	0	0.013	0.11
Model 5	0.161	0.689	1	1.235	0	0.014	0.18
Model 6	0.161	0.689	1	1.170	0	0.013	0.12

Note: Model fit was assessed using the chi-square test (χ^2), p -value, Comparative Fit Index (CFI), Tucker–Lewis Index (TLI), Root Mean Square Error of Approximation (RMSEA) and Standardized Root Mean Square Residual (SRMR). Model fit criteria followed the recommendations of Kline (2015).

TABLE 2 Goodness-of-fit indices and coefficients of determination (R^2) for the six structural equation models (SEM) evaluated in this study.

human proximity, and by vegetation height along NMDS2 (coefficient = -0.37 ; $p = 0.046$), reflecting species turnover along the vegetation structural gradient. Habitat use by this guild was positively affected by distance to residences (coefficient = 0.37 ; $p = 0.011$), being higher in areas farther from human influence.

All six structural equation models met the recommended goodness-of-fit criteria, indicating an excellent fit to the data (Table 2). The proportion of explained variance (R^2) varied among models.

4 | DISCUSSION

Our results demonstrate that both habitat-use intensity and species composition of medium- and large-sized terrestrial mammals in Amazonian *campinaranas* are strongly influenced by environmental and anthropogenic filters, with anthropogenic factors exerting more consistent and widespread effects. Results from the SEM showed that environmental gradients modulate habitat use by the overall mammal assemblage, whereas proximity to houses was the primary driver of habitat-use intensity in the frugivore–herbivore guild. These findings agree with previous evidence that frugivore–herbivorous mammals are particularly sensitive to anthropogenic disturbance (McFarlane et al., 2024; Melo et al., 2015; Rossi et al., 2025).

Contrary to our initial expectations, HAND did not have a direct effect on mammal species composition, suggesting that other environmental variables may play a more prominent role in structuring these assemblages. However, its positive and consistent relationship with vegetation height indicates that plots located at higher distances from drainage support taller vegetation, a pattern previously reported for riparian and non-riparian Amazonian *campinaranas* (Mendonça et al., 2017). Therefore, this finding corroborates the indirect negative effect of HAND on habitat use by mammals in general, illustrating that abiotic variables may influence mammal assemblages indirectly by shaping habitat structure and resource availability.

The greater use of habitats closer to water bodies may be related to environmental conditions that favour some frugivore–herbivorous mammals, such as the spotted paca and collared peccary, which

were among the most frequently recorded species in our study. This interpretation is consistent with Paredes et al. (2017), who reported greater habitat use by these species in areas near water bodies. In addition, lower and more open vegetation typically found near streams may favour the occurrence of termite mounds (Mendonça et al., 2017), an important food resource for insectivorous and omnivorous mammals such as armadillos, anteaters and opossums.

Unexpectedly, vegetation height showed a direct negative effect on habitat-use intensity by mammals in general, as revealed by the SEM. This pattern likely reflects the high frequency of records of habitat- and diet-generalist species, such as opossums (Voss, 2022). Because *campinaranas* with lower vegetation height tend to have a more open canopy (Mendonça et al., 2017), our results align with Brocardo et al. (2023), who reported a positive influence of canopy openness on omnivores. In the study by Brocardo et al. (2023), the common opossum accounted for more than half of the records, reflecting high tolerance to open or secondary environments, consistent with its occurrence in savannas and forest edges (Voss, 2022). Therefore, the negative effect of vegetation height does not imply exclusion from taller forests but rather indicates the relative predominance of opportunistic species in lower and more open vegetation types (Brocardo et al., 2023).

As expected, vegetation structure influenced the composition of the frugivore–herbivore guild. Forests with taller and more structurally complex vegetation generally provide greater food availability and shelter from predators, particularly for large-bodied species such as the lowland tapir and white-lipped peccary (Tardio & Da Silva, 2015). These species depend on continuous forest habitats with abundant food resources, highlighting vegetation structure as an important ecological filter for mammals with specialized habitat requirements (Brandão et al., 2025; Brocardo et al., 2023; Melo et al., 2015; Quintero et al., 2023; Tardio & Da Silva, 2015).

Distance to houses emerged as the main factor structuring overall mammal assemblage composition, indicating that anthropogenic filters can override natural environmental gradients. This pattern is consistent with previous studies showing that mammal species respond differently to human disturbance. For example, large-bodied mammals such as the jaguar, tapir and white-lipped peccary are particularly sensitive to anthropogenic disturbance and

tend to occur farther from houses, where anthropogenic impacts are lower, thereby contributing to the observed variation in mammal assemblage composition (Melo et al., 2015; Rosa et al., 2021; Rossi et al., 2025). This distribution likely reflects both lower anthropogenic disturbance and species life-history traits, including low reproductive rates, large home ranges and high energetic requirements (McFarlane et al., 2024). Conversely, areas closer to houses tend to be characterized by disturbance-tolerant species with higher ecological flexibility, further contributing to shifts in mammal assemblage composition (Ferreira Neto et al., 2023; McFarlane et al., 2024).

Similarly, frugivore–herbivores showed the same response to anthropogenic disturbance, with distance to houses influencing assemblage composition (NMDS1) as well as habitat-use intensity. This result is consistent with the greater sensitivity of large-bodied frugivore–herbivores, such as the lowland red brocket deer, tapir, and white-lipped peccary, to anthropogenic disturbance, particularly hunting pressure, which leads to higher occurrence farther from houses (Ferreira Neto et al., 2023; McFarlane et al., 2024; Melo et al., 2015). Because the white-lipped peccary and red brocket deer were among the most frequently recorded frugivore–herbivores in our study, their distribution likely drove both the observed compositional changes and the greater habitat-use intensity in areas farther from houses. As important ecosystem engineers and seed dispersers, reductions in the occurrence of these large mammals near houses may compromise ecosystem functioning by reducing seed dispersal, nutrient cycling and the maintenance of understory structure (Rosa et al., 2021; Tardio & Da Silveira, 2015).

Although our study demonstrates important effects of environmental and anthropogenic variables on mammal assemblages in Amazonian *campinaranas*, some limitations should be acknowledged. We did not directly quantify food resources (fruits, seeds, leaves, invertebrates), which may affect interpretations regarding species selectivity, as resource availability strongly influences mammal occurrence and habitat use (Brandão et al., 2025; Brocardo et al., 2023). Additionally, anthropogenic pressure, including hunting, domestic dogs, crops, fire, number of households and family size, was inferred indirectly through proximity to residences, despite their known effects on mammal presence and behaviour (Ferreira Neto et al., 2023; McFarlane et al., 2024; Quintero et al., 2023).

Several species included in the ordination occurred infrequently (e.g. $N=5-8$). No transformation or down-weighting of rare species was applied in the construction of the Bray–Curtis dissimilarity matrix, to preserve the original structure of the community data. Because rare species can exert a disproportionate influence on ordination space, particularly at the extremes of NMDS axes, the positioning of some sampling units along compositional gradients may partly reflect their contribution. Consequently, interpretations of axis extremes should be made with caution, as they may represent both the influence of rare species and broader patterns of species turnover.

Finally, in sustainable-use protected areas, where human presence is intrinsic, our results support management strategies that consider distance to houses as a relevant operational metric.

Maintaining areas farther from human occupation is essential for providing refuges for sensitive species. This strategy should be reinforced through long-term monitoring and community-based management to ensure functional conservation and ecosystem resilience (Magnusson et al., 2005; Quintero et al., 2023).

5 | CONCLUSION

1. Assemblages of medium- and large-sized terrestrial mammals in the *campinaranas* were dominated by frugivore–herbivores and generalist species, particularly spotted paca, common opossum and cervids.
2. Hydrological gradients indirectly and negatively influenced habitat use, highlighting the importance of abiotic variables that shape structural heterogeneity and the availability of key resources for wildlife.
3. Anthropogenic influence, inferred from proximity to houses, emerged as the primary factor structuring mammal assemblage composition and habitat use by frugivore–herbivores.
4. These findings underscore the need for spatial management strategies that explicitly account for human presence, combined with long-term monitoring, to maintain refuges for sensitive species and ensure the functional conservation of Amazonian *campinaranas*.

AUTHOR CONTRIBUTIONS

Clarissa Rosa, Rafael Rabelo and Paulo Bobrowiec conceived the ideas and developed the methodology; Renilce Carvalho de Castro, Edney Matos do Nascimento, Renan Ministerio Castro and Sâmia Letícia Reolon da Cruz collected the data; Rafael Rabelo, Paulo Bobrowiec and Renilce Carvalho de Castro analysed the data; Renilce Carvalho de Castro, Clarissa Rosa, Rafael Rabelo, Paulo Bobrowiec and Juliana Schietti contributed to the writing of the manuscript. David Luther contributed to the revision and translation of the final version. All authors critically contributed to the preliminary versions and approved the final manuscript for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data available from the Zenodo repository <https://doi.org/10.5281/zenodo.23066204> (Carvalho de Castro et al., 2026).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

TABLE S1. Shows the mean, standard deviation (SD), and minimum and maximum values of the independent variables.

TABLE S2. Standardized direct and indirect effects estimated by Structural Equation Models (SEM) evaluating the influence of hydrological (HAND), vegetation structure (canopy height), and anthropogenic disturbance (distance to the nearest house) on species composition and habitat use of terrestrial medium- and large-sized mammals. Models 1 and 2 assess the overall species composition based on the first (NMDS1) and second (NMDS2) axes of the NMDS ordination. Model 3 evaluates habitat use by all species. Models 4 and 5 assess the composition of frugivore-herbivore species based on NMDS1 and NMDS2, respectively, and Model 6 evaluates habitat

use by this functional group. Standardized path coefficients (Std. all) and associated *p*-values are shown. Indirect effects represent mediation through canopy height.

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