Research Square

Preprints are preliminary reports that have not undergone peer review.
They should not be considered conclusive, used to inform clinical practice,
or referenced by the media as validated information.

Landscape structure outweighs climate in shaping dietary composition of the maned wolf (Chrysocyon brachyurus, Illiger, 1815) across fragmented Atlantic Forest landscapes

Jean P. Silva[123]

jean.paulo@estudante.ufjf.br

Universidade Federal de Juiz de Fora

Lisandra Mendes Louzada-Camilo[13]

Universidade Federal de Juiz de Fora

M. Fernandes[13]

Universidade Federal de Juiz de Fora

Lênim Faber-Lopes[1]

Universidade Federal de Juiz de Fora

Pedro M. Villa[13]

Universidade Federal de Juiz de Fora

Research Article

Keywords: Diet composition, Landscape structure, Climate variability, Trophic plasticity, Habitat heterogeneity

Posted Date: June 22nd, 2026

DOI: https://doi.org/10.21203/rs.3.rs-9995593/v1

License: This work is licensed under a Creative Commons Attribution 4.0 International License.
Read Full License

Additional Declarations: No competing interests reported.

Abstract

Human-driven environmental changes, particularly land-use change and climate variability, are major drivers of biodiversity patterns. This study investigates how landscape structure and climatic variability influence the diet composition of the maned wolf, a generalist omnivore, in human-modified Atlantic Forest landscapes. We hypothesized that landscape metrics would have a stronger influence than climatic variables (H1), responses would vary among food items (H2), and environmental predictors would explain limited dietary variation (H3). Our results corroborate these hypotheses, showing that landscape structure is the primary driver of dietary composition, with species like *Solanum lycocarpum* and *Maclura tinctoria* positively correlated with edge density and landscape shape index. *Syagrus romanzoffiana* showed sensitivity to both climatic and landscape variables, while *Syzygium cumini* correlated positively with the number of patches. The high dietary richness and evenness in anthropized landscapes highlight the maned wolf's trophic plasticity, enabling its persistence in fragmented mosaics. These findings have significant implications for conservation, emphasizing the importance of landscape connectivity and matrix quality for maintaining diverse food sources and the species' role in seed dispersal.

1. Introduction

Human-driven environmental change is reshaping ecological systems worldwide, with land-use change and climate variability acting as major drivers of biodiversity patterns in the Anthropocene (Foley et al., 2005; IPBES, 2019). Habitat loss and fragmentation alter the spatial structure of ecosystems, influencing species distributions, community composition, and ecological processes across multiple scales (Fahrig, 2003; Haddad et al., 2015). In particular, habitat fragmentation can modify the size, number, shape, and spatial distribution of habitat patches, directly affecting the availability of essential resources required for species persistence (Rybicki et al., 2020). Although these drivers are often investigated separately, their combined effects can generate complex and context-dependent responses that remain difficult to predict (Oliver and Morecroft, 2014). Understanding how organisms respond to interacting with environmental gradients is therefore a central challenge in ecology, particularly in human-modified landscapes where ecological processes are increasingly decoupled from historical baselines (Ellis et al., 2010).

Climatic conditions play a fundamental role in structuring trophic interactions by influencing both the spatial distribution and temporal availability of resources (Parmesan, 2006; Visser and Both, 2005). In mammals, temperature and precipitation regimes affect primary productivity, fruiting phenology, and prey abundance, thereby indirectly shaping dietary composition and foraging strategies (Post et al., 2009; Bogdziewicz et al., 2020). For generalist species, dietary responses to climate are expected to be flexible and context-dependent, reflecting shifts in resource availability across environmental gradients (Sih et al., 2011). In the maned wolf, a well-known opportunistic omnivore, diet composition varies spatially and temporally according to resource availability, with fruits and small vertebrates contributing differently across environmental contexts (Dietz, 1984; Jácomo et al., 2004). Despite this, the role of

climate in shaping dietary composition remains less explored than its effects on species occurrence or abundance (Parmesan, 2006; Oliver and Morecroft, 2014).

Landscape structure is another key determinant of trophic dynamics, particularly in fragmented ecosystems where spatial configuration influences resource distribution and accessibility (Fahrig, 2003; Tscharntke et al., 2012). Metrics such as edge density (ED), number of patches (NP), and landscape shape index (LSI) can alter both the availability of food resources and the movement of consumers across the landscape. (Fahrig, 2013; Fletcher et al., 2018). In mammal communities, fragmentation can modify ecological functions, including predation and seed dispersal, by altering species behavior and interaction networks (Galetti et al., 2013; Dirzo et al., 2014). Moreover, landscape configuration can influence encounter rates between consumers and resources, restructuring trophic interactions even when species persist (Tscharntke et al., 2012; Haddad et al., 2015). Importantly, responses to landscape structure are often species-specific and scale-dependent, reflecting differences in mobility, habitat specialization, and ecological flexibility (Fahrig, 2013; Fletcher et al., 2018).

Despite the substantial body of research linking landscape structure and climate to species occurrence and distribution, much less is known about how these drivers shape trophic structure and resource use, particularly in generalist mammals inhabiting human-modified landscapes (Fahrig, 2003; Tscharntke et al., 2012). Most landscape ecological studies have focused on patterns of species richness, occupancy, or abundance, often overlooking how environmental gradients influence the composition of ecological interactions, such as diet (Haddad et al., 2015; Dirzo et al., 2014). However, shifts in resource use can precede or occur independently of changes in species occurrence, with important consequences for ecosystem functioning and resilience (Estes et al., 2011; Galetti et al., 2013). In fragmented landscapes, changes in habitat configuration and connectivity can alter resource availability and accessibility, potentially restructuring feeding behavior even when species persist (Tscharntke et al., 2012; Fletcher et al., 2018). At the same time, climatic conditions can modulate resource phenology and distribution, further influencing dietary patterns at broad spatial scales (Parmesan, 2006; Post et al., 2009).

In this study, we investigate how landscape structure and climatic variability influence the composition of diet in the maned wolf a highly generalist and opportunistic carnivore in Atlantic Forest. Specifically, we ask: (i) do landscape configuration and climatic gradients influence the occurrence of different food items in the diet? and (ii) are these effects consistent across resource types or context-dependent? We hypothesize that (H1) landscape metrics related to habitat configuration will exert stronger effects on diet composition than climatic variables due to their direct influence on resource accessibility; (H2) responses will vary among food items, reflecting differences in ecological traits and resource dynamics and (H3) environmental predictors will explain only a limited proportion of dietary variation, consistent with the trophic plasticity expected in generalist species. By focusing on dietary composition rather than species occurrence, this study provides a novel perspective on how environmental gradients shape ecological interactions in human-modified landscapes.

2. Materials and methods

2.1 Study Area

The study was conducted in three distinct landscapes within the Atlantic Forest domain of southeastern Brazil, specifically in the Itabapoana River basin (Fig. 1). These areas (Guaçuí, Celina, and Bom Jardim) represent a gradient of anthropogenic disturbance and land-use configuration, which were characterized using data from MapBiomas Collection 8 (Fig. 1). The study was conducted in three landscapes located within the Atlantic Forest biome domain of southeastern Brazil, in the Itabapoana River basin and adjacent regions along the border between the states of Espírito Santo and Rio de Janeiro (Fig. 1). These areas represent distinct contexts of land-use composition, landscape structure, and anthropogenic disturbance within the inland Atlantic Forest. All sampling sites occur within remnants of Seasonal Semideciduous Atlantic Forest, one of the dominant forest formations in this portion of the biome. The regional climate is classified as tropical mesothermic sub-humid, with mean annual temperatures around 20°C and annual precipitation close to 1,200 mm.

The three sampling landscapes Guaçuí, Celina, and Bom Jardim are located in the middle and lower portions of the Itabapoana River basin (Fig. 1). Site selection was based on previous field surveys and independent records of maned wolf occurrence. The distances among landscapes range from 20 to 48 km, ensuring spatial independence. Land-use and land-cover data were obtained from MapBiomas Collection 8 (2024) and used to characterize landscape composition. The regional matrix is dominated by pasturelands, small-scale agriculture, secondary vegetation, and remnant forest patches, forming a typical forest–agriculture mosaic of the interior Atlantic Forest. The three landscapes represent a gradient of anthropogenic disturbance, despite sharing the same original vegetation type. Guaçuí includes relatively larger and more continuous forest patches associated with the Rosal Hydroelectric Reservoir. Celina represents an intermediate condition, with a mosaic of pasturelands and fragmented forest remnants. Bom Jardim is the most anthropogenically modified landscape, dominated by agricultural lands and highly fragmented forest patches.

2.2 Data Collection

Sampling effort was standardized across the three study landscapes (Fig. 1) through two complementary strategies: intensive field stays (24-h campaigns) and standard field surveys (9-h campaigns). The 24-h campaigns consisted of multi-day camping periods within the study areas, a strategy designed to maximize the probability of locating fresh fecal samples by allowing access to sampling sites during early morning and late afternoon periods that coincide with the maned wolf's peak activity (Dietz, 1984; Jácomo et al., 2004). While the 24-h campaigns involved continuous presence in the field, active search effort was conducted during standardized windows of daylight to ensure comparability across all sampling units. Surveys were conducted over a total of 66 sampling days, representing an overall field residence time of 654 hours and resulting in the collection of 77 fecal samples. Similar sampling intensity among landscapes ensured consistent comparisons of diet composition (Massara et al., 2012; Silva et al., 2025).

In the laboratory, fecal samples were washed using a 1-mm mesh sieve and manually sorted with forceps to recover undigested food remains, including seeds, hair, feathers, bones, and other materials (Fig. 2). Dietary items were identified to the lowest possible taxonomic level using reference collections and specialized literature (Jácomo et al., 2004), and all records were subsequently grouped into predefined dietary categories. To confirm the identity of samples with uncertain attribution to the maned wolf, particularly those collected after rainfall when morphological characteristics were less distinct, guard hairs present in the feces were examined (Miranda et al. 2009). Whenever possible, dietary items were identified to the species level.

Although individual identification was not performed, field observations and independent records consistently indicated the presence of multiple maned wolf individuals within each landscape. Maned wolves are known to use communal latrines for scent marking and communication (Kleiman, 1972; Dietz, 1984), suggesting that multiple individuals, potentially from overlapping home ranges, may deposit feces at the same sites. Furthermore, the spatial separation among the study areas, coupled with previous genetic evidence demonstrating restricted gene flow and population structuring in human-modified landscapes (Rodriguez-Castro and Lemos, 2022), strongly suggests that the sampled feces likely originated from individuals belonging to distinct local populations rather than repeated sampling of a single animal. Additionally, road-killed individuals were recorded in or near all three study areas, further supporting the occurrence of multiple individuals across the landscape gradient. Sampling points were also spatially distributed within each landscape, reducing the likelihood of strong pseudoreplication associated with the repeated use of the same latrine sites (Massara et al., 2012).

2.3 Principal Component Analysis: landscape and climate variables

To explore multivariate relationships among climatic conditions, landscape structure, and diet composition, we performed a Principal Component Analysis (PCA) using standardized environmental predictors and food-occurrence variables (Fig. 2). PCA was applied to reduce dimensionality and identify the main ecological gradients structuring variation among sampling landscapes previously defined according to the study areas. Prior to analysis, all variables were centered and scaled to account for differences in units of measurement and variance.

Environmental predictors included climatic variables obtained from the WorldClim database, namely annual mean temperature (AMT), mean diurnal range (MDR), temperature annual range (TAR), precipitation seasonality (PS), and precipitation and temperature variables describing seasonal regimes. Landscape predictors were derived from MapBiomas Collection 8 (2024) and included six metrics describing habitat structure and spatial configuration extracted from the standardized landscape units (~ 40 km²; Fig. 1): percentage of landscape (PLAND), aggregation index (AI), number of patches (NP), edge density (ED), landscape shape index (LSI), and Euclidean nearest neighbor distance (ENN)(fig S1). These metrics represent complementary dimensions of habitat amount, aggregation, fragmentation, edge availability, spatial complexity, and patch isolation/connectivity. Dietary variables included the

occurrence of the main food items identified in fecal samples, represented as presence–absence data for each sampling unit. By integrating dietary, climatic, and landscape variables within the same ordination framework, the PCA allowed visualization of associations among food resources and environmental gradients (Fig. 2).

The first principal components were retained to summarize the dominant gradients of variation in the dataset. In the ordination biplot (Fig. 2), variable vectors represent the magnitude and direction of contribution of each predictor to the principal components, with longer vectors indicating stronger contributions to explained variance. The angle between vectors was used to infer correlations among variables, where acute angles indicate positive associations, obtuse angles indicate negative associations, and orthogonal vectors suggest weak or no correlation. Sampling groups were projected into multivariate space to assess patterns of similarity and separation among landscapes, whereas the vertices of the ordination represent ecological extremes defined by combinations of environmental conditions and dietary composition. The proportion of variance explained by each principal component was used to evaluate the relative importance of the ordination axes.

2.4 Data Processing

Data processing involved the organization, validation, and spatial standardization of all sampling records. Geographic coordinates of sampling points were verified and processed in QGIS, ensuring consistency in spatial reference systems across datasets. When necessary, coordinates originally recorded in geographic format (WGS84) were reprojected to the SIRGAS 2000 / UTM Zone 24S coordinate system to allow accurate spatial analyses, including distance calculations and buffer generation. Sampling points were used to define landscape units based on a standardized spatial extent (~ 40 km²) (Fig. 1), within which environmental variables were extracted. Land-use and land-cover data were obtained from MapBiomas Collection 8 (2024), from which a raster layer was generated in QGIS at a spatial resolution of 30 × 30 m, maintaining compatibility with the original dataset resolution. The raster was subsequently imported into R for landscape analyses, and metrics were calculated using the landscapemetrics package (Hesselbarth et al., 2019) to characterize habitat structure across sampling areas.Given the relatively limited spatial extent of the study landscapes (~ 40 km² per sampling unit), land-use classes were not reclassified prior to analysis. This approach was adopted to preserve the original landscape heterogeneity and thematic detail provided by the MapBiomas dataset, while maintaining sufficient accuracy for landscape metric estimation at the spatial scale considered.

Climatic variables were obtained from the WorldClim database and processed in R using the terra package (Hijmans, 2024). The analytical database used in R integrated dietary composition data of the maned wolf, considering food items recorded per latrine, with geospatial variables extracted from field-collected geographic coordinates associated with each sampled latrine. This integration enabled the assessment of relationships between dietary composition and local environmental conditions. To evaluate relationships among environmental predictors and assess potential multicollinearity, Pearson correlation matrix analyses were performed using the complete set of climatic and landscape variables. Correlation patterns were examined to identify overlapping environmental gradients and support

interpretation of model outcomes. Because models were fitted independently for each predictor, highly correlated variables were not excluded a priori. Instead, predictor influence was evaluated based on recurrence and explanatory performance across independent quasibinomial models.

2.5 Statistical Analysis

To evaluate how landscape structure and climatic conditions influence variation in diet composition, we modeled the occurrence of each food item as a function of environmental predictors using generalized linear models (GLMs) with a quasibinomial error distribution (McCullagh and Nelder, 1989; Crawley, 2013). Each food item (e.g., *Syagrus romanzoffiana*, insects, small mammals) was treated as a binary response variable (presence/absence in each fecal sample), allowing estimation of how occurrence probabilities varied along environmental gradients. Modeling diet components as binary responses is commonly applied in scat-based dietary studies, where individual occurrences are used to infer patterns of resource use (Klare et al., 2011; Williams et al., 2012).

We adopted a quasibinomial family to account for potential overdispersion, which is common in ecological presence–absence datasets due to unmeasured heterogeneity, spatial clustering of samples, and individual-level variation in resource use (Crawley, 2013; Zuur et al., 2009). This approach relaxes the assumption of fixed variance and provides more robust standard errors and inference under overdispersed conditions (McCullagh and Nelder, 1989). To control for systematic differences among sampling landscapes, the categorical variable *Group* (Guaçuí, Celina, and Bom Jardim) was included as a fixed effect in all models.

Landscape and climatic predictors were modeled separately rather than combined within a single model to reduce risks of multicollinearity, overparameterization, and model instability associated with correlated environmental gradients and limited sample sizes (Dormann et al., 2013; Zuur et al., 2009). Independent models also facilitated clearer interpretation of the relationship between individual predictors and food occurrence, an approach commonly adopted in exploratory ecological analyses aimed at identifying general ecological patterns rather than building predictive multivariate models (Burnham and Anderson, 2002). For each model, we extracted coefficient estimates, standard errors, p-values, and pseudo-R^2 values to evaluate explanatory performance. Given the exploratory nature of the study and the high variability typical of dietary datasets derived from fecal analyses, interpretation focused primarily on effect direction and consistency across food items rather than strict statistical significance thresholds (Burnham and Anderson, 2002; Johnson, 1999).

To summarize overall predictor performance, we quantified predictor importance based on their recurrence and ranking among the best-supported models for each food item. Higher scores indicate predictors that consistently explained variation in dietary occurrence across multiple food items, providing an integrated assessment of environmental influences on diet composition.

Generalized linear mixed models of diet-environment relationships

To evaluate how landscape structure and climatic conditions influence variation in diet composition, we modeled the occurrence of each food item as a function of environmental predictors using generalized linear models (GLMs) with a quasibinomial error distribution (McCullagh and Nelder, 1989; Crawley, 2013). Each food item (e.g., *Syagrus romanzoffiana*, insects, small mammals) was treated as a binary response variable (presence/absence in each fecal sample), allowing us to estimate how the probability of occurrence varied along gradients of landscape configuration and climate. Predictor variables included six landscape metrics (PLAND, AI, NP, ED, LSI, and ENN) and a suite of bioclimatic variables describing temperature and precipitation regimes(tab S2). Modeling diet components as binary responses is a common approach in studies based on scat analysis, where individual occurrences are used to infer patterns of resource use (Klare et al., 2011; Williams et al., 2012).

We used a quasibinomial family instead of a standard binomial model to account for potential overdispersion in the data, which is frequently observed in ecological presence–absence datasets (Crawley, 2013; Zuur et al., 2009). Overdispersion arises when the variance exceeds that expected under a binomial distribution, often due to unmeasured ecological heterogeneity, spatial clustering of samples (e.g., latrine sites), or individual-level variation in diet. Such conditions are particularly common in studies of carnivore feeding ecology, where samples may be non-independent and reflect heterogeneous resource use (Klare et al., 2011). The quasibinomial approach relaxes the assumption of fixed variance and provides more robust standard errors and inference under these conditions (McCullagh and Nelder, 1989; Zuur et al., 2009). To account for systematic differences among landscapes, the categorical variable *Group* (Guaçuí, Celina, and Bom Jardim) was included as a fixed effect in all models. This allowed us to control baseline differences in diet composition across the disturbance gradient while testing the independent effects of continuous environmental predictors.

Models were fitted independently for each food item and predictor combination to avoid issues of multicollinearity among landscape and climatic variables, which often represent overlapping ecological gradients (Dormann et al., 2013). For each model, we extracted coefficient estimates, standard errors, and p-values for the focal predictor. Because the primary goal was to identify general patterns rather than to build predictive models, we interpreted results cautiously, focusing on effect direction and relative consistency across food items rather than relying solely on statistical significance. This approach is particularly appropriate in ecological datasets with limited sample sizes and high variability, where strict significance thresholds may fail to capture biologically meaningful trends (Burnham and Anderson, 2002; Johnson, 1999).

Models were fitted separately for each predictor rather than combining landscape and climatic variables within the same model. This approach was adopted to avoid issues of multicollinearity and overparameterization, which are common when using multiple environmental predictors that often capture overlapping ecological gradients (Dormann et al., 2013). Many climatic and landscape variables are inherently correlated, either directly or indirectly, through shared underlying environmental processes (Fahrig, 2013). Additionally, given the relatively limited sample size and the high variability typical of diet data derived from scat analyses, including multiple predictors and interaction terms in a single model

would increase the risk of model instability, convergence issues, and unreliable parameter estimates (Zuur et al., 2009). This is especially relevant for binomial and quasibinomial models, where sparse data and low variation in the response can lead to quasi-complete separation and inflated coefficients. By fitting models independently, we aimed to isolate the effect of each predictor on the occurrence of individual food items, providing a clearer interpretation of how specific environmental gradients are associated with dietary composition. This approach is widely used in exploratory ecological analyses where the goal is to identify general patterns rather than to build predictive multivariate models (Burnham and Anderson, 2002).

To provide an integrated assessment of model outcomes, we quantified the relative importance of predictors based on their recurrence and ranking among the top quasibinomial models for each food item. The importance score reflects a weighted frequency of selection, in which predictors appearing more often among the best-supported models and at higher ranks receive greater values. Thus, higher scores indicate predictors that consistently explain variation in dietary occurrence across multiple food items, rather than stronger effects within a single model, following approaches that emphasize model support across candidate sets (Burnham and Anderson, 2002). The corresponding table of top models summarizes, for each food item, the predictor with the highest explanatory power based on pseudo-R^2 and statistical support, providing a complementary view of predictor performance at the individual-response level. This approach is particularly relevant in ecological datasets with high variability, where statistical significance alone may not capture biologically meaningful patterns (Johnson, 1999), and where predictors may represent correlated environmental gradients (Dormann et al., 2013).

3. Results

Landscape and climate gradient

The first two PCA axes explained 72.5% of the total variation in dietary composition and environmental variables, with PCA1 accounting for 59.0% and PCA2 for 13.5% of the variance (Fig. 5). The ordination revealed a clear separation among the three landscapes, indicating substantial differences in environmental conditions and dietary composition. The first axis (PCA1) represented a gradient primarily associated with landscape configuration, climatic conditions, and dietary composition. Positive scores on PCA1 were strongly associated with TAR ($R = 0.994$, $p = 0.001$), NP ($R = 0.994$, $p = 0.001$), LSI ($R = 0.990$, $p = 0.001$), ED ($R = 0.990$, $p = 0.001$), ENN ($R = 0.977$, $p = 0.002$), AI ($R = 0.757$, $p = 0.001$), annual precipitation (AP; $R = 0.926$, $p = 0.001$), precipitation of the driest quarter (PDriQ; $R = 0.742$, $p = 0.001$), small mammals ($R = 0.791$, $p = 0.001$), and *Syagrus romanzoffiana* ($R = 0.651$, $p = 0.001$). In contrast, negative scores were associated with minimum temperature of the coldest month (MinTCM; $R = -0.951$, $p = 0.001$), mean temperature of the wettest quarter (MeTWetQ; $R = -0.919$, $p = 0.001$), maximum temperature of the warmest month (Mac_tm; $R = -0.960$, $p = 0.001$), *Syzygium cumini* ($R = -0.961$, $p = 0.001$), *Genipa americana* ($R = -0.999$, $p = 0.001$), and insects ($R = -0.937$, $p = 0.001$), indicating an opposing gradient between landscape structure and these climatic and dietary variables.

The second axis (PCA2) captured variation mainly related to climatic seasonality and resource composition. Positive values were associated with precipitation seasonality (PS; R = 0.864, p = 0.001), temperature seasonality (TEMP_S; R = 0.898, p = 0.001), percentage of landscape (PLAND; R = 0.884, p = 0.001), *Syagrus romanzoffiana* (R = 0.759, p = 0.001), and small mammals (R = 0.611, p = 0.001). Negative values were associated primarily with *Cordia magnoliifolia* (R = − 0.969, p = 0.001), *Solanum lycocarpum* (R = − 0.940, p = 0.001), precipitation of the driest quarter (PDriQ; R = − 0.670, p = 0.001), and annual precipitation (AP; R = − 0.376, p = 0.001), indicating differences in resource composition under contrasting climatic regimes.

The ordination clearly separated Bom Jardim, Celina Alegre, and Guaçuí, indicating landscape-specific dietary configurations. Bom Jardim was associated with higher occurrences of *Genipa americana*, *Syzygium cumini*, insects, and other fruit resources. Guaçuí was associated with landscapes characterized by higher values of AI, NP, ENN, ED, LSI, TAR, and climatic seasonality variables, as well as greater occurrences of *Syagrus romanzoffiana* and small mammals. Celina occupied an intermediate position in the ordination space but showed a stronger association with *Solanum lycocarpum* and precipitation-related variables. Together, these results indicate that dietary composition varies among landscapes according to both climatic conditions and landscape structure, supporting the existence of landscape-specific trophic assemblages.

Dietary diversity across landscapes

Rarefaction and extrapolation analyses revealed consistent differences in dietary diversity among the three study landscapes (Fig. 3). Sampling coverage approached 1.0 in all areas, indicating high sampling completeness and allowing robust comparisons among landscapes. Across all Hill numbers, Bom Jardim consistently exhibited the highest diversity values, Celina showed intermediate values, and Guaçuí presented the lowest diversity. This pattern remained stable across the entire coverage gradient and was observed for species richness (q = 0), Shannon diversity (q = 1), and Simpson diversity (q = 2). At maximum sample coverage, estimated richness (q = 0) reached approximately nine food items in Bom Jardim, compared with five in Celina and three in Guaçuí. Similar differences were observed for q = 1 and q = 2, with effective diversity values remaining highest in Bom Jardim and lowest in Guaçuí. Confidence intervals showed limited overlap among landscapes at high sample coverage, indicating consistent differences in dietary diversity among study areas. The same ranking among landscapes (Bom Jardim > Celina > Guaçuí) was maintained across all diversity orders evaluated (Fig. 3).

The rarefaction curves standardized by sampling coverage showed consistent differences in food diversity between the areas (Fig. 4). When comparing the areas under equivalent levels of sampling completeness (≈ 0.80–1.00), Bom Jardim presented the highest diversity values for all Hill numbers evaluated (q = 0, 1 and 2), followed by Celina, while Guaçuí presented the lowest values.

For species richness (q = 0), diversity in Bom Jardim increased from approximately 6 to 9 species as coverage approached 1.0. Celina presented intermediate values (≈ 4–5 species), while Guaçuí maintained the lowest values (≈ 2–3 species). When considering metrics that incorporate relative

abundance (q = 1 and q = 2), the same pattern was maintained. The difference between the areas became more evident at q = 2, indicating a greater dominance of a few food items in Guaçuí and, to a lesser extent, in Celina, while Bom Jardim showed greater evenness in diet composition. The limited overlap of the confidence intervals suggests that the differences observed between the areas are consistent and do not result solely from variation in sampling effort, reinforcing that the pattern detected reflects real differences in diet structure among the environments evaluated.

At maximum sample coverage, estimated richness (q = 0) reached approximately nine food items in Bom Jardim, compared with five in Celina and three in Guaçuí. Similar differences were observed for q = 1 and q = 2, with effective diversity values remaining highest in Bom Jardim and lowest in Guaçuí. Confidence intervals showed limited overlap among landscapes at high sample coverage, indicating consistent differences in dietary diversity among study areas. The same ranking among landscapes (Bom Jardim > Celina > Guaçuí) was maintained across all diversity orders evaluated (Fig. 3).

Diet-Climate relationships

Climatic predictors generally showed weaker effects compared to landscape metrics, but some important relationships were identified. The occurrence of *Solanum lycocarpum* was strongly and positively associated with mean annual temperature (AMT: estimate = 0.047 ± 0.009, $p < 0.001$), suggesting a preference for warmer conditions. In contrast, *Syagrus romanzoffiana* showed consistent negative relationships with climatic variables, including mean annual temperature (AMT: estimate = − 0.014 ± 0.006, $p = 0.0251$), mean diurnal range (MDR: estimate = − 5.729 ± 2.761, $p = 0.0477$), and temperature annual range (TAR: estimate = − 3.612 ± 1.321, $p = 0.0109$), indicating reduced occurrence under higher temperature variability. A marginal positive effect of temperature annual range was observed for *Syzgium cumini* (TAR: estimate = 4.131 ± 2.158, $p = 0.0662$), suggesting a potential but weak influence of climatic variability on this food item. For most other food categories (e.g., insects, birds, small mammals, and *Genipa americana*), climatic predictors were not statistically significant, and effect sizes were generally small or highly variable.

Diet-landscape relationships

Overall, environmental predictors showed heterogeneous and generally weak effects on diet composition, with most models presenting low explanatory power and non-significant relationships. However, consistent patterns emerged for specific food items, particularly in relation to landscape structure. The relative importance analysis revealed that both climatic and landscape predictors were recurrently selected among top models, although their effects varied markedly across food items(fig S2). Strong and consistent effects of landscape structure were observed for some food items. The occurrence of *Solanum lycocarpum* was positively associated with multiple landscape metrics, including edge density (ed: estimate = 0.039 ± 0.016, $p = 0.0226$), landscape shape index (lsi: estimate = 0.690 ± 0.285, $p = 0.0224$), and number of patches (np: estimate = 0.192 ± 0.075, $p = 0.0163$)(Tab S1). These results indicate that this key dietary resource increases in more structurally complex and fragmented landscapes.

Similarly, *Maclura tinctoria* showed positive responses to landscape configuration, particularly for edge density (ed: estimate = 0.014 ± 0.006, p = 0.0332), landscape shape index (lsi: estimate = 0.258 ± 0.114, p = 0.0328), and number of patches (np: estimate = 0.046 ± 0.014, p = 0.0026). A marginal positive effect was also detected for temperature annual range (TAR: estimate = 2.548 ± 1.492, p = 0.099), suggesting a combined influence of landscape structure and climatic variability. In contrast, *Syagrus romanzoffiana* exhibited consistent negative relationships with landscape metrics, including edge density (ed: estimate = − 0.021 ± 0.006, p = 0.0019), landscape shape index (lsi: estimate = − 0.368 ± 0.107, p = 0.0019), and number of patches (np: estimate = − 0.048 ± 0.024, p = 0.0516). These results suggest that this resource is more associated with less fragmented landscapes. For fishes, a negative effect of the number of patches was detected (np: estimate = − 0.438 ± 0.175, p = 0.0188), indicating reduced occurrence in more fragmented environments.

4. Discussion

The results collectively indicate that landscape structure plays a more prominent role than climatic variability in shaping the dietary composition of the maned wolf across fragmented Atlantic Forest landscapes. Although most individual predictor-resource relationships exhibited modest explanatory power, multiple analytical approaches converged on the same ecological pattern. Rarefaction analyses revealed clear differences in dietary diversity among landscapes, the PCA demonstrated a marked reorganization of dietary resources along environmental gradients, and the quasibinomial models identified landscape configuration metrics, such as particularly edge density, landscape shape index, and number of patches, as the predictors most consistently associated with variation in food-item occurrence (Fig. 2). Together, these findings support our first hypothesis (H1) and reinforce the view that, in fragmented ecosystems, the spatial arrangement of habitat remnants can be as important as habitat amount in determining resource accessibility and consumer responses (Fahrig, 2013; Tscharntke et al., 2012; Haddad et al., 2015).

The results also support our second hypothesis (H2), as environmental effects varied substantially among food items (Figs. 5 and 6). While some resources, such as *Solanum lycocarpum* and *Maclura tinctoria*, were positively associated with increasing landscape complexity and fragmentation, others, including *Syagrus romanzoffiana* and fishes, showed opposite responses. Several food categories exhibited little or no detectable association with environmental predictors. This heterogeneity suggests that environmental gradients influence dietary composition through resource-specific ecological processes, reflecting differences in habitat requirements, phenology, spatial distribution, and availability among food resources (Sih et al., 2011; Dennis et al., 2013). Rather than producing a uniform dietary response, landscape and climatic variation appear to reorganize the relative contribution of individual resources to the diet. At the same time, the maintenance of relatively high dietary diversity across all study areas, particularly in the more anthropogenic landscapes, highlights the remarkable trophic flexibility of the maned wolf and supports our third hypothesis (H3). Rather than exhibiting strong dependence on a restricted set of resources, the species appears capable of adjusting resource use according to local environmental conditions, reinforcing its ecological role as a highly adaptable

generalist within heterogeneous forest-agriculture mosaics (Dietz, 1984; Jácomo et al., 2004; Sih et al., 2011).

Landscape structure as the primary driver of dietary composition

One of the most consistent findings of this study was that landscape structure exerted stronger influences on dietary composition than climatic variables. Although most individual predictor–food item relationships explained only a modest proportion of variation, landscape metrics appeared more frequently among the best-supported models and accounted for most statistically significant effects (Figs. 5 and 6). Edge density, landscape shape complexity, and patch subdivision were repeatedly associated with variation in the occurrence of key dietary resources, indicating that the spatial configuration of habitats can influence resource use even when overall habitat availability remains relatively constant (Fahrig, 2003; Fischer and Lindenmayer, 2007; Haddad et al., 2015).

The contrasting responses observed among food items suggest that fragmentation does not simply reduce resource availability but rather restructures the distribution of resources across the landscape. For example, *Solanum lycocarpum* and *Maclura tinctoria* increased in occurrence in landscapes characterized by higher edge density and greater patch subdivision, whereas *Syagrus romanzoffiana* showed the opposite trend. Such patterns are consistent with the well-documented effects of fragmentation on plant communities, where disturbance-tolerant and edge-associated species often become more abundant while forest-dependent species decline (Laurance et al., 2002; Tabarelli et al., 2010). Consequently, changes in the wolf's diet likely reflect shifts in resource availability generated by landscape modification rather than direct avoidance or selection of particular habitat configurations by the species itself (Fahrig, 2017).

Landscape configuration may also influence the accessibility of resources. Maned wolves regularly move across large home ranges and exploit multiple habitat types during foraging movements, frequently crossing forest edges, agricultural areas, and open vegetation formations (Dietz, 1984; Lyra-Jorge et al., 2010). Under such conditions, metrics such as patch number and landscape complexity may determine how easily individuals encounter different food resources across the landscape mosaic. Therefore, the effects detected here are likely to emerge from a combination of changes in resource abundance and changes in resource accessibility, highlighting the importance of considering landscape structure when evaluating trophic responses in highly mobile mammals (Turner, 2005; Fahrig, 2013).

Dietary plasticity and resource complementation in anthropogenic landscapes

Despite the importance of landscape structure for some food resources, the predominance of non-significant relationships across models suggests that dietary composition is only partially explained by individual environmental predictors (tab S2). This result is notable because it indicates that environmental variation does not impose a uniform constraint on resource use. Instead, the maned wolf appears capable of maintaining a relatively broad dietary niche across contrasting environmental conditions, reinforcing its reputation as one of the most trophically flexible carnivores of South America

(Dietz, 1984; Jácomo et al., 2004; Rodrigues et al., 2007). The ecological success of the species in modified landscapes has often been attributed to its omnivorous habits and its ability to exploit resources from multiple trophic levels simultaneously. Throughout its distribution, maned wolves consume fruits, insects, small vertebrates, birds, and anthropogenic resources, often shifting the relative importance of these food categories according to local availability (Motta-Junior et al., 1996; Bueno and Motta-Junior, 2004; Ferreira et al., 2020). Such flexibility may reduce dependence on any single food resource and buffer populations against environmental fluctuations that affect individual prey or fruit species (Dennis et al., 2013; Ripple et al., 2014).

This interpretation is supported by the coexistence of positive and negative responses among different dietary items observed in the present study. Whereas some resources became more frequent in fragmented landscapes, others declined, suggesting a process of resource substitution rather than a generalized reduction in food availability. This phenomenon is consistent with the concept of resource complementation, in which organisms combine resources originating from different habitat types to satisfy their ecological requirements (Dunning et al., 1992; Gehring and Swihart, 2003). Under this framework, landscape modification alters the composition of consumed resources without necessarily reducing the overall capacity of individuals to obtain food. Such compensatory mechanisms may help explain the persistence of maned wolves in human-modified landscapes throughout much of their contemporary range (Coelho et al., 2008; Lyra-Jorge et al., 2010).

Landscape-specific reorganization of food resources

The rarefaction and multivariate analyses revealed that environmental gradients were associated with marked differences in dietary composition among landscapes. Importantly, these differences were detected even after standardization by sample coverage, indicating that the observed patterns were not artifacts of unequal sampling effort. Across all Hill numbers, Bom Jardim consistently exhibited the highest dietary diversity, followed by Celina, whereas Guaçuí showed the lowest values (Fig. 4). Because Hill numbers integrate richness, abundance, and dominance in a unified framework, these results indicate that landscapes differed not only in the number of food resources consumed but also in the relative distribution of those resources within the diet (Chao et al., 2014).

The stronger separation among areas at higher orders of diversity ($q = 1$ and $q = 2$) suggests that differences in resource dominance may be particularly important. In Guaçuí, lower effective diversity indicates that a smaller subset of food resources accounted for a larger proportion of dietary records, whereas diets in Bom Jardim were characterized by greater evenness. Such patterns are consistent with ecological theory predicting that environmental simplification often reduces the diversity of available resources and promotes greater reliance on a limited number of dominant species (Olden et al., 2004; Newbold et al., 2020).

The PCA further demonstrated that landscapes differed not only in diversity but also in the identity of consumed resources. Food items associated with fruit consumption, insects, and landscape metrics occupied distinct positions along the principal environmental gradients, indicating that each landscape

supported a unique dietary configuration (Fig. 2). This result supports the idea that environmental change affects trophic structure primarily through species turnover and resource replacement rather than through a simple loss of resources. Similar reorganization of trophic interactions has been reported in fragmented ecosystems worldwide, where species persistence is often accompanied by substantial modifications in ecological networks and resource-use patterns (Tylianakis et al., 2008; Valiente-Banuet et al., 2015).

Conservation implications in fragmented Atlantic Forest landscapes

The results presented here highlight the importance of moving beyond traditional occurrence-based approaches when evaluating the ecological consequences of habitat modification. Although maned wolves were present across all landscapes studied, clear differences emerged in dietary diversity, resource composition, and environmental associations. These findings demonstrate that species persistence alone may conceal substantial ecological changes occurring within populations, particularly those related to trophic interactions and resource use (McGill et al., 2015; Newbold et al., 2020). The stronger influence of landscape structure compared with climate suggests that local habitat configuration remains a major determinant of trophic opportunities at the spatial scale examined in this study. As fragmentation progresses, changes in patch arrangement, edge availability, and habitat complexity may modify the accessibility and distribution of food resources even when populations remain present. Consequently, conservation planning focused exclusively on habitat amount may underestimate the ecological importance of landscape configuration for maintaining functional processes such as foraging and seed dispersal (Fahrig, 2013; Haddad et al., 2015).

At the same time, the ability of maned wolves to exploit distinct resource assemblages across landscapes reinforces the role of trophic plasticity as a key mechanism promoting persistence in human-modified ecosystems. However, long-term dependence on a narrower subset of resources, particularly in more simplified landscapes, could increase vulnerability to future environmental disturbances affecting those key resources. Maintaining heterogeneous landscapes that preserve a diversity of native food resources and habitat types may therefore be essential for sustaining both the ecological resilience of maned wolf populations and the ecosystem functions they perform as omnivorous consumers and seed dispersers within Atlantic Forest landscapes (Dietz, 1984; Bueno et al., 2002; Frick et al., 2022).

5. Conclusion

This study demonstrates that landscape structure is the primary driver of the maned wolf's diet composition in human-modified Atlantic Forest landscapes, outweighing the influence of climatic variability. Our findings confirm that metrics of habitat configuration, such as edge density and landscape shape index, directly shape the availability and consumption of key food items like *Solanum lycocarpum* and *Maclura tinctoria*. The high dietary richness and evenness observed in anthropized areas underscore the species' remarkable trophic plasticity and its ability to adapt to fragmented mosaics.

The results highlight the dual role of the maned wolf as both a generalist survivor and a critical mobile link for seed dispersal in degraded ecosystems. The positive association between certain food items and fragmentation metrics suggests that the species effectively exploits anthropogenic edges, which may facilitate its persistence in forest–agriculture matrices. However, the sensitivity of resources like *Syagrus romanzoffiana* to both climate and landscape indicates that future environmental changes could impose complex constraints on resource availability. From a conservation standpoint, our study emphasizes the importance of maintaining landscape connectivity and managing matrix quality to support diverse food sources. Preserving the maned wolf's ecological functions requires strategies that go beyond protecting isolated forest remnants, focusing instead on the restoration of landscape elements that enhance resource accessibility. Future research should further investigate the long-term impacts of climate-landscape interactions on the species' foraging behavior to ensure its continued role in maintaining the resilience of tropical ecosystems.

Declarations

Declarations (Ethics, Conflict of Interest)

All procedures involving field sampling and data collection were conducted under permits issued by Sistema de Autorização e Informação em Biodiversidade (SISBIO permit Nos. 97632-1 and 97632-2), in accordance with Brazilian environmental regulations.

Funding

This study was supported by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) and IDEA WILD GRANT through financial support and field equipment grants.

Author Contribution

Jean Paulo Silva: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Writing – original draft, Writing – review & editing.Lisandra Mendes Louzada Camilo: Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing – review & editing.Marjory Cristina de Magalhães Fernandes: Data curation, Formal analysis, Methodology, Software, Validation, Visualization, Writing – review & editing.Lenim Faber-Lopes: Investigation, Methodology, Project administration, Supervision, Visualization, Writing – review & editing.Pedro Manuel Villa: Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing.

Acknowledgement

We thank all researchers involved in this study for their collaboration and support throughout the project. We are especially grateful to Redi Itabapoana for field assistance and logistical support, and to Probiodiversa Brasil for statistical assistance. We also sincerely thank Juliana Silveira dos Santos and her team at the Instituto Nacional da Mata Atlântica for their guidance and valuable contributions regarding landscape metrics analyses. In addition, we thank Thiago Cardoso and Marjory Magalhães from the Universidade Federal de Juiz de Fora for his support in map production and spatial data organization. Furthermore, we acknowledge Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) and IDEA WILD Grant for financial support and field equipment. We also thank Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA) for providing data, and Companhia Energética de Minas Gerais (CEMIG) for granting access to the study areas. Research permits were issued through Sistema de Autorização e Informação em Biodiversidade (SISBIO). Finally, we are deeply grateful to local landowners and residents, especially Mr. Adilson and the Florestan Fernandes community, for their hospitality, trust, and continued support during field activities.

Data availability

The data that support the findings of this study are available from the corresponding author upon reasonable request.

References

1. Bogdziewicz M, Kelly D, Thomas PA, Lageard JG, Hacket-Pain A (2020) Climate warming disrupts mast seeding and its fitness benefits in European beech. Nat Plants 6(2):88–94. https://doi.org/10.1038/s41477-020-0592-8
2. Bogdziewicz M, Kelly D, Thomas PA, Lageard JG, Hacket-Pain A (2020) Climate warming disrupts mast seeding and its fitness benefits in European beech. Nat Plants 6(2):88–94. https://doi.org/10.1038/s41477-020-0592-8
3. Crawley MJ (2013) Multivariate analysis. The R book, 2nd edn. Wiley, 809 – 13, Hoboken
4. Crouzeilles R et al (2025) Restoration of landscape elements to enhance resource accessibility for Neotropical carnivores. Biological Conservation. (In press)
5. de Almeida Jácomo AT, Silveira L, Diniz-Filho JAF (2004) Niche separation between the maned wolf (*Chrysocyon brachyurus*), the crab-eating fox (*Dusicyon thous*) and the hoary fox (*Dusicyon vetulus*) in central Brazil. J Zool 262(1):99–106. https://doi.org/10.1017/S0952836903004473
6. Dietz JM (1984) Ecology and social organization of the maned wolf. Smithson Contrib Zool 392(392):1–51. https://doi.org/10.5479/si.00810282.392
7. Dirzo R, Young HS, Galetti M, Ceballos G, Isaac NJ, Collen B (2014) Defaunation in the Anthropocene. Science 345(6195):401–406. https://doi.org/10.1126/science.1251817
8. Dirzo R, Young HS, Galetti M, Ceballos G, Isaac NJ, Collen B (2014) Defaunation in the Anthropocene. Science 345(6195):401–406. https://doi.org/10.1126/science.1251817

9. Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, Lautenbach S (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36(1):27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x
10. Ellis EC, Goldewijk K, Siebert K, Lightman S, D., Ramankutty N (2010) Anthropogenic transformation of the biomes, 1700 to 2000. Glob Ecol Biogeogr 19(5):589–606. https://doi.org/10.1111/j.1466-8238.2010.00540.x
11. Estes JA, Terborgh J, Brashares JS, Power ME, Berger J, Bond WJ, Wardle DA (2011) Trophic downgrading of planet Earth. Science 333(6040):301–306. https://doi.org/10.1126/science.1205106
12. Estes JA et al (2011) Trophic downgrading of planet Earth. Science 333(6040):301–306. https://doi.org/10.1126/science.1205106
13. Evidence on scaling forest restoration from the Atlantic Forest Restoration Pact in Brazil. Available at
14. Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annu Rev Ecol Evol Syst 34(1):487–515. https://doi.org/10.1146/annurev.ecolsys.34.011802.132419
15. Fahrig L (2013) Rethinking patch size and isolation effects: the habitat amount hypothesis. J Biogeogr 40(9):1649–1663. https://doi.org/10.1111/jbi.12130
16. Fahrig L (2013) Rethinking patch size and isolation effects: The habitat amount hypothesis. J Biogeogr 40(9):1649–1663. https://doi.org/10.1111/jbi.12130
17. Fletcher RJ Jr, Didham RK, Banks-Leite C, Barlow J, Ewers RM, Rosindell J, Haddad NM (2018) Is habitat fragmentation good for biodiversity? Biol Conserv 226:9–15. https://doi.org/10.1016/j.biocon.2018.07.022
18. Foley JA, DeFries R, Asner GP, Barford C, Bonan G, Carpenter SR, Snyder PK (2005) Global consequences of land use. Science 309(5734):570–574. https://doi.org/10.1126/science.1111772
19. Galetti M, Guevara R, Côrtes MC, Fadini R, Von Matter S, Leite AB, Jordano P (2013) Functional extinction of birds drives rapid evolutionary changes in seed size. Science 340(6136):1086–1090. https://doi.org/10.1126/science.1233774
20. Galetti M et al (2013) Functional extinction of birds drives rapid evolutionary changes in seed size. Science 340(6136):1086–1090. https://doi.org/10.1126/science.1233774
21. Haddad NM, Brudvig LA, Clobert J, Davies KF, Gonzalez A, Holt RD, Townshend JR (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci Adv 1(2):e1500052. https://doi.org/10.1126/sciadv.1500052
22. Haddad NM et al (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci Adv 1(2):e1500052. https://doi.org/10.1126/sciadv.1500052
23. Hesselbarth MHK, Sciaini M, With KA, Wiegand K, Nowosad J (2019) landscapemetrics: An open-source R tool to calculate landscape metrics. Ecography 42(10):1648–1657. https://doi.org/10.1111/ecog.04617

24. Hijmans RJ, Brown A, Barbosa M (2026) terra: Spatial Data Analysis. R package version 1.9–24. https://github.com/rspatial/terra
25. IPBES (2019) Global assessment report on biodiversity and ecosystem services. Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. https://doi.org/10.5281/zenodo.3831673
26. IUCN (2020) Global Standard for Nature-based Solutions. IUCN
27. IUCN Global Standard for Nature-based Solutions. Available at
28. Johnson DH (1999) The insignificance of statistical significance testing. J Wildl Manag 763–772. https://doi.org/10.2307/3802789
29. Klare U, Kamler JF, Macdonald DW (2011) A comparison and critique of different scat-analysis methods for determining carnivore diet. Mammal Rev 41(4):294–312. https://doi.org/10.1111/j.1365-2907.2011.00186.x
30. Kleiman DG (1972) Social behavior of the maned wolf (*Chrysocyon brachyurus)* and bush dog (*Speothos venaticus*): A study in contrast. J Mammal 53(4):791–806
31. Lê S, Josse J, Husson F (2008) FactoMineR: an R package for multivariate analysis. J Stat Softw 25:1–18. https://doi.org/10.18637/jss.v025.i01
32. Lombardi JA, Motta-Junior JC (1993) Seed dispersal of *Solanum lycocarpum* St. Hil. (Solanaceae) by the maned wolf. Ciência e Cultura 45(2):126–127*Chrysocyon brachyurus* Illiger (Mammalia, Canidae
33. Magioli M, Ferraz KMPMB, Setz EZF, Percequillo AR, Lousada MLC, Gasparotto VP, Martinelli LA (2019) Human-modified landscapes alter mammal resource and habitat use and trophic structure. Proceedings of the National Academy of Sciences, 116(37), 18466–18472. https://doi.org/10.1073/pnas.1904384116
34. Massara RL, Paschoal AMO, Bailey LL, Jr D, P. F., Chiarello AG (2012) Diet and habitat use by maned wolf outside protected areas in tropical landscapes. Trop Conserv Sci 5(3):284–300. https://doi.org/10.1177/194008291200500305
35. Massara RL, Paschoal AMO, Bailey LL, Doherty PF, Chiarello AG (2012) Diet and habitat use by maned wolf outside protected areas in tropical landscapes of Brazil. Trop Conserv Sci 5(3):284–303. https://doi.org/10.1177/194008291200500305
36. McCullagh P, Nelder JA (1989) Generalized linear models, 2nd edn. Chapman & Hall
37. Miranda GHB, Rodrigues FHG, Paglia AP (2009) Guia de identificação de pelos de mamíferos brasileiros. Editora UFMG
38. Motta-Junior JC, Martins K (2002) The frugivorous diet of the maned wolf, *Chrysocyon brachyurus*, in Brazil: Ecology and conservation. In: Levey DJ, Silva WR, Galetti M (eds) Seed dispersal and frugivory: Ecology, evolution and conservation. CABI Publishing, pp 291–303
39. Motta-Junior JC, Talamoni SA, Lombardi JA, Simokomaki K (1996) Diet of the maned wolf, *Chrysocyon brachyurus*, in central Brazil. J Zool 240(2):277–284. https://doi.org/10.1111/j.1469-7998.1996.tb05284.x

40. Motta-Junior JC, Talamoni SA, Lombardi JA, Simokomaki K (1996) Diet of the maned wolf, *Chrysocyon brachyurus*, in central Brazil. J Zool 240(2):277–284. https://doi.org/10.1111/j.1469-7998.1996.tb05284.x
41. Oliver TH, Morecroft MD (2014) Interactions between climate change and land use change on biodiversity: Attribution problems, risks, and opportunities. Wiley Interdisciplinary Reviews: Clim Change 5(3):317–335. https://doi.org/10.1002/wcc.271
42. Parmesan C (2006) Ecological and evolutionary responses to recent climate change. Annu Rev Ecol Evol Syst 37:637–669. https://doi.org/10.1146/annurev.ecolsys.37.091305.110100
43. Porto LMV, Rui AM (2019) Diet and habitat use by two sympatric canids in the Pampas of South America. Neotropical Biology Conserv 14(1):1–12. https://doi.org/10.3897/neotropical.14.e34828
44. Post E, Forchhammer MC, Bret-Harte MS, Callaghan TV, Christensen TR, Elberling B, Schmidt NM (2009) Ecological dynamics across the Arctic associated with recent climate change. Science 325(5946):1355–1358. https://doi.org/10.1126/science.1173113
45. Post E et al (2009) Ecological dynamics across the Arctic associated with recent climate change. Science 325(5946):1355–1358. https://doi.org/10.1126/science.1173113
46. Rodriguez-Castro RC, Lemos FG (2022) Human highly modified landscapes restrict gene flow of the largest neotropical canid, the maned wolf. Biodivers Conserv 31(5):1229–1245. https://doi.org/10.1007/s10531-022-02388-z
47. Rybicki J, Abrego N, Ovaskainen O (2020) Habitat fragmentation and species diversity in competitive communities. Ecol Lett 23(3):506–517. https://doi.org/10.1111/ele.13450
48. Sih A, Ferrari MCO, Harris DJ (2011) Evolution and behavioural responses to human-induced rapid environmental change. Evol Appl 4(2):367–387. https://doi.org/10.1111/j.1752-4571.2010.00166.x
49. Sih A, Ferrari MC, Harris DJ (2011) Evolution and behavioural responses to human-induced rapid environmental change. Evol Appl 4(2):367–387. https://doi.org/10.1111/j.1752-4571.2010.00166.x
50. Silva BC, de Oliveira LA, Clauss, Costa M (2025) C. G. Digestive anatomy and diet of free-ranging maned wolf (*Chrysocyon brachyurus*). Mammalian Biology. Advance online publication. https://doi.org/10.1007/s42991-025-00493-z
51. Silva JP, Villa PM, Camilo LML, Faber-Lopes L, Fernandes MCM (2026) Diet shifts across fragmented Atlantic Forest landscapes reveal trophic plasticity in the maned wolf *(Chrysocyon brachyurus*). Food Webs, e00342
52. Silva KGD, Santos ARD, Silva AGD, Peluzio JBE, Fiedler NC, Zanetti SS (2015) Análise da dinâmica espaço-temporal dos fragmentos florestais da sub-bacia hidrográfica do Rio Alegre. ES Cerne 21:311–318
53. Tscharntke T, Tylianakis ME, Rand TA, Didham RK, Fahrig L, Batáry P, Westphal C (2012) Landscape moderation of biodiversity patterns and processes—Eight hypotheses. Biol Rev 87(3):661–685. https://doi.org/10.1111/j.1469-185X.2011.00216.x
54. Tscharntke T et al (2012) Landscape moderation of biodiversity patterns and processes - eight hypotheses. Biol Rev 87(3):661–685. https://doi.org/10.1111/j.1469-185X.2011.00216.x

55. Visser ME, Both C (2005) Shifts in phenology due to global climate change: The need for a yardstick. Proceedings of the Royal Society B: Biological Sciences, 272(1581), 2561–2569. https://doi.org/10.1098/rspb.2005.3356

56. Walther G-R, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Bairlein F (2002) Ecological responses to recent climate change. Nature 416(6879):389–395. https://doi.org/10.1038/416389a

57. Williams RL, Goodenough AE, Stafford R (2012) Can diet be inferred from faecal analysis? A comparison of techniques using domestic dogs. Ecol Inf 7:30–34. https://doi.org/10.1016/j.ecoinf.2011.08.003

58. Zuur AF, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer

Figures

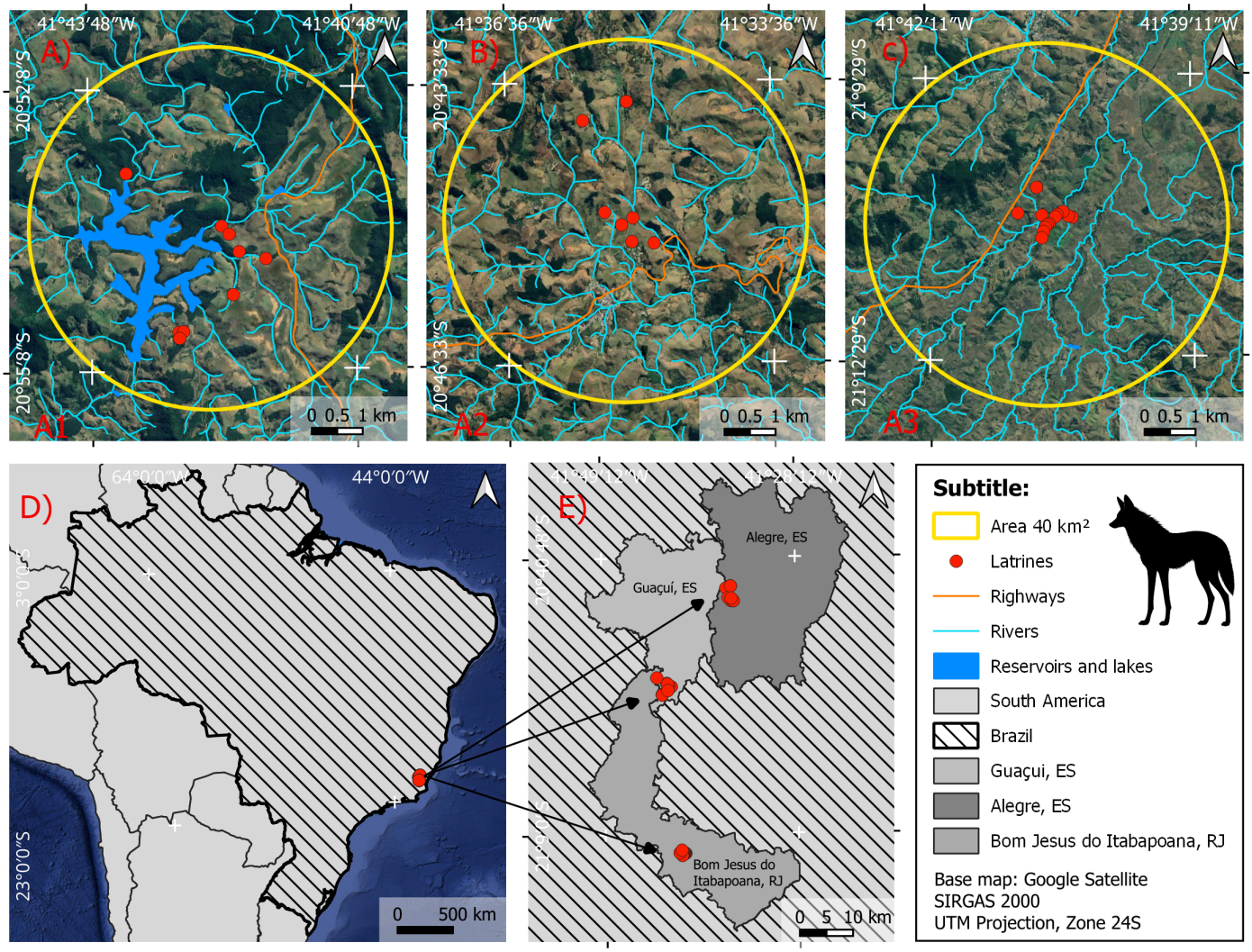


Figure 1

Location of the three study landscapes in the Atlantic Forest domain of southeastern Brazil (D), within the Itabapoana River basin along the border between the states of Espírito Santo and Rio de Janeiro (E). The sampling areas include Guaçuí(A1), Celina(A2), and Bom Jardim(A3).

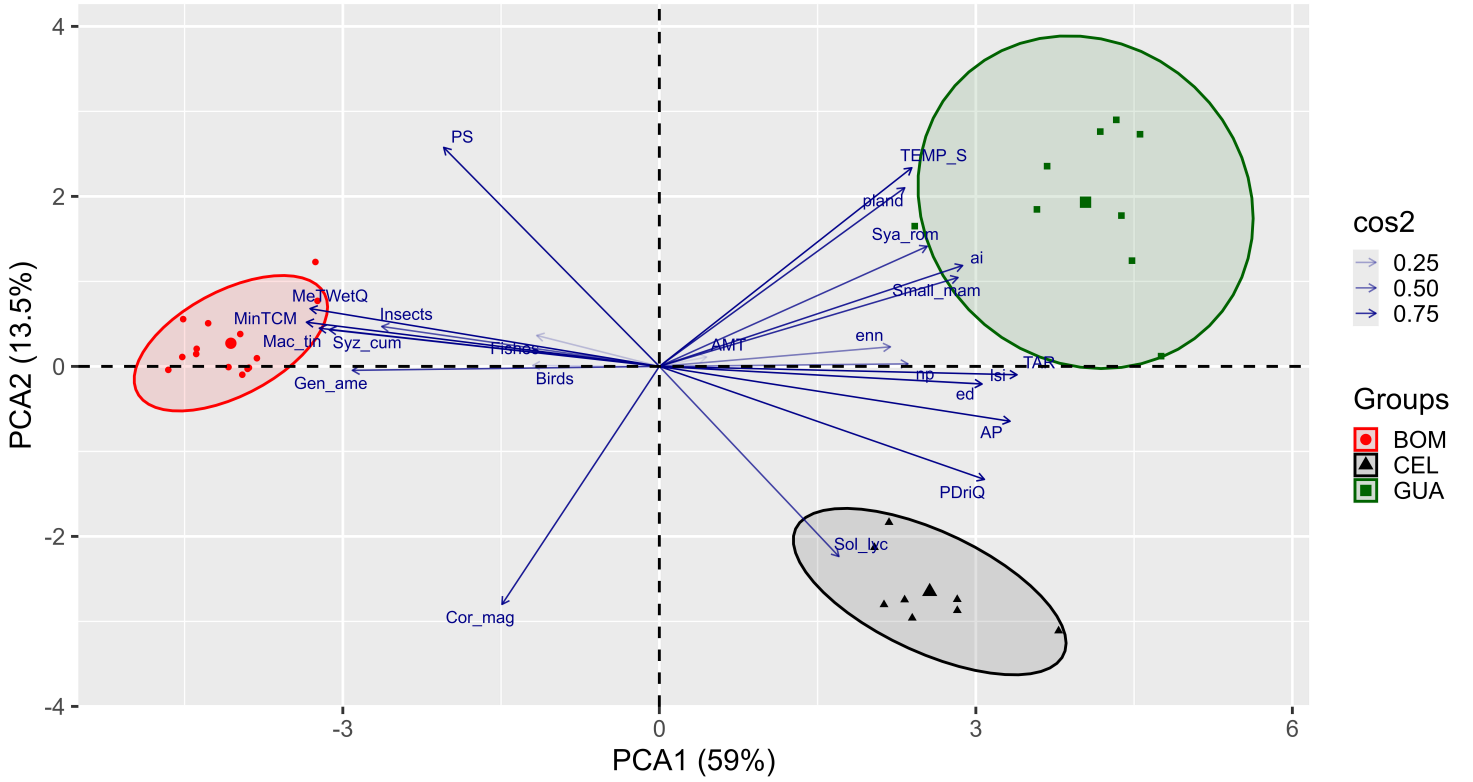


Figure 2

Principal Component Analysis (PCA) ordination of maned wolf latrines based on climatic predictors, landscape metrics, and dietary composition variables. Principal Components 1 and 2 explained 72.5% of the total variation (PCA1 = 59.0%; PCA2 = 13.5%). The intensity of vector color represents the quality of variable representation in the ordination space (cos^2). Climatic variables included AMT (annual mean temperature), TEMP_S (temperature seasonality), MeTWetQ (mean temperature of the wettest quarter), MinTCM (minimum temperature of the coldest month), Mac_tm (maximum temperature of the warmest month), AP (annual precipitation), PDriQ (precipitation of the driest quarter), and PS (precipitation seasonality). Landscape metrics comprised pland (percentage of landscape), np (number of patches), lsi (landscape shape index), ed (edge density), enn (Euclidean nearest-neighbor distance), TAR (total area ratio), and fisi (fragmentation/isolation metric, if applicable). Dietary variables corresponded to food items identified in latrines, including Insects (insects), Birds (birds), Small_mam (small mammals), Sya_rom (*Syagrus romanzoffiana*), Sol_lyc (*Solanum lycocarpum*), Cor_mag (*Cordia magnoliifolia*), Gen_ame (*Genipa americana*), Syz_cum (*Syzygium cumini*).

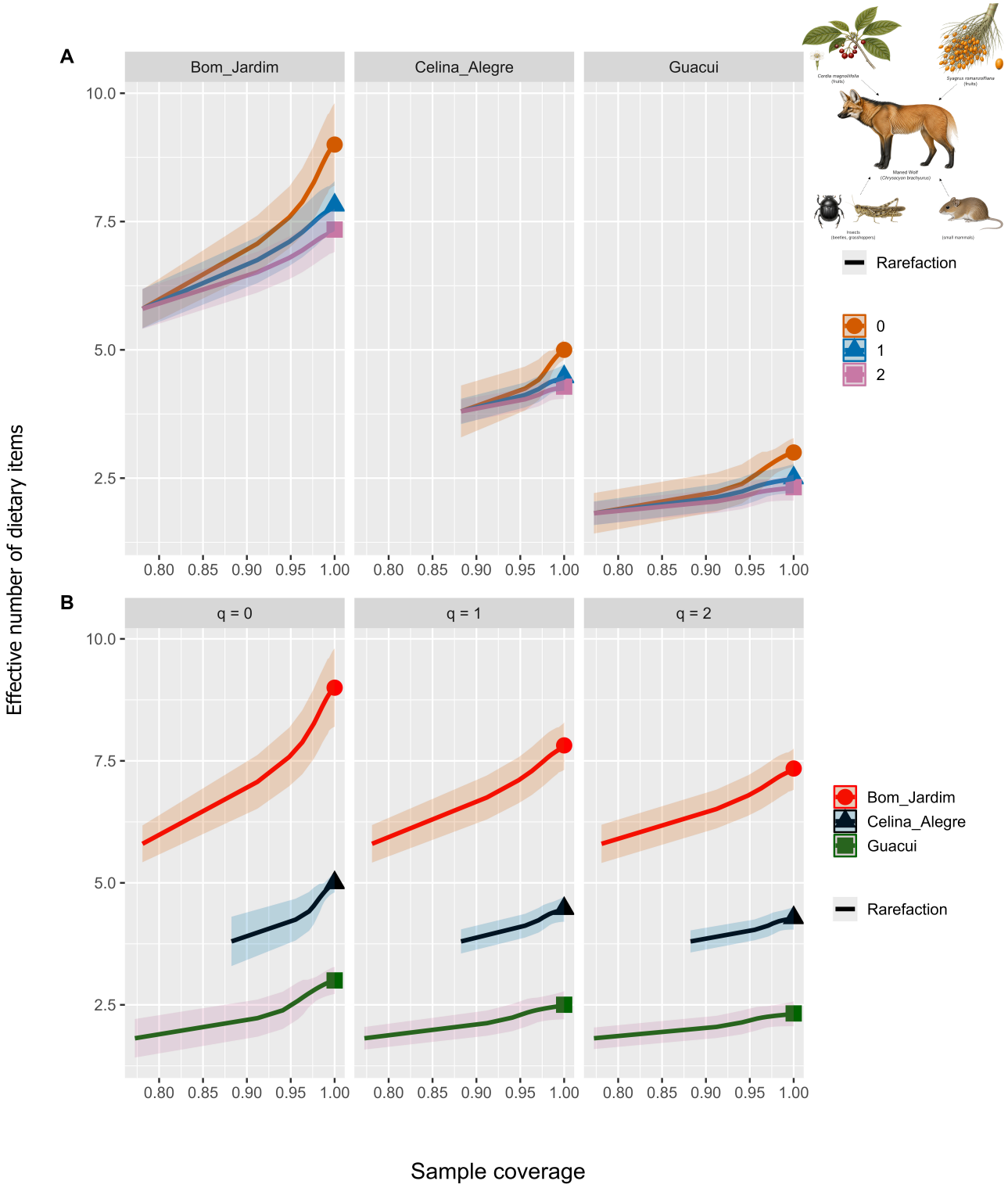


Figure 3

Effective number of dietary items (q = 0, 1 and 2) as a function of sampling coverage in the areas of Bom Jardim, Celina and Guaçui

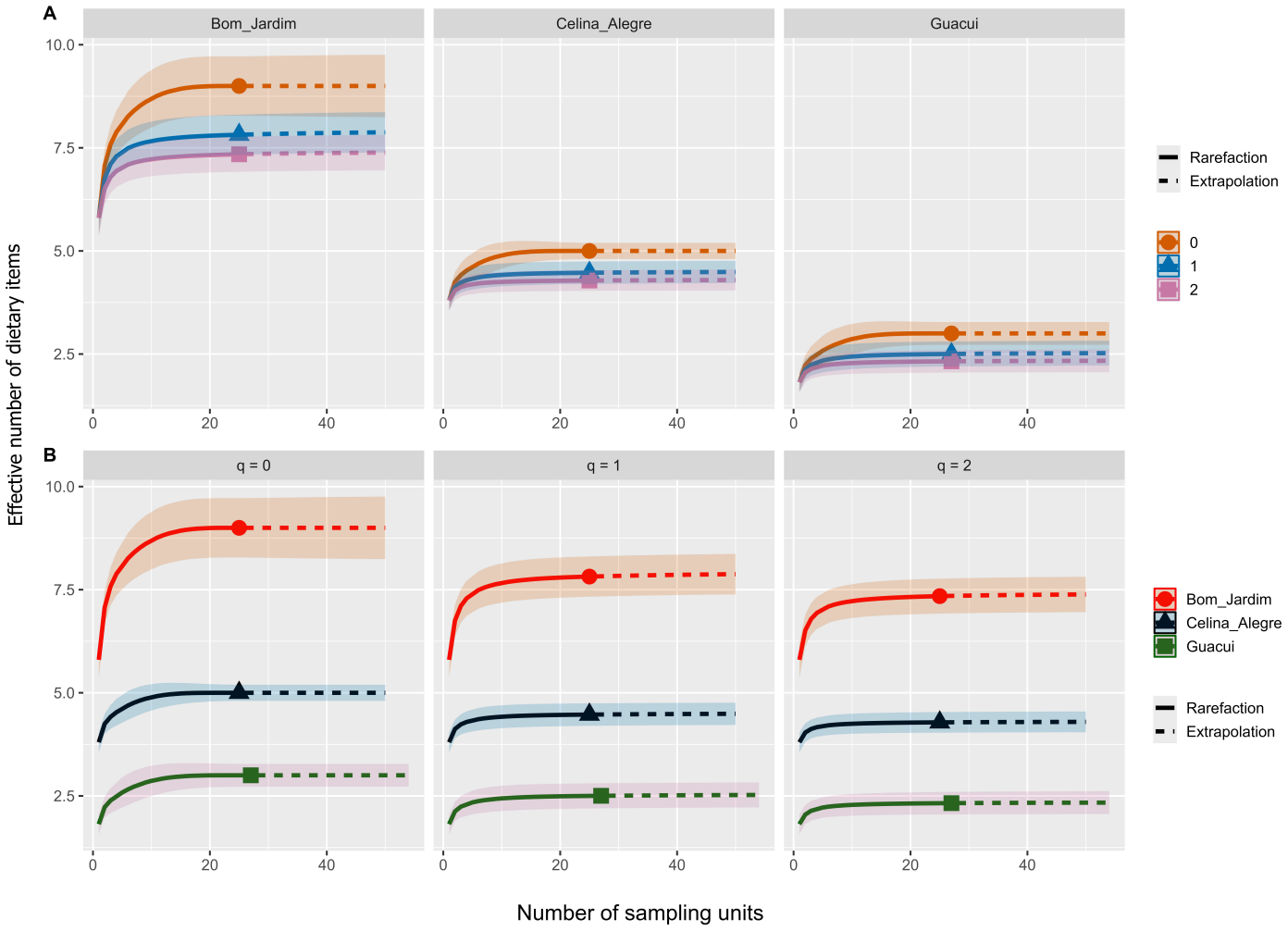


Figure 4

Rarefaction and extrapolation analyses revealed consistent differences in dietary diversity among the three study landscapes (Figure 3). Sampling coverage approached 1.0 in all areas, indicating high sampling completeness and allowing robust comparisons among landscapes. Across all Hill numbers, Bom Jardim consistently exhibited the highest diversity values, Celina showed intermediate values, and Guaçuí presented the lowest diversity. This pattern remained stable across the entire coverage gradient and was observed for species richness (q = 0), Shannon diversity (q = 1), and Simpson diversity (q = 2).

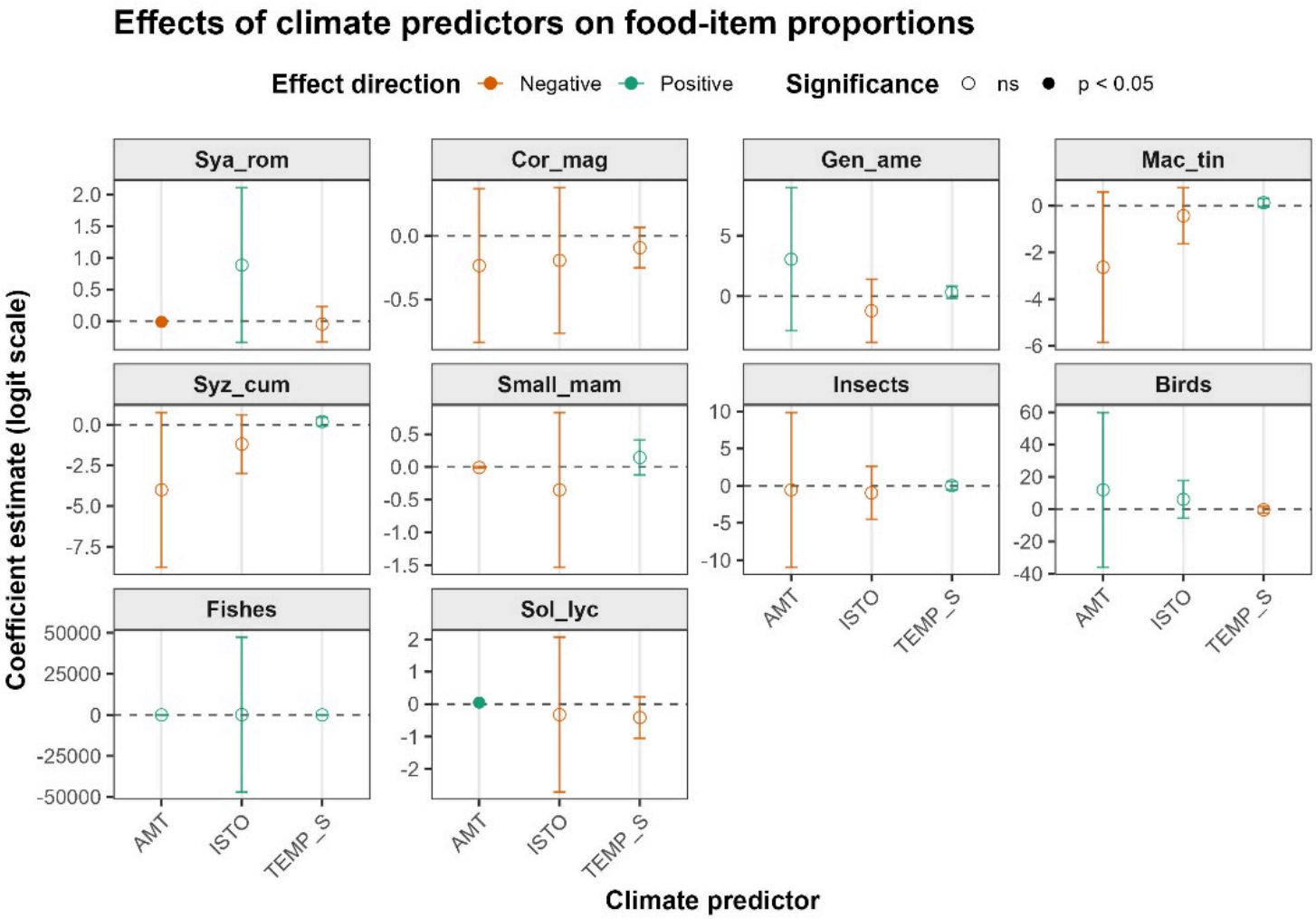


Figure 5

Effects of climate predictors on the occurrence of food items in the diet of the maned wol,, based on quasibinomial generalized linear models. Points represent coefficient estimates (logit scale) for each predictor, and horizontal bars indicate 95% confidence intervals. Colors indicate effect direction (green = positive; orange = negative), while symbols denote statistical significance (filled circles: $p < 0.05$; triangles: $0.05 \leq p < 0.1$; open circles: non-significant). Vertical dashed lines represent zero effect. Panels correspond to individual food items, illustrating variation in the direction, magnitude, and consistency of climatic effects across diet components.

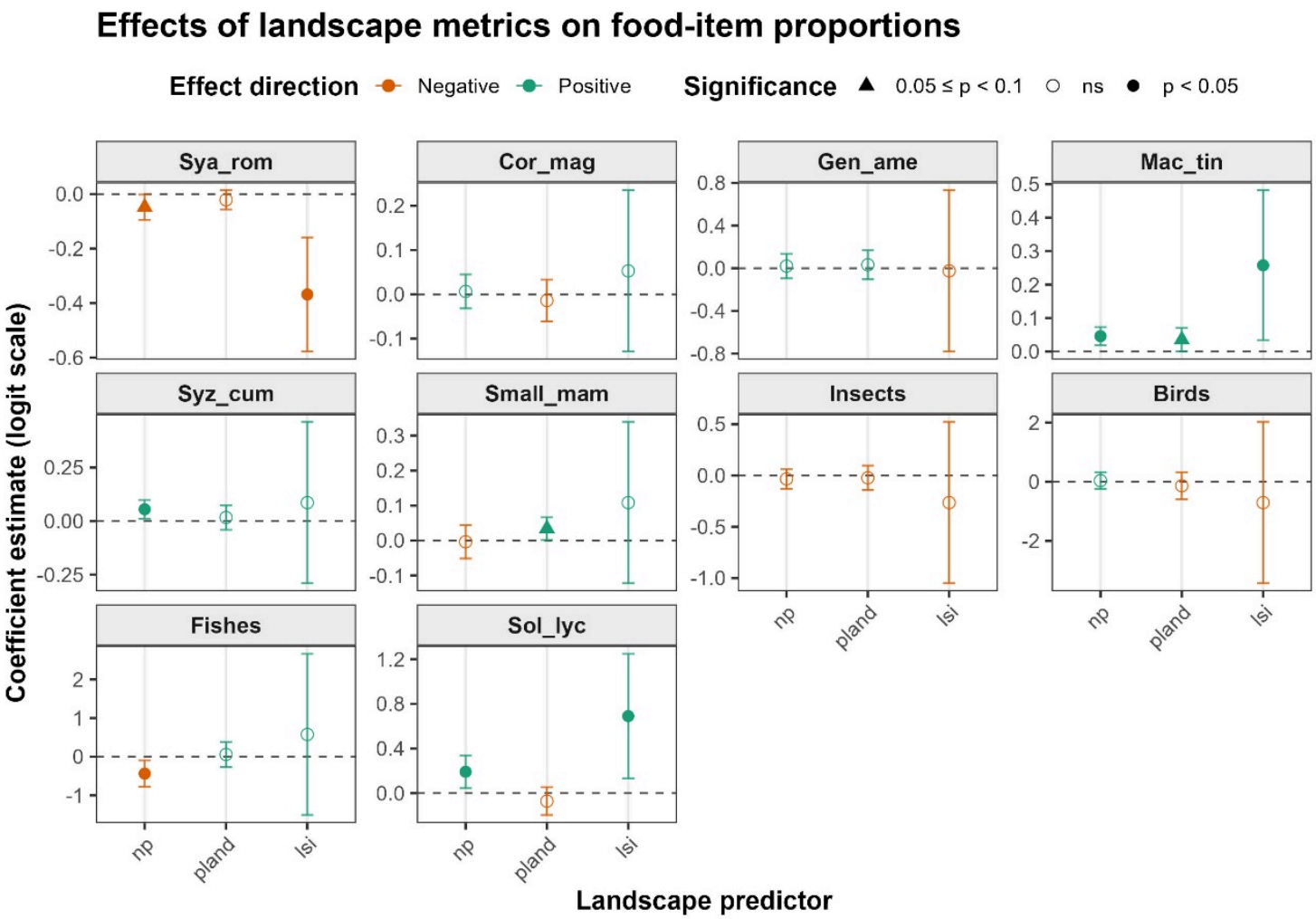


Figure 6

Effects of landscape metrics on the occurrence of food items in the diet of the maned wolf, based on quasibinomial generalized linear models. Points represent coefficient estimates (logit scale), and horizontal bars indicate 95% confidence intervals. Colors denote effect direction (green = positive; orange = negative), while symbols indicate statistical significance (filled circles: $p < 0.05$; triangles: $0.05 \leq p < 0.1$; open circles: non-significant). The dashed vertical line represents a null effect. Panels correspond to individual food items, illustrating variation in the magnitude, direction, and consistency of landscape effects across dietary components.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- supplementarymaterial.docx