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Mammalian diet as indicator of landscape modification

La dieta de mamíferos como indicador de la modificación del paisaje

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Research Article

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Abstract

The modification of primary environments due to human activities imposes different challenges on animal species living in sympatry, which may respond with behavioral and ecological adjustments to survive. Omnivorous mammals, unlike carnivores or herbivores, require special attention due to their constant intake of diets based on vertebrates, invertebrates, and plants. Strategies to obtain food may vary among omnivore species according to the degree of habitat disturbance. For this reason, there is a need to understand how different omnivores respond, in terms of feeding ecology, when subjected to the same anthropogenic pressures within a shared habitat. In this study, we examined the diet of sympatric medium-sized mammals living in a coniferous forest in Veracruz, Mexico, which has been subject to anthropogenic pressures. We focused on ringtail (*Bassariscus astutus*), common opossum (*Didelphis marsupialis*) and gray fox (*Urocyon cinereoargenteus*). We predicted that dietary patterns would differ between habitat types (conserved vs disturbed) and seasons (dry and rainy), being the species with a more specialized diet more affected by landscape modification. We collected and examined scats of the three mammal species. Overall, the most common food item consumed was plants, followed by invertebrates and, to a lesser extent, vertebrates. Food intake frequency was similar between conserved and disturbed zones; however, we recorded a higher invertebrate intake during the rainy season. *Bassariscus astutus* and *D. marsupialis showed* a higher frequency of plant intake, followed by vertebrate and invertebrate items, whereas in *U. cinereoargenteus*, plant and vertebrate items showed equal frequency, followed by invertebrates. Considering each species, the type of consumed food item differed among species and between sampled areas, and an interaction between species and seasons was also found.

Keywords: food, medium-sized mammals, niche, protected area

Resumen

La modificación de los ambientes primarios, como consecuencia de las actividades humanas, impone diferentes desafíos a las especies animales que viven en simpatría, las cuales pueden responder con ajustes conductuales y ecológicos para sobrevivir. Los mamíferos omnívoros, a diferencia de los carnívoros o herbívoros, requieren atención especial debido a la ingesta constante de dietas basadas en vertebrados, invertebrados y plantas. Las estrategias para obtener alimento pueden variar entre las especies omnívoras según el grado de perturbación. Por esta razón, es necesario comprender cómo responden los diferentes omnívoros en términos de ecología alimentaria al estar sujetos a las mismas presiones antrópicas en un hábitat compartido. En este estudio, examinamos la dieta de *Bassariscus astutus*, *Didelphis marsupialis* y *Urocyon cinereoargenteus*, mamíferos medianos simpátricos que viven en un bosque de coníferas en Veracruz, México, el cual ha estado sujeto a actividades humanas. Predecimos que los patrones dietéticos diferirán según el tipo de hábitat (conservado o perturbado) y la estación (seca y lluviosa), siendo las especies con una dieta más especializada las más afectadas por la modificación del paisaje. En general, el alimento más común consumido por los mamíferos fueron las plantas, seguidas de los invertebrados y, en menor medida, los vertebrados. La frecuencia de consumo de los alimentos fue similar entre las zonas conservadas y perturbadas; sin embargo, se registró un mayor consumo de invertebrados en la época de lluvias. *Bassariscus astutus* y *D. marsupialis* mostraron mayor ingesta de plantas seguida de vertebrados e invertebrados; mientras que

para *U. cinereoargenteus*, los ítems de plantas y vertebrados mostraron la misma frecuencia, seguidos de los invertebrados. Considerando cada especie, el tipo de ítem alimenticio consumido fue diferente entre especies y entre áreas muestreadas. También se encontró una interacción entre especies y estaciones.
Palabras clave: alimento, mamíferos medianos, nicho, área protegida

Introduction

The intensification of human activities, such as agriculture, livestock production, and urbanization, among others, changes multiple components of the landscape, including soil properties, landforms, climate, fauna and flora, resulting in a modified environment characterized by loss and degradation of original biological resources (Need et al., 2021). One of the most important attributes of human-modified landscapes is how these components are distributed (Li et al., 2022), influencing the ability of animals to find food resources and suitable habitat (Driscoll et al., 2013). Therefore, severe land transformation could explain changes in animal community structure and diversity, habitat preference and use, and dietary patterns (Magioli et al., 2016, 2019).

Knowledge about the effects of modified landscapes on animal communities is extensive (Fahrig, 2003; Fahrig et al., 2019; Li et al., 2021; Yan et al., 2023), and special attention has been given to mammal species since they play a key role in the food web and, therefore, in ecosystem dynamics (Jones & Safi, 2011; Sinclair, 2003). It is well known that in modified landscapes the structure of mammal communities changes. For example, abundance and species richness tend to decrease, and species composition and diet tend to be simplified (Gámez-Virués et al., 2015; Heroldová et al., 2007).

Herbivorous, carnivorous, and omnivorous animals vary in their degree of dietary specialization and food mixing, including mammals (Reuter et al., 2023), for which single resources feeders are exceptional (Pineda-Muñoz & Alroy, 2014). Mammalian dietary patterns (i.e. the consumed items and their variability) are modulated by parasitism, competition, energy reward, food web dynamics, among other factors (Singer & Bernays, 2003). Species distribution and environmental seasonality may also influence food item acquisition (Cunningham et al., 2006). Recent studies have demonstrated that environmental disturbance can generate a readjustment of food item types (vertebrates, invertebrates, and plants) and the amount of food ingested. Thus, in a modified landscape, variation in mammalian responses to disturbance type and the degree of habitat conservation is expected (Zúñiga et al., 2020).

Omnivorous mammals deserve special attention because within this guild there are species with many combinations of dietary specialization and distinct degrees of vertebrate, invertebrate, and plant intake. These animals feed on different food components such as plant parts, fruits, seeds, as well as invertebrate and vertebrate prey. Reuter et al. (2023) proposed a classification of eight omnivore dietary guilds, revealing that omnivorous species should be less energetically constrained, since they rely on both plant and animal resources. Additionally, omnivores that feed on invertebrate prey have smaller bodies than those that feed on vertebrate prey (Carbone et al., 1999). These findings indicate that, within the omnivore guild, diversification of macroevolutionary and macroecological trends has been essential to adjust the physiological and ecological strategies of current mammalian species (Reuter et al., 2023).

Feeding ecology shows that levels of food mixing and their range of variation are also observed in disturbed landscapes and can serve as indicators of the role of mammals in modified environments (Weideman et al., 2020; Zúñiga et al., 2020). For instance, in agricultural fragments, omnivorous species tend to increase the intake of small vertebrates and invertebrates, while carnivores may suffer negative effects from exposure to or bioaccumulation of toxicants such as pesticides, persistent organic pollutants and heavy metals (Fritsch et al., 2011; Magioli et al., 2016, 2019; Smith et al., 2007). This understanding is ecologically relevant because it sheds light on the mammalian niche differentiation among trophic guilds across different habitat types and their ability to adapt to modified landscapes (Gámez-Virués et al., 2015; Gorczynski et al., 2021).

In this study, we examined the diet of sympatric medium-sized mammal species (1-7 kg; Tucker et al., 2018), in a modified landscape in Veracruz, Mexico. We aimed to identify and compare variation in mammalian diets and their associations with habitat type and season. We predicted that mammalian dietary patterns would differ between habitat types (conserved vs disturbed) and seasons (dry vs rainy).

Methods

Study area

We conducted our study on the northwest slope of the Cofre de Perote mountain in the state of Veracruz, within an area of 17.6 ha. This site is located in a small patch of conserved coniferous forest (10.5 ha), which is a privately protected area called "Bosque de los Murmullos" (19° 32' 20" N; 97° 14' 10" W, Fig.1). The area is a pine-oak forest, composed of evergreen species, such as *Pinus oocarpa*, *P. hartwegii*, *P. teocote*, and *Quercus rugosa*, which are used in the region as timber material and firewood. Near this site there are anthropogenically transformed areas, such as corn (*Zea mays*) and bean (*Vicia faba*) crops, as well as tourism and recreation areas (7.1 ha) (Hernández-Sánchez, 2016). We categorized the study area into two types: conserved (CZ) and disturbed (DZ) zones, characterized by the maintenance of natural coniferous forest structures in CZ, and the presence of human activities (crops, pasture, livestock, roads, and touristic constructions) in DZ, respectively. The study area is located at altitudes between 2,514 and 2,598 masl. The annual temperature ranges between 18 ºC and 22ºC, with two climatic seasons: rainy (from October to May) with average annual precipitation of 193.8 mm, and dry (from June to September) with a precipitation of 47.2 mm (Weather Spark, 2020).

Sampling design and laboratory methods

Conserved and disturbed zones were simultaneously sampled between June and September (rainy season) and between October and May (dry season) of 2017 and 2018, in periods of 10 consecutive days per month. In CZ and DZ, we first searched for mammal latrines, feces or by direct sightings of individuals to determine their location. We only collected fresh feces manually, which were stored in plastic bags and transported

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to the Facultad de Biología, Universidad Veracruzana, Mexico. Feces were dried for 48 hours at 36°C using a drying oven (Binder EDO056UL-120V), then processed and weighed (Phoenix®, 0.001g) to identify the mammal species to which they belonged (following Aranda, 2012; Elbroch, 2003; and personal experience) and to determine the types of food items consumed. Following the modified protocol of Pineda-Munoz and Alroy (2014), the food content was categorized into plant (P), invertebrate (I) and vertebrate (V) items. This was only possible due to the presence of reliable material, such as seeds, parts of insects, hair, nails or bones, that allowed identification at the order, family, genus or, in exceptional cases, species level.

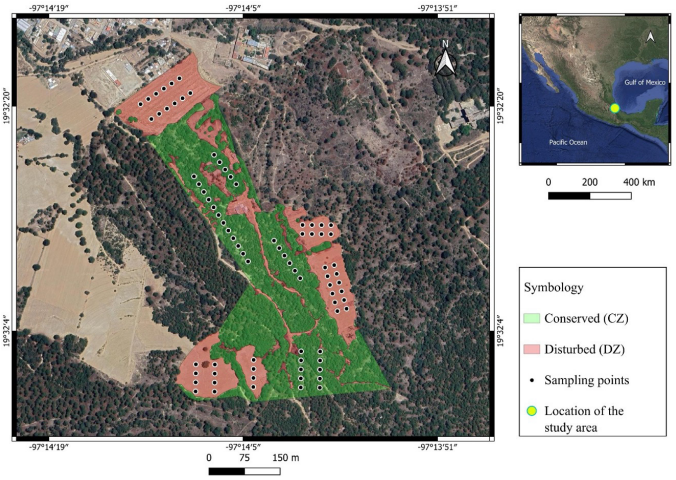

Figure 1. Study area and sampling points of mammal scats in conserved (CZ) and disturbed (DZ) zones within a modified landscape in Veracruz, Mexico.

Data analysis

We calculated fecal volume, weight, and three parameters for each food category: the relative frequency of occurrence (FO%), the relative volume (V%), and the importance value (IV%, Table 1). We used Mann-Whitney non-parametric tests to compare total scat frequency and weight between zones (CZ and DZ) and between seasons (rainy and dry). Additionally, we evaluated differences between food categories (plant, vertebrates, and invertebrates) through the Kruskal-Wallis rank-sum test; whether significant, we then used a post hoc Dunn's test to obtain its representation of dominance, for which we created ranks using FO% data and relative weight for the recorded taxa (Dinno & Dinno, 2017). All analysis were performed in R software (Dinno & Dinno 2017; R Core Team, 2019).

Using food item frequency data, we estimated the similarity of diet composition between site types and seasons. For this, we used an analysis of similarity based on Jaccard distance, which reflects the proportion of similarity among samples and is a robust method to compare composition (Wolda, 1981). To test significance, we used a one-way analysis of similarity (ANOSIM) with 9,999 permutations, which measures the association between samples by the R value, where higher R values represent greater differences in diet composition between samples (Clarke, 1993). To visualize diet composition groups by site and season, we constructed an ordination in two-dimensional space using non-metric multidimensional scaling (NMDS). Diet composition analysis was performed in R software (R Core Team, 2019).

Results

Our field observations showed that three medium-sized species were frequent in the study zone: ringtail (*Bassariscus astutus* Lichtenstein, 1830), opossum (*Didelphis marsupialis* Linnaeus, 1758), and gray fox (*Urocyon cinereoargenteus* Schreber, 1775). We collected a total of 95 scats, mostly from *B. astutus* (74.7%), followed by *D. marsupialis* (15.7%), and *U. cinereoargenteus* (15.7%) (Table 2). Among species, *B. astutus* ($n_{Conserved}$ = 54; $n_{Disturbed}$ = 17) and *U. cinereoargenteus* ($n_{Conserved}$ = 7; $n_{Disturbed}$ = 2) scats were more frequently found in conserved zones, while *D. marsupialis* ($n_{Conserved}$ = 7; $n_{Disturbed}$ = 8) scat frequency was similar between zones.

In general, more feces were collected in disturbed (n = 69) than in conserved (n = 26) zones (Fig. 2), but this difference was not significant (W = 280.5, p = 0.8771 Fig. 2). During the sampling period, the number of scats collected tended to increase ($n_{mín}$ = 6; n_{max} =14), with peaks in June and December (Fig. 3), but no difference was found between seasons (n_{rainy} = 47; n_{dry} = 48, W = 376, p = 0.24, Fig, 2). Mean scat weight was 9.21 ± 1.42 mg (mean ± SE) for *B. astutus*, 5.99 ± 2.36 mg for *D. marsupialis*, and 26.82 ± 9.87 mg for *U. cinereoargenteus*. Feces weight was similar between zones (W = 957.5, p = 0.39) but not between seasons (W = 1338, p = 0.047, Fig. 2).

We recorded seeds and stems of plants, hair of vertebrates, and limbs of invertebrates. Of all analyzed scats, 56 (58.9%) contained exclusively plant items, five contained exclusively invertebrates (5.2%), and one contained exclusively vertebrate items (1%). Only three scats, one of each species, contained simultaneously plant, vertebrate and invertebrate items. The food item type more frequently found was plant material (FO = 92.6 %), followed by invertebrates (FO = 34.7 %), and vertebrates (FO = 10.5 %; Table 2). The intake frequency was similar between conserved and disturbed zones with no statistical differences (plant: FOCZ = 88.8%, FODZ = 92.7%; W= 243, p = 0.82; invertebrates: FOCZ = 40.7%, FODZ = 31.8%; W= 310.5, p = 0.18; vertebrates: FOCZ = 18.5%, FODZ = 7.24%; W= 294, p = 0.12); however, we recorded higher invertebrate intake in the rainy season (plant: FO_{Rainy} = 93.6%, FO_{Dry} = 91.6%; W= 378, p = 0.73; invertebrates: FO_{Rainy} = 46.8%, FO_{Dry} = 22.9%; W= 583, p = 0.01; vertebrates: FO_{Rainy} = 14.8%, FO_{Dry} = 6.25%; W= 410, p = 0.67).

The frequency of food items was different among species. *Bassariscus astutus* and *D. marsupialis* showed the same item frequency, which was higher for plants, followed by vertebrate, and invertebrate items, while *U. cinereoargenteus* showed an equal frequency of plant and vertebrate items, followed by invertebrates (Table 2). At the community level, the relative volume (V%) and importance value (IV%) were higher for plants (Table 2). Dunn's test revealed that plant consumption was dominant at the community level (Table 3; Fig. 4). Additionally, for *U. cinereoargenteus*, Dunn's test revealed no dominance between invertebrate and plant food items, nor between invertebrate and vertebrate categories (Table 3, Fig. 4).

Diet species composition varied between site type and season (Table 4). Plant species composition recorded in mammal diets included *Prunus capulli*, *Juniperus deppeana*, *Miconia argentea*, and *Relbunium hypocarpyum* (Table 4). Two genera of vertebrates were identified: *Sylvilagus* and *Peromyscus*. Five invertebrate taxa were identified from scats: Anthicidae, Scarabaeidae, Coreidae, Litobiomorpha, and Scolopendromorpha (Table 4). Based on the frequency of

each species, NMDS and ANOSIM analysis showed that species composition was similar between zones (R = 0.006; p = 0.485; Fig. 5A) but different between seasons (R = 0.501; p = 0.0001; Fig. 5B).

Table 1. Description of the formulas used to estimate parameters for each food item category recorded in scats of medium-sized mammals in a modified landscape in Veracruz, Mexico.

Parameters	Formulas
Frequency of occurrence (FO%)	$FO_{item\%} = \frac{Number\ of\ scats\ in\ which\ the\ food\ item\ occurred}{Total\ number\ of\ scats}$
Relative volume (V%)	$V_{item\%} = \frac{\sum Percent\ volume\ of\ each\ food\ item\ per\ scat}{Number\ of\ scats\ in\ which\ the\ food\ item\ occurred}$
Importance value (IV%)	$IV_{item\%} = \frac{FO\%\ of\ item\ x\ V\%\ of\ item}{100}$

Table 2. Food group frequency (FO%), relative volume (V%) and importance value (IV%) of each food item category recorded in scats of medium-sized mammals in a modified landscape in Veracruz, Mexico.

Food item	Community			Species								
	Total (n = 95)			*Bassariscus astutus* (n = 71)			*Urocyon cinereoargenteus* (n = 9)			*Didelphis marsupialis* (n = 15)		
	FO%	V%	IV%	FO%	V%	IV%	FO%	V%	IV%	FO%	V%	IV%
Plant	92.6	91	84.2	95.7	95	90.9	77.7	82	63.7	86.6	81	70.2
Invertebrate	34.7	7	0.7	26.7	4	1	77.7	13	10.1	46.6	18	8.4
Vertebrate	10.5	2	0.6	5.63	1	0.05	22.2	5	1.1	26.6	1	1.2

Table 3. Mean rank test for dominance (Dunn's test) performed to evaluate diet at the overall community level and for each medium-sized mammal species in a modified landscape in Veracruz, Mexico.

	Community		Species					
			B. astutus		*D. marsupialis*		*U. cinereoargenteus*	
Food categories	**I**	**V**	**I**	**V**	**I**	**V**	**I**	**V**
P	Z = - 5 .236 **p < 0**	Z = 8.589 **p < 0**	Z = -9.962 **p < 0**	Z = 11.563 **p< 0**	Z = -3.365 **p = 0.001**	Z = 4.113 **p < 0**	Z = -1.586 p = 0.212	Z = 3.033 **p = 0.007**
V	Z = 3.353 **p = 0.0008**		Z = 1.601 p = 0.109		Z = 0.747 p = 0.454		Z = 1.447 p = 0.147	

Note. Food item categories: P = plants, V = vertebrates, I = invertebrates. Bold values indicate statistical significance (p ≤ 0.05).

Table 4. Diet composition recorded in scats of medium-sized mammal species in a modified landscape in Veracruz, Mexico.

Food item category	Mammal species					
	B. astutus		*D. marsupialis*		*U. cinereoargenteus*	
	Season					
Plant[a]	**Dry**	**Rainy**	**Dry**	**Rainy**	**Dry**	**Rainy**
Juniperus deppeana	X	X	X		X	
Miconia argentea		X		X		X
Prunus capulli		X		X		X
Relbunium hypocarpyum		X				
Vertebrate[b]						
Sylvilagus				X		X
Peromyscus	X	X	X	X	X	X
Invertebrate[c]						
Anthicidae	X		X			
Scarabaeidae	X	X		X	X	X
Coreidae	X		X		X	
Litobiomorpha		X				X
Scolopendromorpha		X				X

Note. The "X" indicates the presence of each food item category for each species. Levels of taxonomic identification: a species, b genus and c family and order.

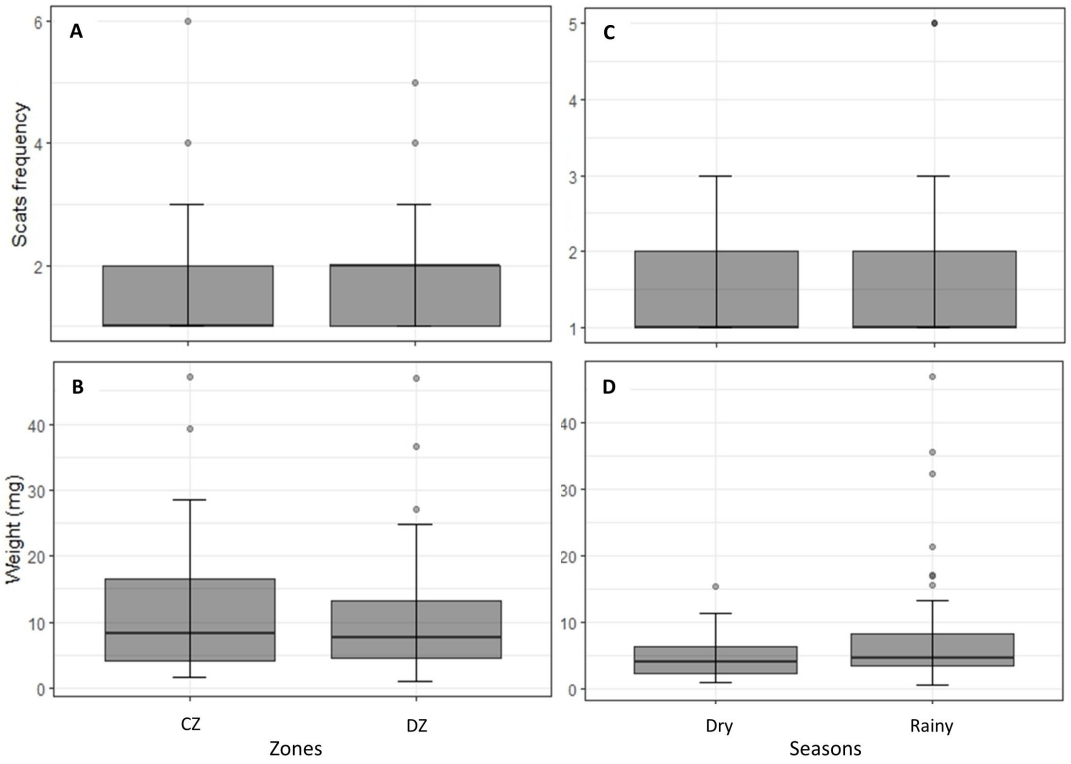

Figure 2. Scat frequency and weight of medium-sized mammals in conserved (CZ) and disturbed (DZ) zones (A and B) and between dry and rainy seasons (C and D) in a modified landscape in Veracruz, Mexico.

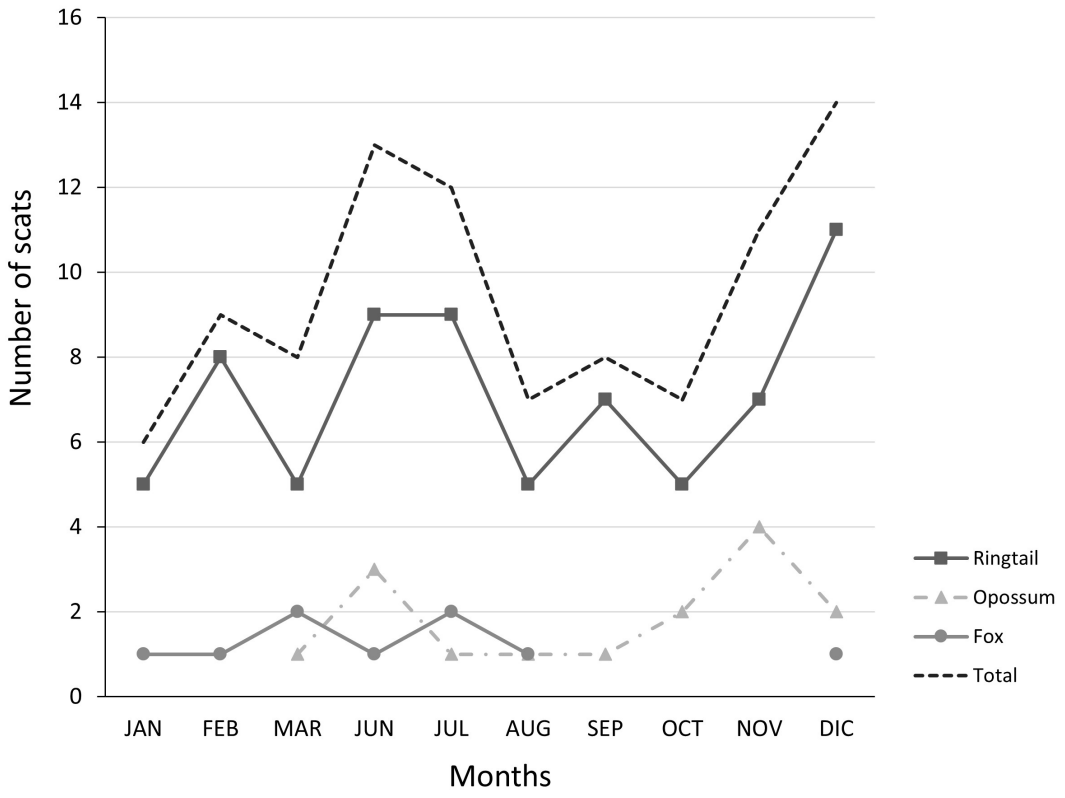

Figure 3. Number of scats recorded for the mammal community, and for each mammal species in a modified landscape in Veracruz, Mexico.

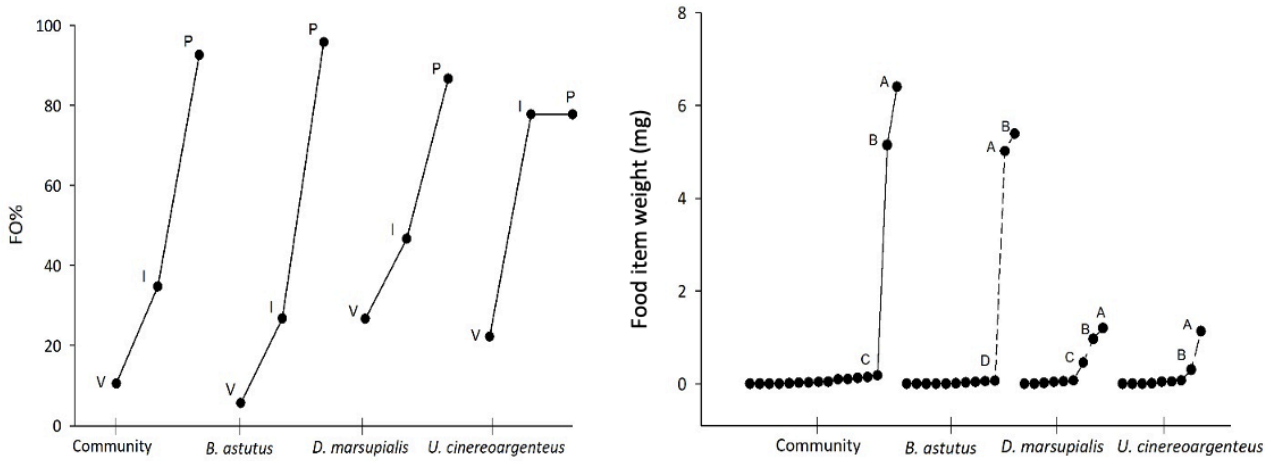

Figure 4. Dominance rank of food categories (P = plant, V = vertebrate, and I = invertebrate), based on frequency of occurrence (FO%, left panel) and weight (right panel), for identified taxa consumed by the mammal community and by each mammal species in a modified landscape in Veracruz, Mexico. Identified taxa: A) *Prunus capulli*, B) *Juniperus deppeana*, C) *Miconia argentea*, and D) *Scarabaeidae*.

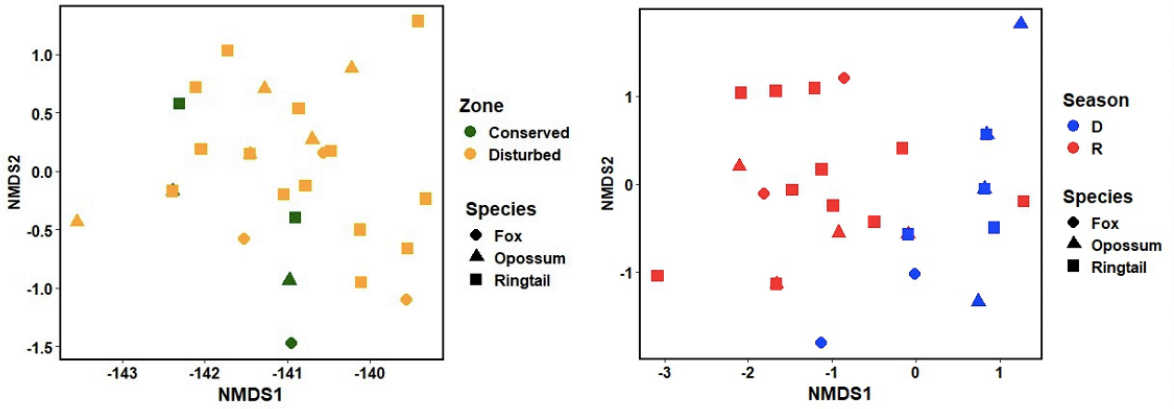

Figure 5. Dietary species composition of medium-sized mammals, based on presence-absence data, between conserved (CZ) and disturbed (DZ) zones (left panel), and between seasons (right panel), in a modified landscape in Veracruz, Mexico.

Discussion

Our prediction was partially supported, since mammal dietary composition varied between seasons, but not between zones, with similar composition among mammal species, dominated by plant items. Regarding the mammal community structure and interactions, the similarity of dietary content between *B. astutus* and *D. marsupialis* suggests that these species act as direct competitors, in both zone types, occupying the same trophic level. In contrast, *U. cinereoargenteus* appears to occupy a different trophic level, with no apparent strong influence on the other two species. Knowledge of mammal dietary composition provides a useful framework for understanding and predicting mammal community dynamics and species vulnerability to environmental changes, particularly in areas under anthropic pressure (Gorczynski et al., 2021).

The three medium-sized mammal species recorded in this study, *B. astutus*, *D. marsupialis* and *U. cinereoargenteus*, are frequently found in communities of conserved and disturbed areas and are well known to be omnivorous species (Cortés-Marcial & Briones-Salas, 2014; Guerrero et al., 2002; Wong-Smer et al., 2022). Regarding dietary composition, no differences in food item intake frequency were detected between conserved and disturbed zones; however, higher invertebrate intake was recorded during the rainy season. These results should be interpreted with caution, because finding feces in a given zone does not necessarily mean that an animal uses exclusively that type of zone. Therefore, species home range, distribution, and biological traits related to habitat use must be considered to fully understand the ecological implications of our results. In this sense, similarities in food intake between zones could be initially explained by species requirements, since omnivorous diets are mostly based on plant intake (Reuter et al., 2023). Second, omnivorous mammals are generally less affected by landscape modifications, especially in areas with crops or forest remnants, such as our study area (Prugh et al., 2008; Magioli et al., 2019). Also, the higher intake of invertebrates during the rainy season could be explained by seasonal increase in the availability of this type of prey, which reflects a reconfiguration of dietary patterns between seasons (Zúñiga et al., 2020). Finally, the similarities in food intake between zones and the increased intake of invertebrates during the rainy season may also suggest a simplification in the local food

supply, reducing the variability of other food resources, such as animal prey, across both spatial and temporal scale in the landscape (Zúñiga et al., 2020).

We observed that *B. astutus* and *D. marsupialis* have a diet dominated by plants, followed by invertebrates. *Bassariscus astutus* is an abundant species in mammal communities, frequently recorded as a common or dominant species because individual occurrence is associated with food provision, and not with habitat type (Cortés-Gutiérrez et al., 2019; Hagar, 2007). *Didelphis marsupialis* is a species with a generalist diet and habitat preference, and a recent study has revealed this species as a predator of *Philander opossum*, another possum species (Rojas-Sánchez et al., 2023), which further increases the knowledge on *D. marsupialis* diet. Based on our dietary data, *B. astutus* and *D. marsupialis* can be classified within the same omnivore guild, primarily characterized as herbivore-insectivore (Pineda-Muñoz & Alroy, 2014). In terms of community dynamics, occupying the same trophic level could indicate some degree of niche overlap and potential direct interspecific competition between species (Silva-Pereira et al., 2011).

Urocyon cinereoargenteus, on the other hand, showed a diet dominated by both plants and invertebrates, indicating that this species is more generalist, behaving as an opportunistic mesopredator, as observed in other studies (Méndez-Ramirez & Serna-Lagunes, 2024). We believe that the dietary pattern of *U. cinereoargenteus* is influenced by the study area, because differences in dietary composition have been reported between populations inhabiting urban areas – where diet are dominated by invertebrates, vertebrates and plant (Morales et al., 2008) – and forest landscapes, where diet are dominated by plant, invertebrates and vertebrates (Guerrero et al., 2002; Wong-Smer et al., 2022). In general, an opportunistic diet corresponds to a broader and unspecialized diet, and thus, to a wider niche than other guilds (Pineda-Munoz & Alroy, 2014). For *U. cinereoargenteus*, this premise is likely valid, since this species has higher mobility, which gives individuals the ability to exploit various habitats and resources (Bateman & Fleming, 2012; Pasch & Kattán, 2019).

Diet composition was similar between zones and different between seasons, as shown by NMDS results. The first result could be explained by the similar use of space by the omnivorous species, especially by *B. astutus* and *D. marsupialis*, which are both terrestrial and arboreal, and also by their access to a wide variety of plant and animal species, or a combination of both, from which omnivorous mammals can obtain energy and nutrition (Balestrieri et al., 2019). This could be an ecological strategy to reduce negative effects of diet overlap, especially in altered environments (Zúñiga et al., 2020). On the other hand, changes in diet composition between seasons are expected, since in seasonal forests plants and invertebrate species show phenological patterns of occurrence and abundance, with higher availability during the rainy season (Picazo & García-Collazo, 2019).

The dietary patterns recorded in this study suggested a reduction in resources variety and availability at the landscape level, which could modify local food chain structure or functional diversity as a result of habitat simplification. In turn, the reduction in functional diversity may drive animal communities toward trait homogenization, an ecological phenomenon that is relatively rare for mammal communities and has been reported in studies focused on dietary patterns (Gámez-Virués et al., 2015; Weideman et al., 2020).

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