ESCOLA SUPERIOR DE CONSERVAÇÃO AMBIENTAL E SUSTENTABILIDADE

WHAT THE CANOPY KEEPS: INTERNAL FOREST STRUCTURE SHAPES THE FUNCTIONAL COMPOSITION OF AN ATLANTIC FOREST HERBIVORE ASSEMBLAGE

Por

JADE HUGUENIN RIOS

NAZARÉ PAULISTA, 2026

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“Aos moradores das florestas – em toda a sua diversidade de tamanhos, formas e cores. Que possam continuar existindo muito além das nossas páginas.”

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LIST OF ABBREVIATIONS

AICc	Akaike Information Criterion corrected for small sample sizes
ANOVA	Analysis of variance
BP	Breusch–Pagan test (for heteroscedasticity)
CFLS	Complexo Florestal Linhares-Sooretama
CI	Confidence interval
CR	Critically Endangered (IUCN category)
CV	Coefficient of variation
CM	Unweighted Community Mean
df	Degrees of freedom
EN	Endangered (IUCN category)
ES	Espírito Santo (state, Brazil)
FD	Functional diversity
FDiv	Functional divergence
FRic	Functional richness
FSp	Functional specialization
FUn	Functional uniqueness
FUSE	Functionally Unique, Specialized and Endangered (index)
GE	Global endangerment (threat status component of FUSE)
GLS	Generalized least squares
HC3	Heteroscedasticity-consistent standard errors (type 3)
IEMA	Instituto Estadual de Meio Ambiente e Recursos Hídricos (Espírito Santo)
IUCN	International Union for Conservation of Nature
LC	Least Concern (IUCN category)
LSFC	Linhares-Sooretama Forest Complex

MMA	Ministério do Meio Ambiente (Brazil)
MODIS	Moderate Resolution Imaging Spectroradiometer
OLS	Ordinary Least Squares
PCoA	Principal coordinates analysis
PNHR	Private Natural Heritage Reserve
R^2adj	Adjusted coefficient of determination
SD	Standard deviation
SE	Standard error
VIF	Variance inflation factor
VNR	Vale Natural Reserve (Reserva Natural Vale)
VU	Vulnerable (IUCN category)

ABSTRACT (PORTUGUESE)

Resumo do Trabalho Final apresentado ao Programa de Mestrado Profissional em Conservação da Biodiversidade e Desenvolvimento Sustentável como requisito parcial à obtenção do grau de Mestre

O QUE O DOSSEL GUARDA: A ESTRUTURA INTERNA DA FLORESTA MOLDA A COMPOSIÇÃO FUNCIONAL DE UMA ASSEMBLEIA DE HERBÍVOROS NA MATA ATLÂNTICA

Por

JADE HUGUENIN RIOS

Setembro, 2026

Orientador: Prof. Dr. André Valle Nunes

Aspectos da diversidade funcional (DF), como a composição funcional, podem enriquecer as estratégias analíticas e auxiliar na demonstração do valor dos dados de biodiversidade, especialmente em estudos de ecossistemas e de espécies ameaçadas, como os da Mata Atlântica. Neste estudo, buscamos avaliar aspectos da diversidade funcional da assembleia de herbívoros de médio e grande porte em um dos maiores remanescentes de Mata Atlântica madura, o Complexo Florestal Linhares-Sooretama (CFLS), relacionando-os à estrutura interna da floresta (altura do dossel) e à configuração da paisagem, e propondo o uso de uma ferramenta de priorização para ações locais de conservação – o índice FUSE. Para esse conjunto de dados, obtidos por meio de registros de armadilhas fotográficas, calculamos os índices de espaço funcional e de diversidade funcional da comunidade, determinamos variáveis da paisagem e da estrutura do habitat, modelamos as relações entre índices funcionais e variáveis da paisagem por meio de regressão linear (Mínimos Quadrados Ordinários – OLS), com um conjunto de modelos definido a priori com base em nossas hipóteses ecológicas para a área (comparado por AICc), e caracterizamos e comparamos dois setores com proteção diferencial no CFLS (Leste vs. Oeste). Por fim, calculamos o índice FUSE para as espécies ameaçadas, que combina unicidade, especialização e grau de ameaça. Nossos principais resultados sugerem que áreas florestadas no CFLS com dossel mais alto estão

associadas a uma maior depredação de sementes ponderada pela comunidade. A independência dessa relação em relação à riqueza de espécies sugere que é a composição funcional que está associada à estrutura local do habitat. Os setores com históricos distintos de proteção não diferiram na composição funcional; a variação esteve associada sobretudo à estrutura do dossel dos fragmentos florestais, e não ao setor. A paisagem no entorno foi um preditor fraco da diversidade funcional. Para as espécies ameaçadas registradas, o índice FUSE foi calculado em escala regional, resultando em um ranking de quatro herbívoros prioritários para a conservação, com a anta (*Tapirus terrestris*) no topo, seguida da cutia (*Dasyprocta leporina*) – funcionalmente distinta apesar do menor grau de ameaça – e dos dois pecaris. A gestão das áreas protegidas no CFLS e os atores-chave do território devem priorizar a qualidade estrutural da floresta nas iniciativas de conservação, e não apenas a cobertura florestal.
Palavras-chave: composição funcional; armadilha fotográfica; priorização para a conservação

ABSTRACT (ENGLISH)

Abstract of the Final Paper presented to the Professional Master's Program in Biodiversity Conservation and Sustainable Development as a partial requirement for obtaining the Master's degree

WHAT THE CANOPY KEEPS: INTERNAL FOREST STRUCTURE SHAPES THE FUNCTIONAL COMPOSITION OF AN ATLANTIC FOREST HERBIVORE ASSEMBLAGE

By

JADE HUGUENIN RIOS

September 2026

Advisor: Prof. Dr. André Valle Nunes

Aspects of functional diversity (FD) can enrich analytical strategies and help demonstrate the value of biodiversity data, especially in studies of ecosystems and threatened species, such as those in the Atlantic Forest. Here, we evaluated aspects of the functional diversity of the medium- and large-sized herbivore guild in one of the largest remnants of mature Atlantic Forest, the Linhares–Sooretama Forest Complex (CFLS), relating them to internal forest structure (canopy height) and landscape configuration, and proposing a state-scale adaptation of the FUSE index for conservation prioritization. From camera-trap records, we computed the functional space and per-cell functional-diversity indices — volume (functional richness and divergence) and composition — determined habitat-structure and landscape variables, modeled their relationships with linear regression (Ordinary Least Squares – OLS) using a model set defined a priori (AICc), and compared the two forest sectors (East vs. West). Functional composition shifted with canopy height: community-weighted seed predation increased in taller forest, independently of species richness, indicating that it is functional composition that tracks local habitat structure. Sectors with different protection histories did not differ in composition; the variation was associated mainly with canopy structure rather than with sector. The surrounding landscape was a weak predictor of functional diversity. Among threatened species, the state-scale FUSE prioritized four herbivores, with the lowland tapir (*Tapirus terrestris*)

ranked highest, followed by the red-rumped agouti (*Dasyprocta leporina*) — functionally distinctive despite a lower threat level — and the two peccaries. Management of protected areas in the CFLS and key regional stakeholders should prioritize structural forest quality in conservation initiatives, rather than forest cover alone.
Keywords: functional composition; camera trap; conservation prioritization

(ARTICLE) WHAT THE CANOPY KEEPS: INTERNAL FOREST STRUCTURE SHAPES THE FUNCTIONAL COMPOSITION OF AN ATLANTIC FOREST HERBIVORE ASSEMBLAGE

1. INTRODUCTION

The functional diversity (FD), linking community structure to ecosystem processes by capturing organisms' functional roles, can add another layer of ecological meaning to biodiversity data (Petchey & Gaston, 2006; Mouillot et al., 2013). While species richness quantifies the number of taxa in a community (Chao & Chiu, 2016; Magurran, 2021), FD measures diversity of organismal characteristics (Violle et al., 2007). These individual characteristics position species in a community's functional space (Mason et al., 2005; Petchey & Gaston, 2006; Mouchet et al., 2010; Mouillot et al., 2013) and reflect interactions with abiotic and biotic environmental variables. FD comprises several complementary aspects (Mouchet et al., 2010; Mouillot et al., 2013): the extent and variation of trait space occupied by a community (such as functional richness and divergence; Villéger et al., 2008), as well as its functional composition, which refers to which trait values or ecological guilds predominate in a community, typically represented by community-weighted means or the proportion of species fulfilling specific ecological roles (Garnier et al., 2004).

These aspects may respond independently to environmental gradients, allowing environmental filters to alter a community's dominant functions without changing the overall functional space it occupies. Mammals can be considered excellent models for studying FD metrics, since their well-documented traits and ecological roles (e.g., herbivory, predation, and seed dispersal) can help relate community composition to ecosystem processes (Sukma et al., 2019) and help reveal how these functions respond to environmental changes (Rega-Brodsky et al., 2023). The emphasis on mammals is also warranted by conservation urgency. Among vertebrates, they represent some of the highest numbers of threatened species, with medium- and large-sized mammals (>1 kg) being particularly impacted by the global defaunation crisis (Jorge et al., 2013; Dirzo et

al., 2014), precisely the species responsible for key landscape-scale functions, such as long-distance seed dispersal and top-down population control. So, beyond describing functional patterns, trait-based metrics offer promising ways to identify species whose loss would most severely impair ecosystem function. Tools such as the FUSE index (Functionally Unique, Specialized and Endangered; Pimiento et al. 2020) combine a species' functional distinctiveness with its extinction classification risk to identify species whose functional roles are both unique and endangered, helping prioritize guilds or taxa for conservation in critical and hazardous ecosystems.

Like other tropical forests, marked by degradation (Borgo et al., 1996; Gibson et al., 2011), the Brazilian Atlantic Forest is, in many respects, enduring its reality. Its forest cover is now restricted to 23% of its original extent, with 97% of its natural remnants reduced to small patches (<50 ha) (Vancine et al., 2024). Even amid ongoing systematic species loss (Dirzo et al., 2014), it remains a vital refuge for biodiversity (Mittermeier et al., 2004; Bovo et al., 2018). Because FD and functional composition capture shifts in ecological function associated with landscape structure, they are particularly sensitive tools for assessing the functional integrity of threatened ecosystems.

In these natural areas of interest, FD of mammal communities can be modulated by environmental filters operating at multiple scales. Landscape factors, such as forest cover, forest continuity, and remnant arrangement and shape, help determine which species’ functions are present and can remain in a region (Magioli et al., 2015; Bogoni et al., 2017; Rios et al., 2022). Within forest remnants, structural factors such as canopy height and vegetation complexity represent local habitat quality and resource availability (Tews et al., 2004; Santos & Henriques, 2010), functioning as a filter that thereby influences mammal assemblages (Püttker et al., 2008; Estrada et al., 2026), principally for those species that depend directly on the main resources evaluated (e.g., seed dispersers and seed predators). In this case, the more structural complexity a habitat has, the more likely it is to support mammal communities that are not only richer in species (Estrada et al., 2026) but also more diverse in their roles (Sukma et al., 2019; Rega-Brodsky et al., 2023).

Large forest herbivores and frugivores often depend directly on the abundant food resources provided by mature, intact forests, such as large fruits, leaves, and seeds (Galetti et al., 2006; Keuroghlian & Eaton, 2009). Some of these species also require extensive home ranges and lower distances to watercourses (Altrichter et al., 2012; Oshima, 2019). For these guilds, structural degradation, especially at forest edges, depletes these resources by replacing large-fruited trees with pioneer species that produce small seeds (Magnago et al., 2014), affecting their access to adequate resources. In contrasting roles in plant interactions, some species act as seed predators that destroy most of the seeds they ingest, while others act as dispersers (Bodmer, 1991; Vacari et al., 2025). Either way, these species depend on habitat structure to persist, and the balance between their roles depends on the size and hardness of available seeds; canopy structure is expected to filter the composition of plant–animal interactions within the guild, shifting the balance between seed dispersal and seed predation.

Although the FD of tropical forest mammal communities is consistent at broad to intermediate scales (Rovero et al., 2020), these patterns are less understood at finer scales, where local habitat features such as canopy structure operate within a continuous forest block (Rovero et al., 2020). This study addresses one of the facets of this gap by examining how internal canopy structure influences the FD of the herbivore assemblage within a large, continuous Atlantic Forest block. We evaluated how forest canopy and landscape structure the functional diversity of the terrestrial medium- and large-sized herbivore guild, in both functional volume (richness and divergence) and composition, in one of the largest remaining complexes of mature Atlantic Forest. We also evaluated whether the surrounding landscape context and water availability shape herbivore functional diversity, testing anthropogenic cover, landscape heterogeneity (Shannon index of land-use diversity), and distance to watercourses as competing candidate predictors in our model set.

Considering that taller, structurally more mature forests offer a broader set of resources and niches, we tested whether (H1) functional richness and divergence increase with canopy structure (height); (H2) Functional composition varies with canopy structure: canopy filters the community-weighted composition of seed-related plant–animal

interactions within the guild; and (H3) landscape configuration and environmental context (forest and anthropogenic cover, distance to watercourses, forest edges, roads, and sector continuity) structure the functional diversity of the herbivore guild, such that the more continuous forest sector and cells with greater forest cover and lower anthropogenic pressure support higher functional richness and divergence and a distinct functional composition. We further proposed an adaptation of the FUSE index using state-scale threat status to identify conservation-priority herbivore species. The results are discussed in light of their implications for the conservation of the Linhares-Sooretama Forest Complex (LSFC) and for understanding the ecological processes that structure herbivore assemblages in large Atlantic Forest remnants.

3. METHODS

3.1 - Study Area

The LSFC, located in the northern part of Espírito Santo, southeastern Brazil, is a large complex of Atlantic Forest that covers approximately 50,000 hectares. Its area encompasses the Sooretama Biological Reserve (SBR; 27,859 ha) under public protection, and the Vale Natural Reserve (VNR; 21,787 ha), the Recanto das Antas Private Natural Heritage Reserve (PNHR; 2,201.60 ha), the Mutum-Preto PNHR (378.73 ha), the Cupido & Refúgio Farm (70 ha), and mandatory legal reserves on rural properties under private protection. The region's geological foundation presents sedimentary deposits that create the "coastal tablelands", characterized by features that are typically flat or gently undulating (Fontana et al., 2016). Given its characteristics, the most prominent vegetation type of the LSFC is classified as Evergreen Seasonal Forest (Jesus & Rolim, 2005), also known as the “Tabuleiro” forest (Rizzini, 1997; Garbin et al., 2017).

The surroundings of the LSFC reveal a landscape characterized by intense fragmentation, multiple land uses, and dynamic potential, particularly in areas dedicated to pasture for dairy and beef cattle farming, silviculture, as well as to coffee cultivation and the production of papaya, banana, coconut, rubber tree, and other crops (INCAPER,

2023; Torres et al., 2026; see Figure 1). The LSFC is bisected longitudinally by the BR-101 Highway, which divides the forest block into two sectors with distinct landscape characteristics (east and west). This combination of factors makes the LSFC highly significant for the conservation of the mammal fauna, and it is considered a priority area for the protection of large mammals in the Atlantic Forest (Galetti et al., 2009).

3.2 - Sampling with camera trapping

Sampling was carried out across five areas that together encompass the forest remnants of the LSFC: the Sooretama Biological Reserve (SBR; 27,858 ha; 19°05′S; 40°15′W), the Recanto das Antas Private Natural Heritage Reserve (PNHRRA; 2,212 ha), the Mutum-Preto PNHR (PNHRMP; 379 ha), the Vale Natural Reserve (VNR; ~20,000 ha), and the Cupido & Refúgio Farm (180 ha; Figure 1). SISBIO/Chico Mendes Institute for Biodiversity Conservation granted authorization for the study (No. 32565-5).

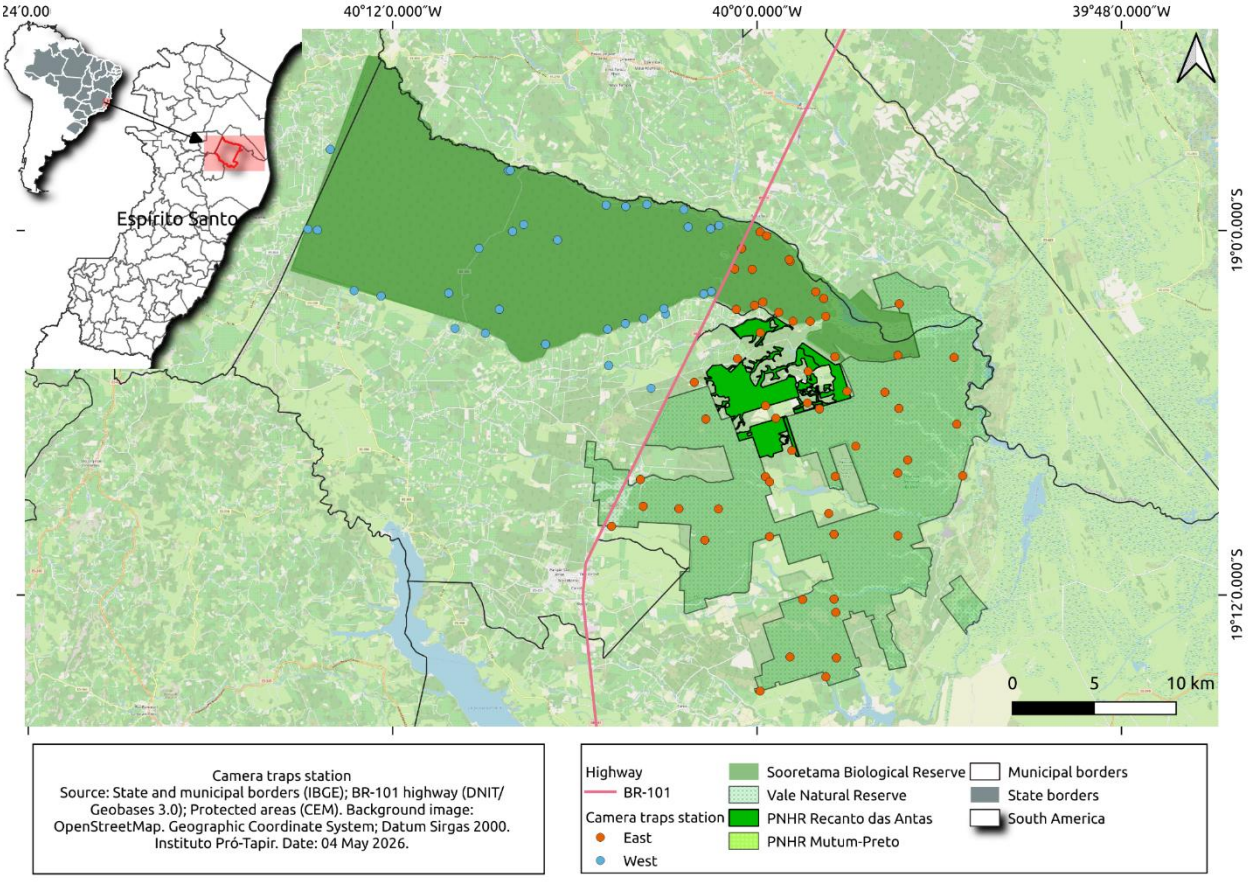

Figure 1. Camera-trap monitoring stations of the Pró-Tapir Institute for Biodiversity at the LSFC, for the sampling designs conducted in 2016 and 2017. Data sources: state and municipal borders (IBGE, 2020); BR-101 highway (DNIT/Geobases, 2019); protected areas (CEM, 2021); Basemap:

©OpenStreetMap Contributors (ODbL). Geographic Coordinate System, Datum SIRGAS 2000. Elaboration: Pró-Tapir Institute for Biodiversity, 2026.

The sampling was conducted in three periods, between February 2016 and December 2017, as detailed below.

2016 Sampling Design: Between February and April 2016, 21 camera traps were installed at fixed stations randomly selected in a grid of 4 km² square cells within the SBR area and its surroundings. The camera traps remained active 24 h/day, resulting in a sampling effort of 807 camera-nights. The 2016 campaign shows high spatial overlap with the 2017/01 campaign, with several stations located in the same 4 km² cells. Consequently, the 2016 data were incorporated as complementary sampling efforts within the shared grid, rather than as an analytically independent campaign.

2017/01 Sampling Design: Between January and March 2017, 41 camera traps were installed across the SBR, PNHRRA, PNHRMP, VNR, and other adjacent private areas. A grid of 4 km² cells was established for the study area, and cells with installed cameras were randomly selected. The installed camera traps remained active 24h/day, resulting in a sampling effort of 1,769 camera-nights.

2017/02 Sampling Design: Between August and December 2017, 32 camera traps were installed following a sampling design protocol based on the Random Encounter Model (REM) methodology; selected via a random draw from 3.7 km² grid cells established across the SBR, VNR, PNHRMP, and PNHRRA. Note that the sites were re-aggregated in the analysis to the established 4 km² grid (see Section 3.3). The installed camera traps remained active 24h/day throughout the period, resulting in a sampling effort of 3,082 camera-nights.

Data acquisition and processing criteria

Field sampling totaled 5,658 camera-nights across the three campaigns; no bait was used to attract species to the sampling points. After accounting for one stolen camera trap and

excluding two cells outside forested areas, 67 cells and 5,531 camera-nights were selected to conduct the analysis.

Records for each herbivore species were classified as independent records based on Tobler et al. (2008), which counts a record per species span within an hour. Undefined records of brocket deer (potential genera *Mazama*, *Passalites,* or *Subulo*) were excluded due to the impossibility of reliable species-level identification in some records. Sex was not differentiated, as the sex of most species cannot be reliably identified from camera records. Based on the independent records, a species presence/absence matrix per cell was constructed (with each species considered present or absent in each 4 km² cell), regardless of the number of records.

3.3 - Sampling unit and completeness

To compare campaigns with different sampling designs, sampling points/stations were integrated into a regular 4 km² (2 × 2 km) grid, constructed using the SIRGAS 2000 UTM Zone 24S reference system. In cases where stations were located on the grid edge, they were assigned to the nearest cell using the `st_nearest_feature()` function from the “sf” package (Pebesma, 2018) in R (R Core Team, 2026). Under this logic, we aggregated records and sampling effort from stations within the same cell, so each cell represented a single unit of analysis, regardless of the number of campaigns or stations it comprised. We chose not to apply a direct effort correction, but instead explicitly assessed its influence on the main outcome. Sample completeness was assessed using rarefaction/extrapolation (iNEXT; Hsieh et al., 2016).

In total, 67 cells distributed in the study area were used as sampling units. Because the functional indices differ in their requirements, they were computed on nested subsets of these 67 cells, defined a priori according to the minimum number of co-occurring herbivore species each index requires (Section 3.5).

3.4 - Functional traits

Functional traits are intrinsic characteristics measurable at the individual level (e.g., morphological, physiological, or phenological) that influence the performance and fitness of organisms (Violle et al., 2007). To functionally characterize the recorded species, five functional traits with direct ecological relevance to the processes structuring mammal communities in fragmented landscapes were selected (see Table 1).

Table 1. Functional traits used to characterize the functional diversity of large herbivores in the LSFC. Categorical traits were coded as nominal categorical factors.

Trait	Type	Categories / Unit
Activity pattern	Nominal categorical	Diurnal, Cathemeral, Nocturnal
Body mass	Continuous	Grams (log10)
Frugivory	Continuous	% of diet from fruits/seeds (dispersal + depredation; Magioli et al., 2021)
Plant–animal interaction	Continuous	Dispersal − depredation (Magioli et al., 2021); negative = net seed predation, positive = net dispersal
Home range	Continuous	Hectares (log10)

Unlike many FD studies based on historical and general databases (Covre et al., 2022; Pedroso-Santos et al., 2024), we built the functional characterization from the assemblage recorded at the site, cross-checked against primary sources, which provides more representation of the local community's functional structure (Etard et al., 2020).

Activity pattern. The activity pattern (diurnal, nocturnal, cathemeral) was obtained from ATLANTIC MAMMAL TRAITS (Gonçalves et al., 2018) and cross-checked with EltonTraits and Nodari (2016). For two species (*Passalites nemorivagus* and *Tapirus terrestris*), we used primary camera-trap data collected at LSCF (unpublished results from this dataset), which took precedence over the databases.

Body mass. Mass values were obtained from Paglia et al. (2012), using the midpoint of the ranges when provided. To verify the consistency of these values, we compared them with three independent databases — ATLANTIC MAMMAL TRAITS (Gonçalves et al., 2018), EltonTraits (Wilman et al., 2014), and PanTHERIA (Jones et al., 2009). When the midpoint from Paglia et al. (2012) substantially diverged from the consensus of these

databases, we calibrated the value to that consensus (calibrated species: *Subulo gouazoubira*, *Dicotyles tajacu*, *Tayassu pecari*, *Tapirus terrestris*). All values were log-transformed ($\log_{10}$) for analysis.

Frugivory. Frugivory was quantified, for each species, as the proportion of the diet derived from fruits and seeds, obtained from the functional-trait compilation of Magioli et al. (2021) as the sum of its seed-dispersal and seed-depredation contributions. For *Passalites nemorivagus*, which is not included in that compilation, frugivory was derived from primary dietary studies of the species (Bodmer, 1989, 1991; Gayot et al., 2004).

Plant-animal interaction. Rather than assigning species to discrete roles, we characterized each species' contribution to seed fate as a set of continuous diet traits. From the compiled diet dataset of Magioli et al. (2021), we extracted, for each species, the proportion of the diet corresponding to seed dispersal (gut passage of intact small and large seeds) and to seed depredation (destruction of small and large seeds). From these we derived effective frugivory (the summed proportion of fruit and seed consumption, i.e. dispersal + depredation), and we used the community-weighted mean of seed depredation as the primary compositional response (see Section 3.7. Models). Diet proportions for eight of the nine species were taken directly from Magioli et al. (2021). For *Passalites nemorivagus* — reported as *Mazama gouazoubira* in part of the earlier Amazonian literature and not included in that compilation — proportions were derived from primary dietary studies (Bodmer, 1989, 1991; Gayot et al., 2004). For the seven species with dedicated seed-dispersal or seed-predation studies available, these independent sources corroborated the assigned proportions (Motta-Junior et al., 1994; Fragoso et al., 2003; Galetti et al., 2006; Alves-Costa et al., 2007; Keuroghlian & Eaton, 2009; Jansen et al., 2012; Seibert, 2015).

Home range. Home range values were obtained from the global HomeRange database (Broekman et al., 2022). A protocol to ensure standardized extraction and comparability across species was adopted, comprising only individual-level estimates (excluding group and population values); prioritizing the 95% isopleth, and when this was unavailable, using the 100% isopleth; and for each species, calculating the median of the estimates

(a measure robust to outliers). When there were at least five estimates from South American studies (n ≥ 5), we used only these, given their greater relevance to the Neotropical context; otherwise, we used all estimates available in the database. Of the nine species, home ranges for eight were derived directly from the HomeRange database. For *Passalites nemorivagus*, which was absent from the database, we imputed its value from its closest relative, *Subulo gouazoubira*, following the imputation decisions in Johnson et al. (2021).

3.5 - Functional space and functional diversity indices

Functional distances between species were calculated using Gower distance ("mFD" package version 1.0.7; Magneville et al., 2022) for the five functional traits in R (R Core Team, 2026). Functional space quality was assessed using the Mean Absolute Deviation (MAD) criteria. The optimal number of dimensions for this dataset was determined to be three (MAD = 0.015).

Three alpha functional diversity indices were calculated per sampling cell: (i) functional richness (FRic), which measures the volume of the convex functional space occupied by species present in a community (Villéger et al., 2008) and was calculated only for cells with a richness of ≥ 4 species; (ii) Functional divergence (FDiv) quantifies the degree of functional divergence of species within the occupied space, and values close to 1 indicate that species tend to occupy the extremes of the available functional space (Villéger et al., 2008); (iii) unweighted community mean (CM) were calculated for each functional trait, representing the mean trait value across the species present in each cell (Garnier et al., 2004).

Because the functional indices differ in their mathematical requirements, they were computed on nested subsets of the 67 sampling cells. Functional composition (community-weighted means) was calculated for the 56 cells in which at least two herbivore species co-occurred, since a community-weighted mean is only meaningful when more than one species contributes to the aggregation. The volume-based indices (FRic and FDiv) were calculated for the 35 cells containing at least four herbivore species: because functional richness is defined as the volume of the convex hull enclosing the

species in the functional space, a non-degenerate hull in a d-dimensional space requires at least d + 1 vertices, and cells with fewer species cannot delimit a volume. These minimum-richness thresholds were defined *a priori* and determine the sample sizes reported for each facet (composition, n = 56; volume, n = 35).

3.6 - Landscape variables

Canopy height was used as a proxy for structural quality and was derived from the Meta & WRI High Resolution Canopy Height product, containing tree canopy presence and height obtained by satellite imagery spanning from 2009 to 2020 (Tolan et al. 2024; native resolution 1 m, MAE 2.8 m; resampled to 30 m) and masked to forest pixels from land cover and land use data from MapBiomas Collection 10 (reference year was 2017; MapBiomas, 2024), so that it reflected only forested areas; non-forest pixels, present in some cells, were excluded. This decision followed the criteria presented by Estrada et al. (2026), which valued structural metrics (e.g., canopy height) and mitigated coarse heterogeneity from non-forest areas within each cell. The analysis encompassed the mean canopy height of forest-masked canopy pixels within each 4 km² sampling grid cell.

Additional variables were tested to evaluate the influence of landscape structure on functional diversity (forest and anthropogenic cover, distance to watercourses, forest edges, roads, and sector continuity). These were extracted within circular buffers (2 km radius) centered on each sampling cell, chosen to reflect the perceptual and home-range scale of the medium- and large-sized herbivores in our assemblage (Burton et al., 2015; Magioli et al., 2021), as the 2 km radius comprises the home ranges of most species recorded here (see Table S2).

Land cover and land use were obtained from MapBiomas Brazil Collection 10 (reference year 2017; MapBiomas, 2024). The classes were grouped into two categories: forest (comprising natural forest formations and arboreal “restinga”); and anthropogenic cover (comprising silviculture, agriculture/livestock farming, and non-vegetated areas). The variables of interest were forest cover (%), anthropogenic cover (%), and the Shannon diversity index, calculated from land-use classes within the 2-km-radius buffer, as a

measure of landscape heterogeneity. The variables were extracted using the “terra” package (Hijmans, 2023) in R (R Core Team, 2026).

The distance to the nearest permanent watercourse was calculated from each cell centroid using the Ottocoded Hydrographic Database from the National Water Agency (ANA, 2017), filtering drainage segments with a Strahler order of 2 or greater, which corresponds to watercourses with a higher probability of being perennial. Extraction was performed using the “sf” package (Pebesma, 2018) in R (R Core Team, 2026).

Distance to edges and roads served as a proxy for disturbance. These were based on the distance from each cell centroid to the nearest forest edge, derived from the MapBiomas mask, and to the nearest road or highway, obtained from OpenStreetMap (motorway, trunk, primary, secondary, and tertiary road classes) with the “osmdata” package (Padgham et al., 2017) in R (R Core Team, 2026). Because only these higher-order OSM classes were used, the metric reflects primarily the larger public road network rather than internal unpaved management tracks. Edge distance was interpreted as a proxy for edge effects, and road distance as a proxy for anthropogenic disturbance and access.

To assess whether FD reflected the region's landscape configuration and protection history, we assigned each cell to one of two sectors defined by the BR-101 highway, which separates the Complex into two sides: the east sector (which encompasses the majority of the VNR area and the PNHRs), and the west sector (which encompasses the majority of the SBR area). We characterized landscape continuity by the mean distance of cells to forest edges, and forest amount by the proportion of forest cover per cell. Differences between sectors in forest cover, edge distance, canopy height, and the community-weighted seed depredation (composition) were tested with Welch's t-tests. To quantify the independent and shared contributions of sector and canopy height to the community-weighted seed depredation (composition), we used variance partitioning (Peres-Neto et al. 2006) and tested the significance of each fraction using partial redundancy analysis with 9999 permutations (fixed random seed). To verify that any

sector effect was not driven by proximity to the highway, we repeated the partial analysis controlling for both canopy height and distance to roads.

We also tested anthropogenic cover, landscape heterogeneity (Shannon index), and distance to watercourses as candidate predictors; these were not retained in the confidence set of models and are detailed in the Supplementary Material (Table S6).

3.7 - Models

Each landscape predictor was interpreted in relation to a specific facet of disturbance or habitat structure: forest cover as habitat availability; anthropogenic cover as the intensity of land conversion in the surrounding matrix; the Shannon index of land use as the heterogeneity (configurational complexity) of that matrix; distance to the nearest road as a proxy for anthropogenic disturbance and access; distance to the forest edge as a proxy for edge effects; and side of the BR-101 highway as a categorical descriptor of forest sector and landscape continuity.

Relationships between functional indices and landscape variables were modeled using linear regression (OLS). Instead of stepwise selection, whose biases in parameter estimation and instability are well documented (Whittingham et al., 2006), a set of *a priori* defined models was compared using AICc (Burnham & Anderson, 2002), with model averaging applied to the confidence set (ΔAICc < 2). Linear models were adopted because we had no *a priori* expectation of non-linear responses, residual inspection gave no indication of systematic curvilinearity, and the sample sizes available (n = 56 cells for composition and n = 35 for the volume facets) do not support the estimation of more complex functional forms without overfitting. The candidate set comprised nine models: the null (intercept-only) model, a canopy-only model, and seven canopy-plus-one-variable models. The primary response variable was the community-weighted seed depredation (composition), modeled within this a priori AICc framework with model averaging as described above. The remaining functional indices (community means of the other traits, the activity-pattern proportions, FRic and FDiv) were assessed with univariate linear regressions against canopy height, using the same diagnostic cadence (below) and correcting for multiple comparisons (see Results in Table 4).

In parallel, each functional facet (community-weighted seed depredation, functional richness and functional divergence) was regressed univariately against each landscape variable, with p-values corrected for multiple comparisons by the Benjamini–Hochberg procedure across the resulting 21-test family (See Results in Table 5).

Each model was subjected to a fixed diagnostic sequence. Residual normality (Shapiro–Wilk) and homoscedasticity (Breusch–Pagan) were assessed, and heteroscedasticity-robust standard errors (HC3) were used. Spatial autocorrelation in the model residuals was assessed using Global Moran's I with a k-nearest-neighbor scheme (k = 5), implemented in the "spdep" package (Bivand & Wong, 2018) in R (R Core Team, 2026); where residuals showed significant positive autocorrelation, the models were refitted using generalized least squares with an exponential spatial correlation structure (Pinheiro & Bates, 2000). Because several responses had non-normal residuals, each relationship was additionally tested with a two-tailed permutation test (9,999 permutations); for the exploratory responses, permutation p-values were corrected for multiple comparisons using the Benjamini–Hochberg and Holm procedures.

3.8 - Sensitivity tests

To verify that the indices captured dimensions of diversity independent of taxonomic richness, herbivore richness per cell was added as a covariate to each significant model; an effect was retained as compositional only when the predictor of interest remained significant after this control.

A sensitivity analysis assessed the influence of sampling seasonality on the functional indices (FRic and FDiv) using a type-II ANOVA that controlled for herbivore richness and sampling effort; each cell was classified as belonging to the rainy, dry, or mixed season based on the sampling campaigns that contributed to its records. All sensitivity analyses are available in the Supplementary Material.

Also, we assessed whether the functional metrics were sensitive to uneven sampling by (i) correlating each metric with per-cell sampling effort (Spearman), and (ii) refitting the

main canopy–composition model under a series of increasing minimum-effort thresholds and after excluding the most intensively sampled cells (Table S6).

3.9 - FUSE: Functionally Unique, Specialized and Endangered

The Functionally Unique, Specialized and Endangered (FUSE; Pimiento et al., 2020) is an index that combines two components of a species' functional contribution: functional uniqueness (mean distance to its three nearest neighbours in functional space; nb_NN=3) and functional specialization (distance from the functional centroid), each rescaled to 0–1 and weighted by the species' threat status (endangerment score, GE). The index was implemented with the “mFD” package (version 1.0.7; Magneville et al., 2022) in R (R Core Team, 2026), where the GE component was standardized to 0–1 (standGE = TRUE) and adapted to replace the global threat component (IUCN, 2024) with a state-scale component using the Espírito Santo state Decree 5.237-R/2022 of endangered species (IEMA, 2022), as suggested by Pimiento et al. (2020), to prioritize species whose functional loss would be most critical at the regional scale. Species not listed in the state decree were assigned the lowest threat category (Least Concern equivalent).

4. RESULTS

4.1 - Species richness and sampling effort

Throughout the three campaigns analyzed, the nine medium- and large-sized herbivore species that constitute our focal guild were recorded across the 67 4-km² cells (Table 2), obtained by grouping the sampling stations into a regular grid. These herbivores occurred within a broader assemblage of 23 medium- and large-sized mammal species detected in the study area. A total of 4,339 independent records was obtained for the full assemblage (3,260 for the nine focal herbivores; Table 2). Per-cell richness of the full mammal assemblage averaged 6.2 ± 2.9 species (range 1–12). Sampling completeness, assessed for this assemblage, was high: the 23 observed species represented 91% of the estimated asymptotic richness (Chao2 = 25.2; 95% CI 23–35), with a sample coverage of 99.3%. These 23 species represent approximately 64% of the 36 medium- and large-sized mammal species documented in previous studies of the Linhares–

Sooretama Forest Complex (Srbek-Araujo & Kierulff, 2016), and do not include most arboreal mammals confirmed for the region. The complete list is available in the Supplementary Material.

Table 2. Medium- and large-sized herbivore species recorded in the Linhares-Sooretama Forest Complex between 2016 and 2017. No. of cells = 67 4 km² cells with at least one record; IRs = independent records. Some of these records can be accessed in Gatti et al. (2017).

Order	Species	Common name	No. of cells	IRs	East cells	West cells
LAGOMORPHA	*Sylvilagus brasiliensis*	common tapeti	2	56	1	1
RODENTIA	*Hydrochoerus hydrochaeris*	capybara	2	3	1	1
	Dasyprocta leporina	red-rumped agouti	39	844	30	9
	Cuniculus paca	paca	36	350	25	11
	Passalites nemorivagus	Amazonian brown brocket	51	601	34	17
ARTIODACTYLA	*Subulo gouazoubira*	gray-brocket deer	1	3	1	0
	Dicotyles tajacu	collared peccary	36	889	34	2
	Tayassu pecari	white-lipped peccary	7	154	7	0
PERISSODACTYLA	*Tapirus terrestris*	lowland tapir	48	360	35	13

Per-cell species richness increased markedly with sampling effort (Figure 2; Spearman $\rho = 0.78$, $p < 0.001$), a dependence characteristic of camera-trap surveys. This effect is confined to the per-cell scale and is consistent with the high completeness of the pooled inventory (sample coverage 99.3%): cells with lower effort detected fewer species, whereas the assemblage as a whole approached its asymptote. Because raw species counts were therefore effort-sensitive, the functional analyses that follow were based on metrics screened for effort dependence (Section 3.8) rather than on species richness itself.

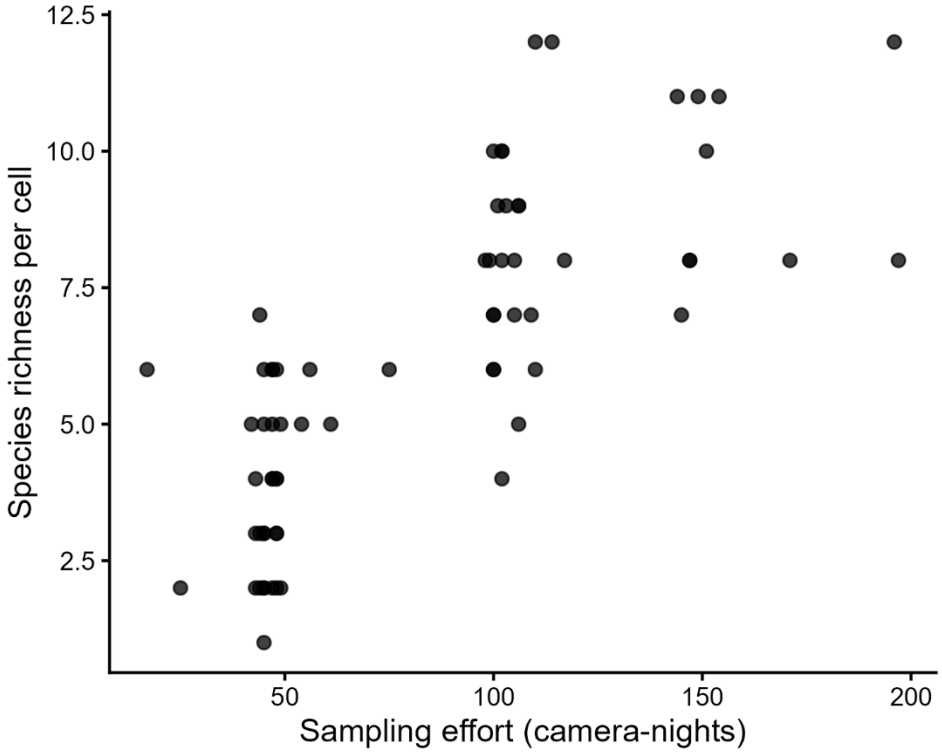

Figure 2. Per-cell species richness of the medium- and large-sized mammal assemblage (23 species) in relation to sampling effort across the 67 grid cells (sampling effort: 17–197 camera-nights per cell). Richness increased with effort (Spearman ρ = 0.78, p < 0.001), a dependence typical of camera-trap sampling. Although per-cell richness was therefore effort-sensitive, assemblage-level completeness was high when cells were pooled (23 observed species, 91% of the Chao2 estimate; sample coverage 99.3%). The functional metrics used in the subsequent analyses were screened for effort sensitivity (Table S6).

4.2 - Functional space and functional volume of the herbivore guild

Gower-based functional distances yielded a three-dimensional space as the optimal representation (MAD = 0.015). All five traits contributed significantly to its organization (Table 3), which was structured primarily by body size and space use: home range (R^2 = 0.93) and body mass (R^2 = 0.82) showed the strongest associations with the functional axes, followed by activity pattern (R^2 = 0.74), frugivory (R^2 = 0.70) and the net seed effect (R^2 = 0.65).

Table 3. Associations between functional traits and the three-dimensional functional space (Gower distances; nine species; MAD = 0.015), fitted by envfit (vegan; 999 permutations). Continuous traits were fitted as vectors, and the categorical trait (activity pattern) as centroids.

Trait	R^2	p
Home range ($\log_{10}$)	0.93	0.001
Body mass ($\log_{10}$)	0.82	0.003
Activity pattern	0.74	0.005
Frugivory	0.70	0.040
Net seed effect	0.65	0.049

Functional volume did not respond to canopy height. Across the 35 cells with ≥ 4 species, functional richness showed a weak, non-significant negative trend (β = −0.016; OLS p = 0.12), which remained non-significant under heteroscedasticity-consistent standard errors (HC3 p = 0.25) and after accounting for spatial autocorrelation (Moran's I p = 0.04; GLS p = 0.23). Functional divergence was likewise unrelated to canopy height (β = −0.003; OLS p = 0.67; HC3 p = 0.74; GLS p = 0.57; Table 4). The volume occupied by the guild in functional space, and the dispersion of species within it, were therefore invariant to canopy structure.

4.3 – Functional composition

Functional composition shifted with canopy height (n = 56 cells with ≥ 2 species). Community-weighted seed depredation increased significantly with canopy height (β = +1.38; OLS p = 0.009; HC3 p < 0.001; GLS p = 0.009; Figure 3A), confirmed by permutation (p = 0.015) and independent of herbivore richness (β = +1.37, p = 0.013; richness contributing nothing, p = 0.96) — indicating a purely compositional response. This relationship was not an artifact of sampling: seed depredation was uncorrelated with sampling effort (Spearman ρ = −0.056, p = 0.68) and remained significant across increasing minimum-effort thresholds (Table S6), and it did not vary across sampling seasons (canopy × season interaction F = 1.23, p = 0.299).

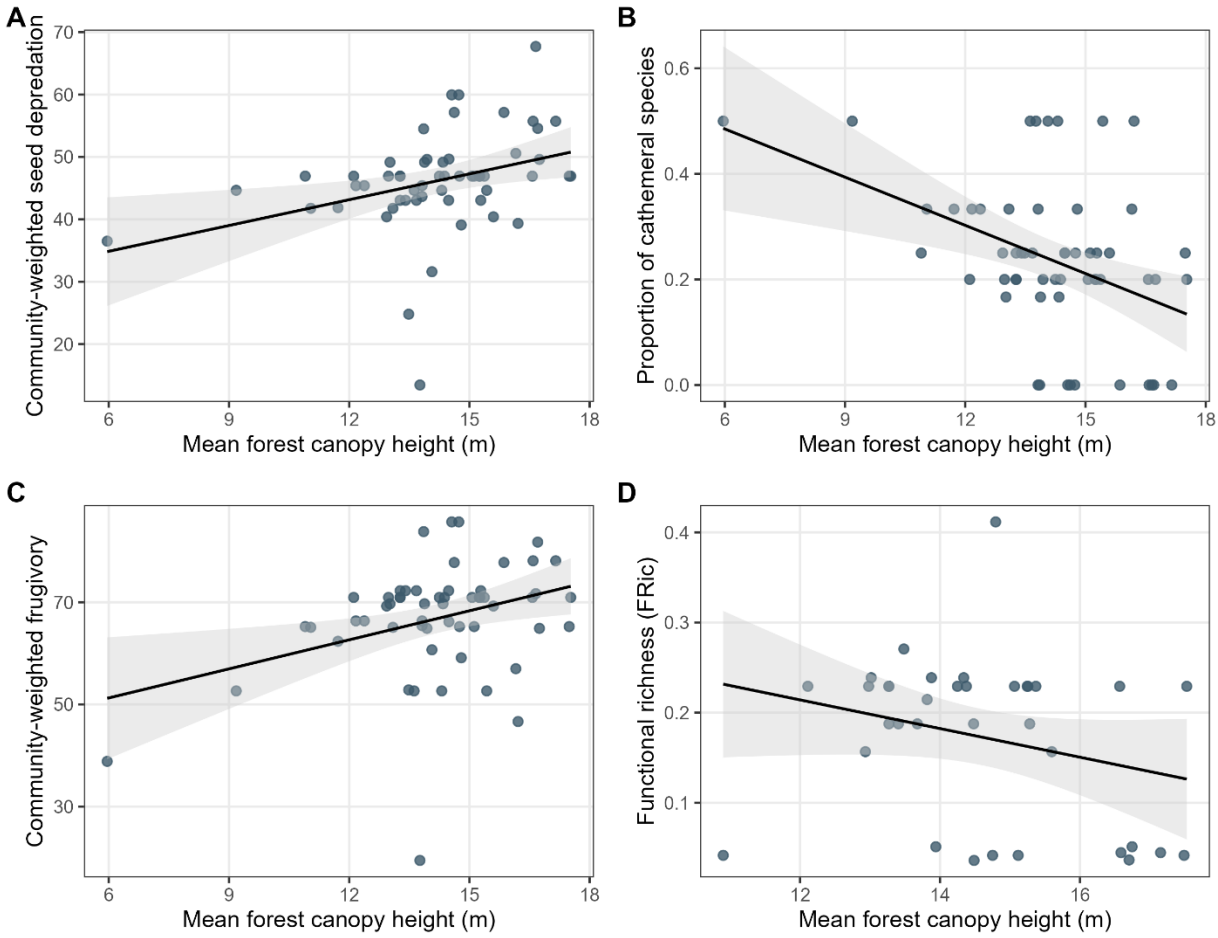

Figure 3. Facets of herbivore functional diversity as a function of mean forest canopy height. Community-weighted seed depredation (A; primary response, n = 56), the proportion of cathemeral species (B; n = 56) and community-weighted frugivory (C; n = 56) shifted with canopy height, whereas functional richness (D; n = 35 cells with ≥ 4 species, spanning a narrower canopy range) did not. Lines show ordinary least-squares fits (shaded areas: 95% confidence intervals); statistical details and robustness checks are in Table 4.

Among the exploratory composition metrics (corrected for multiple testing), activity composition also shifted: the proportion of cathemeral species decreased with canopy height (β = −0.030; HC3 $p < 0.001$; GLS $p = 0.002$; permutation $p = 0.019$, also significant after Holm correction, Figure 3B), mirrored by a complementary increase in diurnal species (the three proportions sum to one; the nocturnal proportion was unchanged, $p = 0.93$); the diurnal increase did not survive the spatial model (GLS $p = 0.09$). Community-weighted frugivory increased with canopy height (β = +1.90; HC3 $p = 0.019$; GLS p =

0.009; BH-corrected p = 0.04; Figure 3C), although part of this signal was attributable to richness (p = 0.038).

The remaining metrics were unrelated to canopy height (Benjamini–Hochberg-corrected permutation p): the net seed effect — the balance between dispersal and depredation — (β = −0.86; p = 0.31), community-weighted body mass (p = 0.23) and home range (p = 0.78), and the nocturnal proportion (p = 0.93; Table 4). Taken together, taller canopies were associated with assemblages weighted toward diurnal, seed-predating herbivores, without changes in functional volume (Figure 3D), body size, or home range.

Table 4. Relationships between facets of functional diversity and canopy height. β, slope per meter of canopy height (OLS). Robustness: Shapiro–Wilk, Breusch–Pagan with HC3 standard errors, Moran's I with spatial GLS (exponential), and a two-tailed permutation test (9,999 permutations). p_n, p-value of herbivore richness added to the model. [a] raw permutation p (pre-specified primary); [b] Benjamini–Hochberg-corrected (exploratory); [c] also significant after Holm; —, not applicable; n.s., not significant. Activity proportions sum to one.

	Facet/response	β	OLS p	HC3 p	GLS p	Perm p	p_n
Volume (n = 35)	Functional richness (FRic)	−0.016	0.12	0.25	0.23	—	—
	Functional divergence (FDiv)	−0.003	0.67	0.74	0.57	—	—
Composition (n = 56) *primary*	Seed depredation (CM)	+1.38	0.009	<0.001	0.009	0.015[a]	n.s. (0.96)
	Cathemeral proportion	−0.030	0.002	<0.001	0.002	0.019[b,c]	0.017
	Frugivory (CM)	+1.90	0.009	0.019	0.009	0.041[b]	0.038
Composition (n = 56) *exploratory*	Diurnal proportion	+0.030	0.015	0.015	0.094	0.041[b]	0.38
	Net seed effect (CM)	−0.86	0.23	0.42	0.23	0.31[b]	—
	Body mass (CM)	−0.024	—	—	—	0.23[b]	—
	Home range (CM)	−0.009	—	—	—	0.78[b]	—
	Nocturnal proportion	+0.001	—	—	—	0.93[b]	—

4.4 – Landscape configuration and continuity

Overall, landscape configuration and continuity were poor predictors of the guild's functional diversity. Of the 21 predictor–response combinations tested (seven landscape

variables × three facets; permutation tests with Benjamini–Hochberg (BH) correction; Table 5), only one (functional richness versus distance to roads) survived correction.

Table 5. Univariate relationships between seven landscape variables and three facets of functional diversity, ordered by raw permutation p-value within each facet. β, slope per unit of the predictor (for sector, western relative to eastern). p, two-tailed permutation (9,999 permutations); BH p, Benjamini–Hochberg-corrected over the 21-test family. NDVI excluded a priori (saturation). † Only relationship surviving BH correction.

Facet/predictor			
Seed depredation (CM) (n = 56)	**β**	**Perm p**	**BH p**
Land-use diversity (Shannon)	−6.6	0.006	0.067
Forest cover (%)	+0.15	0.010	0.067
Anthropogenic cover (%)	−0.17	0.013	0.067
Distance to road	$+4.7 \times 10^{-4}$	0.075	0.263
Distance to edge	-1.3×10^{-2}	0.164	0.382
Sector (west vs east)	−1.86	0.440	0.646
Distance to water	$+6.0 \times 10^{-4}$	0.580	0.716
Functional richness (FRic) (n = 35)	**β**	**Perm p**	**BH p**
Distance to road	-1.1×10^{-5}	0.001	0.027 †
Anthropogenic cover (%)	$+1.3 \times 10^{-3}$	0.288	0.550
Sector (west vs east)	+0.043	0.325	0.568
Distance to water	-1.5×10^{-5}	0.398	0.643
Land-use diversity (Shannon)	+0.030	0.462	0.646
Forest cover (%)	-6.6×10^{-4}	0.537	0.705
Distance to edge	$+5.9 \times 10^{-5}$	0.857	0.947
Functional divergence (FDiv) (n = 35)	**β**	**Perm p**	**BH p**
Distance to road	-4.5×10^{-6}	0.030	0.124
Sector (west vs east)	+0.041	0.091	0.272
Distance to water	-1.4×10^{-5}	0.164	0.382
Anthropogenic cover (%)	$+8.0 \times 10^{-4}$	0.260	0.545
Land-use diversity (Shannon)	$+9.1 \times 10^{-3}$	0.705	0.822
Forest cover (%)	-2.3×10^{-5}	0.971	0.985
Distance to edge	-2.3×10^{-6}	0.985	0.985

No landscape variable was robustly related to community-weighted seed depredation. Seed depredation tended to increase with forest cover (β = +0.15) and to decrease with anthropogenic cover (β = −0.17) and land-use diversity (β = −6.6), but none survived correction (BH-corrected p = 0.07); being strongly intercorrelated (|r| = 0.72–0.95), these describe a single forest-intactness gradient. The AICc comparison (Table 6) was consistent: the confidence set (ΔAICc < 2) comprised the canopy-only model and three models adding land-use diversity, anthropogenic cover or forest cover, but these improved only marginally on the canopy-only model (ΔAICc = 0.68; comparable Akaike weight, 0.17 vs 0.24). Model averaging over the confidence set confirmed the primacy of canopy height (variable importance = 0.98, versus ≤ 0.24 for the cover-based metrics); no landscape coefficient was individually significant in the averaged model, reflecting the shared variance between canopy height and the collinear intactness gradient. Beyond canopy height, therefore, seed depredation showed only a weak, non-decisive tendency to increase in more forested, less heterogeneous landscapes. Distance to water, distance to edges, and forest sector were unrelated to composition (BH-corrected p ≥ 0.38; not retained by AICc, ΔAICc > 2).

Table 6. Candidate models of community-weighted seed depredation (n = 56) selected *a priori*, each combining canopy height with a single landscape variable, compared with canopy-only and null models by AICc. Models within ΔAICc < 2 (above the line) form the confidence set; model averaging over this set gave a variable importance of 0.98 for canopy height and ≤ 0.24 for the landscape variables. df, degrees of freedom; w_i, Akaike weight. The three cover-based metrics were never entered together (collinearity, |r| = 0.72–0.95).

Model	df	logLik	AICc	ΔAICc	w_i
Canopy + land-use diversity	4	−191.13	391.0	0.00	0.24
Canopy + anthropogenic cover	4	−191.32	391.4	0.38	0.20
Canopy only	3	−192.63	391.7	0.68	0.17
Canopy + forest cover	4	−191.63	392.0	1.01	0.15
— confidence-set limit (ΔAICc < 2) —					
Canopy + distance to road	4	−192.49	393.8	2.73	0.06
Canopy + sector	4	−192.61	394.0	2.97	0.06
Canopy + distance to water	4	−192.62	394.0	2.98	0.05
Canopy + distance to edge	4	−192.63	394.0	3.01	0.05
Null (intercept only)	2	−196.16	396.5	5.51	0.02

The two forest sectors did not differ in seed depredation (Welch's $t = 0.74$, $p = 0.47$), forest cover ($t = -1.21$, $p = 0.24$), or edge distance ($t = 0.54$, $p = 0.59$), differing only marginally in canopy height ($t = 1.98$, $p = 0.055$). Variance partitioning confirmed that canopy height uniquely explained the composition (unique adjusted $R^2 = 9.3\%$; partial RDA $F = 6.50$, $p = 0.018$), whereas sector contributed nothing independently (unique adjusted $R^2 \approx 0$; $F = 0.04$, $p = 0.85$), even when distance to roads was additionally held constant ($F < 0.01$, $p = 0.95$).

Functional divergence was unrelated to any landscape variable. Functional richness increased toward roads ($\beta = -1.1 \times 10^{-5}$ per meter; HC3 and GLS $p = 0.001$) — the only relationship surviving correction (BH-corrected $p = 0.03$). This effect was independent of canopy height ($p = 0.005$), sampling effort ($p = 0.002$), forest sector ($p = 0.002$), and sampling season ($p = 0.005$; Table 7), and distance to roads was uncorrelated with forest, anthropogenic, or land-use-diversity cover ($|r| \leq 0.18$). It most likely reflects both the higher detectability of road- and trail-using species and the contribution of open-habitat-adapted species near roads, and the detection component cannot be excluded by the covariates tested.

Table 7. Functional richness increased toward roads across all specifications (n = 35), persisting under HC3 standard errors, spatial GLS (Moran's I of OLS residuals p = 0.73), and controls for canopy height, sampling effort, forest sector, and sampling season. Sampling effort was itself a positive covariate (p = 0.03).

Model	β (distance to road)	p (road)	Covariate p
OLS / HC3 / Spatial GLS	-1.10×10^{-5}	0.001	—
+ canopy height	-1.08×10^{-5}	0.005	canopy = 0.89
+ sampling effort	-1.02×10^{-5}	0.002	effort = 0.03
+ forest sector	-1.24×10^{-5}	0.002	sector = 0.48
+ sampling season (+ richness + effort)	-8.3×10^{-6}	0.005	season n.s.; richness = 0.0005

Overall, the surrounding landscape did not structure the functional composition of the guild — which was modestly explained by internal forest structure (canopy height), with only a weak, non-decisive forest-intactness signal — nor did forest sector add explanatory

power; the single robust landscape effect acted on functional volume (richness) and is most parsimoniously attributed to road-associated detectability and open-habitat species.

4.5 – Sensitivity analyses

The compositional effects were robust to taxonomic richness: adding herbivore richness as a covariate left the canopy–depredation relationship significant ($p = 0.013$), with richness itself contributing nothing ($p = 0.96$). Functional richness and divergence differed with sampling season (type-II ANOVA; FRic $F = 7.17$, $p = 0.003$; FDiv $F = 3.41$, $p = 0.046$; See Supplementary Material); for functional richness, however, this seasonal signal was confounded with distance to roads — once road distance was included, the seasonal term became non-significant ($p \geq 0.24$) while road distance remained significant ($p = 0.005$). Functional divergence retained a marginal seasonal effect ($p = 0.046$). Thus, the volume indices carried a weak seasonal signal that, for functional richness, was largely subsumed by distance to roads.

4.6 - Functional prioritization of threatened species

Among the nine herbivores, four were classified as threatened at the state level and therefore received a non-zero FUSE value. *Tapirus terrestris* showed the highest FUSE (1.060), combining high functional uniqueness and specialization with its Critically Endangered state status, followed by *Dasyprocta leporina* (0.551), *Tayassu pecari* (0.417) and *Dicotyles tajacu* (0.166) (Figure 4; Table 8). *Dasyprocta leporina* ranked second, reflecting its high functional uniqueness (FUn = 0.83), making it the most functionally distinct of the threatened species—combined with its Vulnerable status. The remaining five herbivores were Least Concern at the state level (GE = 0) and therefore received a FUSE of zero; these included *Sylvilagus brasiliensis*, the most functionally unique and specialized species of the entire guild (FUn = FSp = 1.00), which nonetheless contributed nothing under the state-weighted index because it is unlisted at the regional threat scale.

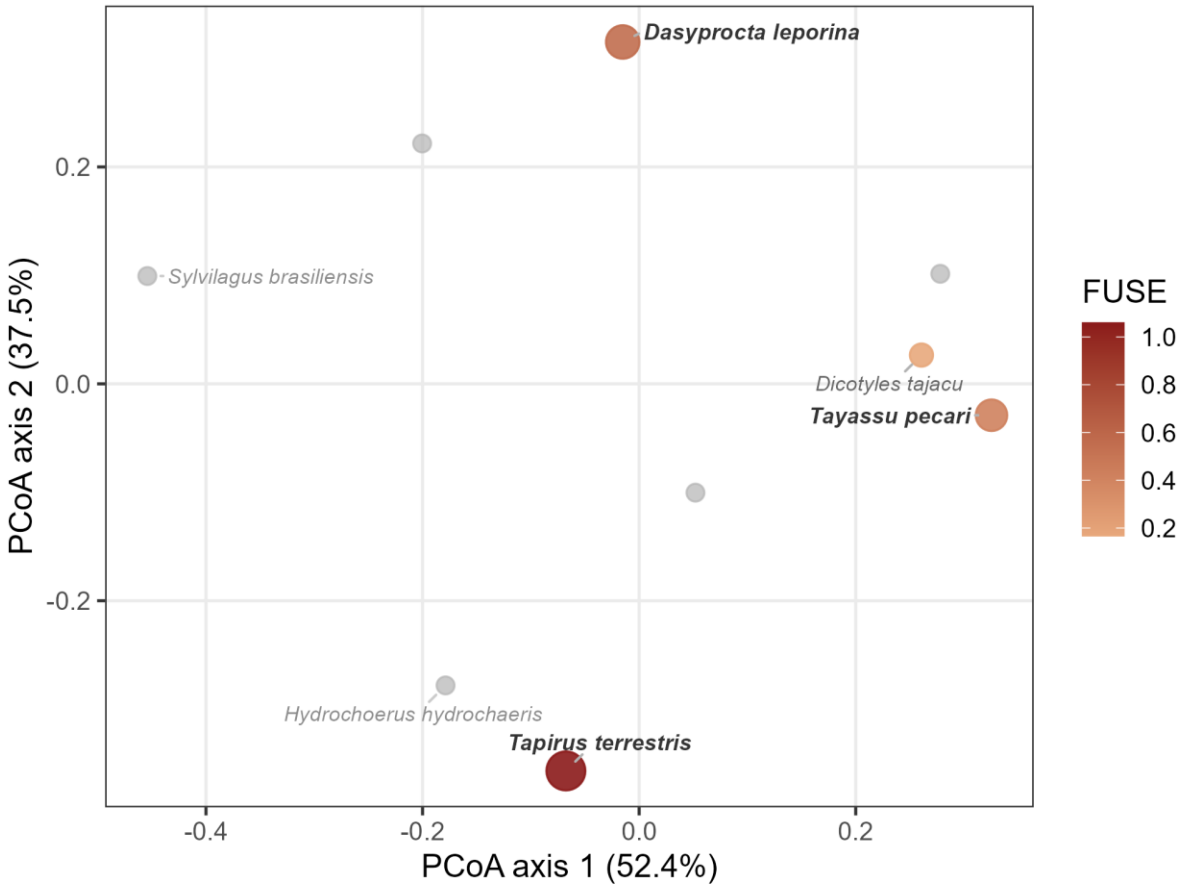

Figure 3. Functional space of the nine medium- and large-sized herbivore species of the Linhares–Sooretama Forest Complex, defined by the first two axes of a three-dimensional PCoA (52.4% and 37.5% of functional variation; see Methods). Each point is a species. The four species threatened at the state level (FUSE > 0) are colored and sized by FUSE value (darker and larger = higher priority); the remaining five species (FUSE = 0) are shown in grey. The three highest-scoring species are labeled in bold italics; *Dicotyles tajacu* — threatened but functionally redundant (functional uniqueness ≈ 0) — and two peripheral, non-priority species (*Sylvilagus brasiliensis*, *Hydrochoerus hydrochaeris*) are labeled in grey italics for reference.

Table 8. Species ranked by FUSE value among the herbivores registered in the Linhares-Sooretama Forest Complex. Threat categories are shown for the assessments consulted (IUCN Red List; national list, MMA Ordinance 148/2022; Espírito Santo state list, IEMA Decree 5.237-R/2022), and FUSE was computed from the state-level status. FUSE sums two functional components (uniqueness and specialization), each rescaled to 0–1, after multiplying each by

normalized threat status and applying a log-transformation. Higher values indicate greater importance for conservation prioritization at the local scale.

Species	IUCN	National (BRA)	State (ES)	FUn (uniqueness)	FSp (specialization)	FUSE
Tapirus terrestris	VU	VU	**CR**	0.746	0.653	1.060
Dasyprocta leporina	LC	LC	**VU**	0.832	0.450	0.551
Tayassu pecari	VU	VU	**EN**	0.160	0.474	0.417
Dicotyles tajacu	LC	LC	**EN**	0.000	0.241	0.166

5. DISCUSSION

Our main result is that within the LSFC, forest cells with greater canopy height tend to support a higher community-weighted level of seed predation across the herbivore guild. Canopy height was by far the most important variable in the model (variable importance = 0.98), and the only other models that were competitive with it included collinear forest-intactness descriptors, which only marginally improved upon the canopy-only model. Its influence was modest in absolute terms, since canopy height explained roughly a tenth of the variation in community-weighted seed predation (adjusted $R^2 \approx 0.10$), so the effect, though statistically robust and consistent, is one of several largely unmeasured influences on the guild's composition. We interpret this as reflecting greater resource availability and habitat integrity in the taller forests, which may be better able to support species with high ecological requirements (Sampaio et al., 2010; Altrichter et al., 2012; Rios et al., 2022). The relationship was independent of species richness ($p = 0.96$), so it appears that the functional composition of the guild tracks local habitat structure. Community-weighted frugivory also increased along with the same gradient. As both seed dispersal and seed predation increased together, the net dispersal-predation balance did not shift, and so the overall level of seed-related interactions simply increased with canopy height.

Importantly, this pattern emerged within a large, continuous, protected forest block, where habitat amount and configuration vary little across cells. With landscape-level variation largely removed, internal structural quality (indexed by canopy height) becomes the

operative gradient on functional composition, one that landscape-level assessments are not designed to capture. In this sense, canopy height acts as an internal “keystone structure” (Tews et al., 2004), associated with shifts in the assemblage’s dominant roles independently of how much habitat is available or how it is arranged — though, as noted above, its quantitative effect on composition was modest. Such internal attributes need not act alone: in structurally complex Atlantic Forest, the composition of the woody-plant community has been found to explain small-mammal composition even more than vegetation structure itself (Skupien et al., 2025), indicating that several internal drivers can operate within a single continuous forest block.

Canopy height had no effect on the volume of functional space occupied by the assemblages. Functional richness was driven by species richness and sampling effort rather than habitat structure (Villéger et al., 2008; Mouchet et al., 2010) and therefore did not reflect shifts in composition. Functional divergence was also uncorrelated with canopy height or any of the landscape variables. The only exception to this was a seasonal signal in functional richness, which disappeared when distance to roads was incorporated into the model. Distance to roads remained significant while the seasonal term was no longer significant, suggesting that the seasonal signal we observed was simply a road-related gradient (probably a detection gradient) rather than a real seasonal effect. Functional divergence showed only a very weak seasonal signal. Overall, these results indicate that, in this system, it is functional composition that responds to internal habitat structure (Mouillot et al., 2013).

This finding complements a well-established branch of work. In fragmented Atlantic Forest landscapes, the functional diversity of terrestrial vertebrates is primarily shaped by broad environmental and landscape variables, such as climatic gradients and human footprint (Pedroso-Santos et al., 2024), fragment size (Magioli et al., 2015; Fornitano et al., 2024), and landscape configuration (Bonfim et al., 2021; Rios et al., 2022) — and human occupation structures mammal functional composition even at the biome scale (Bogoni et al., 2016). Our result is consistent (at a finer scale) with the literature, which has shown that vegetation structural complexity influences the distribution and composition of mammals in forested systems, largely via its association with resource

availability. This has been demonstrated at the micro-scale by Püttker et al. (2008) in the Atlantic Forest, by Sukma et al. (2019) in Australian eucalypts and dry forests, and by Cudney-Valenzuela et al. (2023) in the Lacandón Rainforest, Mexico. Of the landscape descriptors, community-weighted seed predation showed only a very weak and non-significant trend to decrease with land-use heterogeneity and to increase with forest cover; none of these trends were significant after correction for multiple testing, and given the high degree of intercorrelation between them ($|r| = 0.72$ to 0.95), they represent a single, redundant gradient of forest intactness rather than distinct effects. More broadly, because landscape-scale features (cover, heterogeneity, configuration) are relatively constant or redundant within this continuous, protected block, internal structural complexity (in this case, canopy height) becomes the operative filter on functional composition, complementing landscape-scale assessments and identifying structural quality as a conservation target within protected forest blocks.

Our study identifies a robust association between canopy height and the functional composition of the herbivore guild but does not directly test the underlying mechanism. Canopy height integrates both habitat structural configuration and the food resources associated with it. Taller, closed-canopy stands are characteristic of mature interior forest, whereas canopy height is the attribute most degraded at forest edges, accompanied by reductions in aboveground biomass and carbon stocks (Magnago et al., 2014, 2015, 2017). This structural degradation extends beyond physical change: in the same Atlantic Forest region, Magnago et al. (2014) showed that forest edges lose large-fruited tree species, which are replaced by early-successional, small-seeded species, even though overall functional richness remains unchanged. Such a shift in the seed resource base provides a plausible pathway for our result: the large, hard seeds characteristic of mature, tall-canopy forest favor the herbivores that exploit them, intensifying community-weighted seed predation and, in parallel, dispersal in taller stands. We propose, rather than demonstrate, that structural quality operates through resource availability, a mechanistic pathway that remains a hypothesis to be tested with direct measurements of food resources. This functional reorganization may also have consequences for functional redundancy and ecosystem resilience (Magnago et al., 2014). Canopy height should therefore be considered not only a physical attribute but also a proxy for the resources

that sustain the herbivore guild, being most directly linked to the fruits and seeds produced by mature-forest trees.

Forest sector (used here as a proxy for landscape continuity and protection history) did not, in fact, have any independent influence on the guild's functional composition. There was no difference between the two sectors in community-weighted seed predation (Welch's $t = 0.74$, $p = 0.47$), and variance partitioning attributed essentially zero unique explanatory power to sector once canopy height was taken into account (unique adjusted $R^2 \approx 0$; $F = 0.04$, $p = 0.85$). Canopy height was, however, marginally higher in the eastern sector ($t = 1.98$, $p = 0.055$), so that structural quality and protection history are partly confounded. The eastern sector contains the Vale Natural Reserve, whose differential surveillance may have buffered large herbivores against the higher rates of poaching presence historically recorded in the Sooretama Biological Reserve (Chiarello, 1999, 2000; Sousa & Srbek-Araujo, 2017; Fontes et al., 2020) and, in doing so, helped preserve its tall-canopy forest. The operative predictor, nonetheless, is canopy structure itself, not sector. Seen this way, canopy structure is a conservation legacy: Atlantic Forest stands take more than two and a half decades to acquire old-growth structural features (Zanini et al., 2014), and the recovery of mature-forest species composition can require a century or more (Liebsch et al., 2008; Rozendaal et al., 2019), so maintaining and restoring tall, mature forest is a long-term commitment (Cardoso et al., 2022). Sector thus remains a spatial proxy in which protection, structure, and configuration cannot be disentangled.

Beyond this compositional filtering, each species embodies a functional distinctiveness that its apparent redundancy can conceal — fine-scale niche differentiation of the sort described by Srbek-Araujo and Kierulff (2016) for the Vale Natural Reserve mammals. The FUSE index captures precisely this distinctiveness, allowing conservation priorities to reflect not only how threatened a species is but how functionally irreplaceable it would be if lost. Under our state-scale adaptation, Tapirus terrestris emerged as the highest-priority herbivore, combining high functional uniqueness and specialization with its Critically Endangered status in Espírito Santo. The red-rumped agouti (Dasyprocta leporina) ranked second — a result driven less by threat than by functional distinctiveness: as a small-bodied, scatter-hoarding frugivore, it occupies a functionally

unique position within the guild, and its Vulnerable status is sufficient to place it above the two threatened peccaries. As this guild is strongly tied to canopy structure, conserving tall, structurally mature forests is the best way of protecting the habitat of the highest-priority species (Sukma et al. 2019; Cudney-Valenzuela et al. 2023).

At a regional scale, this application of FUSE provides a practical tool for managers and research groups to allocate conservation effort more efficiently. Among the prioritized species, Tayassu pecari illustrates its value: the white-lipped peccary has undergone major range-wide declines and is especially reduced in the Atlantic Forest (Altrichter et al., 2012; Jorge et al., 2013; Maciel et al., 2019), and within the LSFC its distribution is restricted (unpublished data: Projeto Felinos, Instituto Pró-Tapir, and others). As a wide-ranging ecosystem engineer, it depends on large, continuous, well-preserved forest, and Oshima (2019) showed that its habitat selection favors high tree cover, large forest areas, and fragment interiors while avoiding roads and densely populated areas — a selectivity for habitat quality consistent with the structural dependence we highlight. Because large herbivores rank among the most defaunated functional groups (Bogoni et al., 2018), safeguarding high-quality forest is critical; equally, forests that have not yet attained such structure remain essential, since their protection and restoration would, over time, develop the structural quality — including the large-fruited tree communities (Magnago et al., 2014) — that underpins the resource base we associate with the guild's composition (Banbury Morgan & Jucker, 2025). Conservation strategies should therefore safeguard both existing high-quality continuous forests (Rovero et al., 2020) and the successional and restoration pathways that lead to them, accounting for land-use history and landscape forest cover (Rozendaal et al., 2019; Hordijk et al., 2024).

The canopy–composition relationship was robust across all the validation methods (heteroscedasticity- consistent standard errors, spatial GLS, permutation tests, control for herbivore richness and a range of minimum effort thresholds (Table 4; Table S6)), though there are several caveats which limit the interpretation of the results. Although consistent, the effect was small in magnitude: canopy height accounted for only around 10% of the variation in community-weighted seed predation, with the vast majority of variation unexplained. The functional metrics were based on species occurrence rather than

abundance or occupancy, so the community-weighted means are unweighted and vulnerable to detection bias (Burton et al. 2015). The sample size was also fairly small (56 cells for composition, 35 for volume), which limited the power of the secondary indices; these were considered exploratory and, despite correction for multiple comparisons (Benjamini–Hochberg and Holm), the weak associations should be interpreted with caution. The trait values were drawn from a published compilation (Magioli et al. 2021) with the exception of *Passalites nemorivagus,* which was supplemented with primary dietary studies, so there is a degree of trait uncertainty which is then carried through into the composition indices. The volume facets were also measured over a narrower range of canopy than the composition facets, as functional richness requires cells with at least four co-occurring species; the invariance of volume should therefore be interpreted within that narrow range. The study is observational and correlational and so only identifies the structural attributes which co-vary with herbivore composition and does not establish causation nor rule out the presence of unmeasured variables which may be correlated with canopy height. Experimental or longitudinal work, and direct measurement of food resources, would be required to confirm the proposed mechanism. The sampling design may also have limited our ability to detect other guilds (e.g., the rare felids), and so the functional assessment may be somewhat incomplete.

6. CONCLUSIONS

Of the three hypotheses tested, only one was supported. H1 was not supported: functional richness and divergence did not increase with canopy structure. The volume and internal spread of the guild's functional space did not vary with canopy height. H2 was supported: functional composition did vary with canopy structure. The canopy acted as a filter on the community-weighted composition of seed-related plant-animal interactions, resulting in a higher community-weighted level of seed predation and a shift in the assemblage toward diurnal herbivores. The net dispersal-predation balance and the volume facets were unchanged. H3 was not supported: landscape configuration and environmental context were poor predictors of the guild's functional diversity. Neither forest cover, anthropogenic cover, landscape heterogeneity, distance to water or to edge,

nor forest sector were robust predictors of composition. The only landscape relationship to survive correction (a rise in functional richness towards roads) is in the opposite direction to what was predicted and is most parsimoniously explained by the effects of road-associated detectability and open habitat species rather than by any effect of habitat quality. Within this large, continuous forest block, it was therefore the internal structure of the forest that restructured the functional composition, and this did so without any change in functional volume.

Our state-scale adaptation of the FUSE index identified the lowland tapir as the herbivore of highest regional conservation priority, the red-rumped agouti (which is functionally critical even though it is at a lower threat level) and the two peccaries as the next most important, demonstrating that functional importance and threat level don't always align. For the Linhares-Sooretama Forest Complex (one of the largest remaining blocks of mature Atlantic Forest and a key area for large mammal conservation), this has very clear implications: conserving tall, structurally mature forest is the way to ensure the persistence of the herbivore guild and the particular assemblage of plant-animal interactions it performs. More generally, it shows that the functional composition is a very sensitive indicator of how internal habitat quality structures ecological function within large forest remnants and that threat-weighted functional metrics at a regional scale can be used to prioritize the species whose functional roles are most at risk.

The observed functional differences in assemblage composition, which only become apparent when trait identity and local-scale data are considered, can be valuable tools for conservation planning at finer scales, since many medium- to large-bodied Atlantic Forest mammals and their natural habitats are highly threatened.

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SUPPLEMENTARY MATERIAL

This file provides additional data, analyses, and methodological details supporting the results reported in the main text. It is organized into five sections: (1) sampling effort and recorded species, including a sample-based rarefaction/extrapolation curve and the full species list; (2) functional traits of the herbivore guild; (3) FUSE scores for all nine species; (4) sensitivity analyses assessing the robustness of the main result, including screening for sampling-effort dependence; and (5) notes on reproducibility and tool use. All analyses were based on reproducible scripts and derived directly from the underlying data.

1. Sampling and recorded species

Table S1. Sampling effort by campaign and sector at the LSFC.

Campaign	Period	Number of stations	Camera-nights	Seasonality
2016	Feb–Apr	21	766	Rainy
2017/01	Jan–Mar	41	1,769	Rainy
2017/02	Aug–Dec	32	3,082	Dry/transition

Table S2. Medium- and large-sized mammal species recorded in the Linhares-Sooretama Forest Complex between 2016 and 2017. No. of cells = number of 4 km² cells with at least one record; IRs = independent records.

Order	Species	Common name	No. of cells	IRs	East cells	West cells
DIDELPHIMORPHIA	*Didelphis aurita*	black-eared opossum	17	61	13	4
CINGULATA	*Euphractus sexcinctus*	six-banded armadillo	4	4	2	2
	Cabassous tatouay	naked-tailed armadillo	8	9	7	1
	Dasypus novemcinctus	nine-banded armadillo	27	221	20	7
PILOSA	*Tamandua tetradactyla*	collared anteater	18	41	13	5
LAGOMORPHA	*Sylvilagus brasiliensis*	common tapeti	2	56	1	1
PRIMATES	*Sapajus robustus*	crested capuchin	6	17	3	3
RODENTIA	*Hydrochoerus hydrochaeris*	capybara	2	3	1	1
	Dasyprocta leporina	red-rumped agouti	39	844	30	9
	Coendou insidiosus	prehensile-tailed porcupine	1	1	1	0
	Cuniculus paca	paca	36	350	25	11
CARNIVORA	*Eira barbara*	tayra	22	71	14	8
	Nasua nasua	coati	49	501	33	16
	Procyon cancrivorus	crab-eating raccoon	11	22	6	5
	Cerdocyon thous	crab-eating fox	9	103	6	3
	Herpailurus yagouaroundi	jaguarundi	6	6	4	2
	Leopardus guttulus	little spotted cat	1	1	0	1
	Leopardus pardalis	ocelot	12	21	10	2
ARTIODACTYLA	*Passalites nemorivagus*	Amazonian brown brocket	51	601	34	17
	Subulo gouazoubira	gray brocket deer	1	3	1	0
	Dicotyles tajacu	collared peccary	36	889	34	2
	Tayassu pecari	white-lipped peccary	7	154	7	0
PERISSODACTYLA	*Tapirus terrestris*	lowland tapir	48	360	35	13

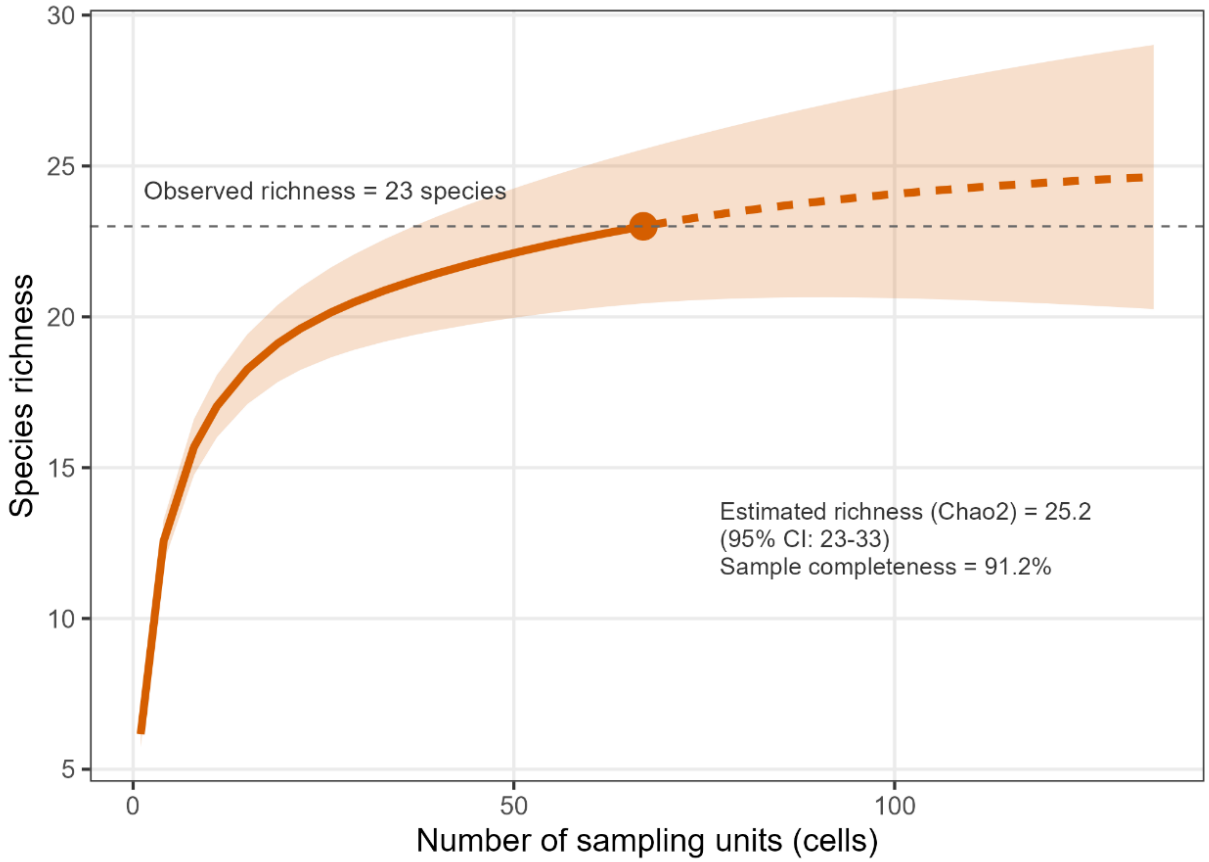

Figure S1. Sample-based rarefaction (solid line) and extrapolation (dashed line) curve of species richness for medium- and large-sized mammals in the Linhares-Sooretama Forest Complex, based on species incidence across 67 sampling cells (4 km²). The point marks the observed richness (23 species); the shaded area represents the 95% confidence interval (200 bootstrap replicates). Extrapolation was projected to twice the reference sample size. Observed richness corresponded to 91% of the estimated asymptotic richness (Chao2 = 25.2; 95% CI: 23–35), indicating high sampling completeness.

2. Functional Traits, FRic and FDiv

Table S3. Functional traits of the nine medium- and large-sized herbivore species used to construct the functional space of the Linhares–Sooretama Forest Complex. Body mass (g) follows EltonTraits (Wilman et al. 2014) and Paglia et al. (2012); home range (ha) was compiled from Broekman et al. 2023; activity pattern and dispersal role were classified based on specific sources and criteria (see Methods); and the diet components — folivory (browsing, grazing) and frugivory, the latter split into seed dispersal and seed depredation of small-seeded ([a]) and large-seeded ([b]) plants — each shown as mean and standard deviation (SD), following Magioli et al. (2021). From these components, we derived the traits used in the analyses as follows: frugivory = seed dispersal + seed depredation; net seed effect = seed dispersal − seed depredation; and seed depredation (the primary compositional response) = seed depredation. NA, standard deviation not available.

Species	Body mass (g)	Activity pattern	Home range (ha)	Folivory				Frugivory (seed interaction)							
				Browsing		Grazing		Seed dispersal				Seed depredation			
				Mean	SD	Mean	SD	Small-seeded [a]	SD	Large-seeded [b]	SD	Small-seeded [a]	SD	Large-seeded [b]	SD
Cuniculus paca	9.300	Nocturnal	10	6,5	8,4	0,0	0,0	2,3	0,2	44,6	3,3	2,3	0,2	44,6	3,3
Dasyprocta leporina	3.200	Diurnal	4	4,9	4,4	0,0	0,0	2,7	0,3	51,3	5,2	1,8	0,2	34,2	3,5
Dicotyles tajacu	22.000	Diurnal	200	25,0	6,2	0,0	0,0	1,9	0,174	1,4	0,1	36,2	3,3	26,2	2,4
Hydrochoerus hydrochaeris	50.000	Cathemeral	100	0,0	0,0	100,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
Passalites nemorivagus	15.000	Diurnal	150	21,3	12,4	0,0	0,0	4,7	NA	0,0	0,0	42,0	NA	31,0	NA
Subulo gouazoubira	21.000	Diurnal	300	85,5	5,5	3,2	4,1	0,4	0,2	0,3	0,1	6,1	2,6	4,5	1,9
Sylvilagus brasiliensis	1.200	Nocturnal	2	40,0	0,0	60,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
Tapirus terrestris	260.000	Cathemeral	470	72,4	16,5	0,0	0,0	7,1	4,2	4,2	2,5	10,3	6,1	6,0	3,6
Tayassu pecari	32.000	Diurnal	2.000	29,1	14,6	0,0	0,0	1,9	0,3	1,3	0,2	35,0	6,0	25,3	4,3

[a] Small-seeded plants; [b] large-seeded plants. SD, standard deviation; NA, not available.

Values for the folivory (browsing, grazing) and frugivory (seed dispersal and depredation) components follow Magioli et al. (2021); see that source for the definition of each item.

Analysis-level traits were derived from these components: frugivory = seed dispersal + seed depredation; net seed effect = dispersal − depredation; seed depredation (primary) = depredation.

Body mass, home range and activity pattern: see Methods for sources.

3. FUSE

Table S4. FUSE values for the nine medium- and large-sized herbivore species recorded in the Linhares–Sooretama Forest Complex, ordered by conservation priority. FUSE (Functionally Unique, Specialized and Endangered; Pimiento et al. 2020) combines functional uniqueness and functional specialization, each rescaled to 0–1 and weighted by threat status (log-transformed and summed). Here, threat status was assigned from the Espírito Santo state list (IEMA Decree 5.237-R/2022) rather than the global IUCN status, to reflect regional conservation priorities. Threat categories from all three assessments consulted are shown for context (IUCN Red List; national list, MMA Ordinance 148/2022; state list, IEMA Decree 5.237-R/2022). Species classified as Least Concern at the state level score zero. Higher values indicate greater conservation priority at the regional scale.

Species	IUCN	National (BRA)	State (ES)	FUn (uniqueness)	FSp (specialization)	FUSE
Tapirus terrestris	VU	VU	**CR**	0.746	0.652	1.060
Dasyprocta leporina	LC	LC	**VU**	0.832	0.450	0.550
Tayassu pecari	VU	VU	**EN**	0.159	0.474	0.417
Dicotyles tajacu	LC	LC	**EN**	0.000	0.241	0.166
Cuniculus paca	LC	LC	**LC**	0.840	0.545	0.000
Hydrochoerus hydrochaeris	LC	LC	**LC**	0.622	0.488	0.000
Passalites nemorivagus	LC	LC	**LC**	0.157	0.369	0.000
Subulo gouazoubira	LC	LC	**LC**	0.000	0.512	0.000
Sylvilagus brasiliensis	EN	LC	**LC**	1.000	1.000	0.000

4. Sensitivity analyses

Table S5. Type-II ANOVA of functional richness (FRic) and functional divergence (FDiv) against sampling season, herbivore richness and sampling effort (n = 35 cells; seasons: rainy, mixed, dry).

Response/term	df	F	p
FRic			
Sampling season	2	7.17	0.003
Herbivore richness	1	10.61	0.003
Sampling effort	1	0.63	0.43
FDiv			
Sampling season	2	3.41	0.046
Herbivore richness	1	0.20	0.66
Sampling effort	1	0.15	0.70

Table S6. Robustness of the functional metrics to variation in sampling effort. Because per-cell species richness was effort-dependent (Figure 2), the functional metrics used in the main analyses were screened for effort sensitivity. (a) Spearman correlations between each functional metric and per-cell sampling effort (camera-nights). (b) The canopy–seed-depredation relationship (community-weighted seed depredation ~ canopy height) refitted under increasing minimum-effort thresholds (excluding progressively less-intensively sampled cells) and, in the last row, after excluding the most intensively sampled cells (upper decile). (c) Leave-one-species-out analysis: community-weighted seed depredation recomputed with each species removed in turn and refitted against canopy height, to confirm that no single species drove the effect. β, OLS slope; R^2adj, adjusted R^2. The primary effect remained significant throughout.

(a) Metric × sampling effort (Spearman)

Metric	ρ	p	n
Seed depredation (CM) — primary	−0.056	0.684	56
Functional richness (FRic)	+0.524	0.001	35
Functional divergence (FDiv)	−0.065	0.710	35
Species richness (assemblage)	+0.78	<0.001	67

(b) Seed depredation ~ canopy height under effort thresholds

Subset	Min. effort (camera-nights)	n	β	p	R^2adj
≥ P0 (all cells)	17	56	1.38	0.009	0.102
≥ P10	45	51	1.43	0.008	0.116
≥ P20	47	46	1.18	0.024	0.091
≥ P30	48	40	1.22	0.039	0.084
≥ P40	61	34	1.22	0.042	0.096
≤ P90 (excl. top 10%) —		50	1.45	0.010	0.111

(c) Leave-one-species-out (seed depredation ~ canopy height)

Species removed	n	β	p	R^2adj
Passalites nemorivagus	47	1.90	0.003	0.166
Subulo gouazoubira	55	1.32	0.003	0.139
Dasyprocta leporina	55	1.73	0.005	0.124
Cuniculus paca	53	1.46	0.008	0.112
Tapirus terrestris	49	1.19	0.009	0.119
Sylvilagus brasiliensis	56	1.34	0.009	0.102
Tayassu pecari	56	1.34	0.011	0.098
Hydrochoerus hydrochaeris	55	1.49	0.018	0.083
Dicotyles tajacu	54	1.01	0.056	0.050
Full model (all nine species)	**56**	**1.38**	**0.009**	**0.102**

5. Notes for publication

During the preparation of this work, the authors used Claude (Anthropic) in order to assist with the organization and structuring of manuscript sections and with the creation and review of analytical scripts. After using this tool, the authors reviewed and edited the content as needed and took full responsibility for the content of the published article.

Statistical analyses were implemented in R (R Core Team, 2026). Analytical scripts (*a priori* model selection by AICc, sensitivity analyses, variance partitioning, spatial GLS, and functional diversity components) were developed with the assistance of Claude (Anthropic, 2026). All analyses were based on reproducible, author-verified scripts, and all results were derived directly from the underlying data. The author reviewed, verified, and validated all outputs.