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Generalist With a Narrow Niche Breadth: Feeding Ecology and Seed Germination Effectiveness of a Large Canid Within a Silvicultural Matrix

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ABSTRACT

Understanding the feeding ecology of key carnivores is essential to unravel their ecological roles and inform effective conservation strategies, especially in human-modified landscapes. In this study, we investigated the feeding ecology of the maned wolf (*Chrysocyon brachyurus*) and its gut passage effects on seed germination in small Cerrado fragments surrounded by silviculture in Brazil. We collected and analysed 84 scats and reviewed the literature to compare the niche breadth and food item richness with other studies. We also conducted germination trials using wolf's fruit (*Solanum lycocarpum*) seeds retrieved from scats and from ripe fruits. We identified 27 food items, with a strong predominance of wolf's fruits, birds, small mammals, Poaceae, and Hymenoptera species. Animal items were more frequent in the dry season, and native plant items in the rainy season. The maned wolf in our study area exhibited a narrow niche breadth (0.122), indicating low evenness in resource use and a diet structured around a few dominant items. Across 21 reviewed studies (24 sites), niche breadth ranged from 0.09 to 0.57 (mean = 0.37), with high variation in the number of consumed items (11–77, mean = 40.96), reinforcing that uneven resource use is common across populations. Seeds from scats showed significantly higher germination rates (52%) than those from ripe fruits (2%). Our findings support the classification of the maned wolf as an opportunistic generalist, whose diet is consistently structured around a subset of key resources rather than evenly distributed across all available items. Conservation strategies within silvicultural matrices should prioritise the preservation and restoration of open Cerrado fragments and the implementation of wildlife-friendly forestry practices, such as maintaining habitat corridors and reducing pesticide use, to secure essential prey populations, native food resources, and the wolf's vital function as a seed disperser.

1 | Introduction

Approximately 27% of mammal species are currently at risk of extinction (IUCN 2025), primarily due to agriculture expansion, logging, hunting, linear infrastructure development, invasive species, pollution, and climate change (Newbold et al. 2015; Ripple et al. 2016; Grilo et al. 2021; Harfoot et al. 2021). Although

most of this biodiversity is safeguarded in protected areas, they cover only 16.51% of the planet's surface (UNEP-WCMC 2025). Furthermore, 70% of the world's forests lie within 1 km of the forest edge, making them highly susceptible to the negative impacts of fragmentation (Haddad et al. 2015). In this context, preserved areas within human-modified landscapes, such as silviculture, pastures, and croplands, are crucial for biodiversity

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conservation, as they facilitate wildlife movement, increase connectivity between forest fragments, and thereby reduce population isolation while increasing matrix permeability (Metzger et al. 2019).

Similar to other Southern hemisphere savannas, such as those in Australia and Southern Africa, the Brazilian Cerrado has been increasingly replaced by intensive production systems, including silviculture matrices. In the Cerrado domain, the silvicultural matrix has expanded dramatically, registering a growth of 446% between 1985 and 2024, while native formations suffered a contraction of 28.5% during the same period (MapBioma 2025). This rapid expansion drives the conversion of vast areas of natural, semi-natural, or productive land into monospecific plantations (Brockhoff et al. 2008), a process associated with the loss of rare native and specialist species of medium and large-sized mammals (Cravino and Brazeiro 2021), small mammals (Čepelka and Dokulilová 2025), birds (Wolswijk et al. 2025), reptiles and amphibians (Cordier et al. 2021).

This rapid conversion not only threatens species persistence but can also alter the fundamental ecological interactions that sustain these ecosystems. Specifically, we still know little about how these landscapes influence mammals' feeding ecology and functional roles (Motta-Junior et al. 2014; Azevedo et al. 2025), as these environments can significantly alter prey availability, plant diversity, and habitat structure (Foley et al. 2005; Newbold et al. 2015; Metz et al. 2024). Also poorly understood is the extent to which these animals can continue performing ecological functions such as seed dispersal or top-down regulation (Triay-Limonta et al. 2024).

The ecological impact of human-modified landscapes can be reflected in shifts in dietary niche breadth. For instance, both the crab-eating fox (*Cerdocyon thous*) and the Pampas fox (*Lycalopex gymnocercus*) have a larger niche breadth outside protected areas (Metz et al. 2024). This shift can be interpreted through the lens of the Optimal Foraging Theory, which states that diet should reflect a strategy to maximize net energy intake, potentially leading to a more specialized niche in environments where high-quality resources are predictable, or search costs for alternative items are high (MacArthur and Pianka 1966; Krebs 2014). Thus, in human-modified landscapes such as silviculture matrices, resource distribution becomes simplified, driving two divergent foraging strategies: (1) niche contraction, where predators specialize on abundant and accessible resources to offset the elevated search costs associated with dense, exotic stands; or (2) niche expansion, characterized by opportunistic generalism, where a scarcity of high-quality prey compels individuals to consume a broader range of low-profitability items.

In a seasonal environment like Cerrado, resource availability is strictly linked to rainfall patterns, consequently influencing niche breadth. While the rainy season typically promotes a peak in fruit production for many native species, the dry season is often characterized by a decrease in plant biomass, which may increase the relative importance of animal prey to fulfill species' energetic requirements (Oliveira and Marquis 2002; Motta-Junior et al. 2014).

A key species for understanding these shifting dynamics is the maned wolf (*Chrysocyon brachyurus*), the largest native canid in South America (Dietz 1985; Cheida et al. 2011), inhabiting Cerrado domain and Pampas (Queirolo et al. 2011). Globally, it is classified as Near Threatened to extinction (Paula and DeMatteo 2015), but in Brazil, the species is considered Vulnerable to Extinction (Ministério do Meio Ambiente 2022). The main threats to population survival include habitat loss and fragmentation, roadkill, retaliatory killings due to presumed predation of domestic fowl, and disease transmission from domestic dogs (de Paula et al. 2013; Paula and DeMatteo 2015). Although the species occur along human-modified landscapes and may be tolerant to some degree of anthropization, they do not occupy them at the same intensity as natural habitats (de Paula et al. 2013). Since maned wolf's range is under high anthropogenic pressures, every potential population is important for the species conservation and should be monitored (Rodríguez-Castro et al. 2022). Especially considering that projections estimate that mammals and birds species pool will shift in the next 100 years to small, fast-lived, highly fecund, insect-eating, generalists (Cooke et al. 2019). Then, understanding the persistence of large-bodied, wide-ranging species like the maned wolf in production landscapes is critical.

The maned wolf is traditionally considered omnivorous, generalist, and opportunistic. It feeds on a wide variety of small vertebrates, such as rodents, marsupials, armadillos, birds, reptiles, and arthropods, as well as plants, especially fruits (Dietz 1984; Motta-Junior et al. 1996; Jácomo et al. 2004; Motta-Junior 2000; Aragona and Setz 2001; Santos et al. 2003; Rodrigues et al. 2007; Emmert 2012; Franceschini 2020). However, some studies have reported some degree of dietary specialization as indicated by low values of Levins' niche breadth index (Bueno and Motta-Junior 2004, 2009; Cheida 2005; Queirolo and Motta-Junior 2007; Campos 2009; Michalski et al. 2013; Soares 2018), reflecting a diet structured around a few dominant items and low resource-use evenness. Despite this, most studies on the maned wolf feeding ecology have been conducted in protected areas, and little is known about the species' feeding ecology in human-modified landscapes, such as silvicultural and agricultural matrices (Motta-Junior et al. 2014).

Beyond dietary shifts, the maned wolf's feeding ecology may influence ecosystem health through seed dispersal. One of the most important plant species in the maned wolf's diet is *Solanum lycocarpum*, commonly known as wolf's fruit, whose seeds are frequently found in faecal samples (Motta-Junior et al. 2014; Silva et al. 2025). Beyond simple consumption, the ingestion and subsequent defecation of these seeds may not only promote their dispersal but also enhance their germination success, highlighting the maned wolf's role as a functional seed disperser (Traveset et al. 2007). This role is particularly vital because, in many anthropized Cerrado landscapes, the maned wolf remains one of the last extant large-bodied frugivores. Unlike smaller birds or rodents, the maned wolf possesses the gape size and gut capacity to ingest and disperse large-seeded fruits that would otherwise face recruitment failure due to a lack of suitable vectors. Although only a few studies have assessed the effectiveness of this animal as a seed dispersal agent (Motta-Junior and Martins 2002; Santos et al. 2003; Reis et al. 2023), there is a clear need to better understand the role of the maned

wolf, and carnivores, as seed dispersers (Calixto et al. 2025). This includes measuring the frequency and effectiveness of seed dispersal, seed viability after gut passage, and the actual contribution of omnivorous carnivores to plant recruitment (Calixto et al. 2025). Understanding seed viability and recruitment is thus essential for restoration ecology, providing the evidence needed to transition from single-species management to the protection of the fundamental ecological processes that sustain the Cerrado.

Our study simultaneously evaluates dietary shifts, compares niche metrics, and functional outcomes within a silviculture-dominated landscape, a matrix that remains understudied for large canids. Our objectives were: (1) to characterize the feeding ecology of the maned wolf, including the diversity and frequency of food items consumed across seasons; (2) to evaluate the dietary niche breadth of the maned wolf in this human-modified landscape; (3) to contextualize the niche breadth through a systematic review across the species' range in Cerrado domain; and (4) to assess the maned wolf's role as a seed disperser, specifically focusing on the germination success of wolf's fruit seeds after passing through the digestive tract. We predict that: (1) diet varies between seasons, with a higher consumption of animal items in the dry season and more plant-based items during the rainy season (Motta-Junior et al. 2014); (2) maned wolves in fragmented and modified landscapes behave as generalist feeders, consuming a wide

variety of plant and animal items (Dietz 1984; Soares 2018; Kotviski et al. 2019); (3) passage through the maned wolf's digestive tract enhances germination success of wolf's fruit seeds compared to seeds from ripe fruits, indicating a functional role as seed dispersal (Santos et al. 2013). This study will not only advance our understanding of the maned wolf's ecology but also contribute to the broader field of carnivore ecology in human-modified landscapes by deepening our understanding of how a canid uses and functions in natural landscapes surrounded by silvicultural matrices.

2 | Material and Methods

2.1 | Study Area

The study area encompasses native vegetation areas within Fazenda Nova Monte Carmelo (FNMC) (18°49'30"S, 47°51'45"W) in the Cerrado domain, Minas Gerais state, Brazil (Figure 1). This property, owned by LD Celulose, covers a total area of 58 000 ha, of which 46 000 ha are dedicated to eucalyptus plantations and 12 000 ha are designated for native vegetation conservation (Soares et al. 2015). The forest plantations are established on previously disturbed lands, primarily used for live-stock grazing and agriculture. The study area is characterized by Cerrado *strictu sensu*, Vereda transitioning to gallery forest, and Parque de Cerrado (Ribeiro and Walter 2008). We collected

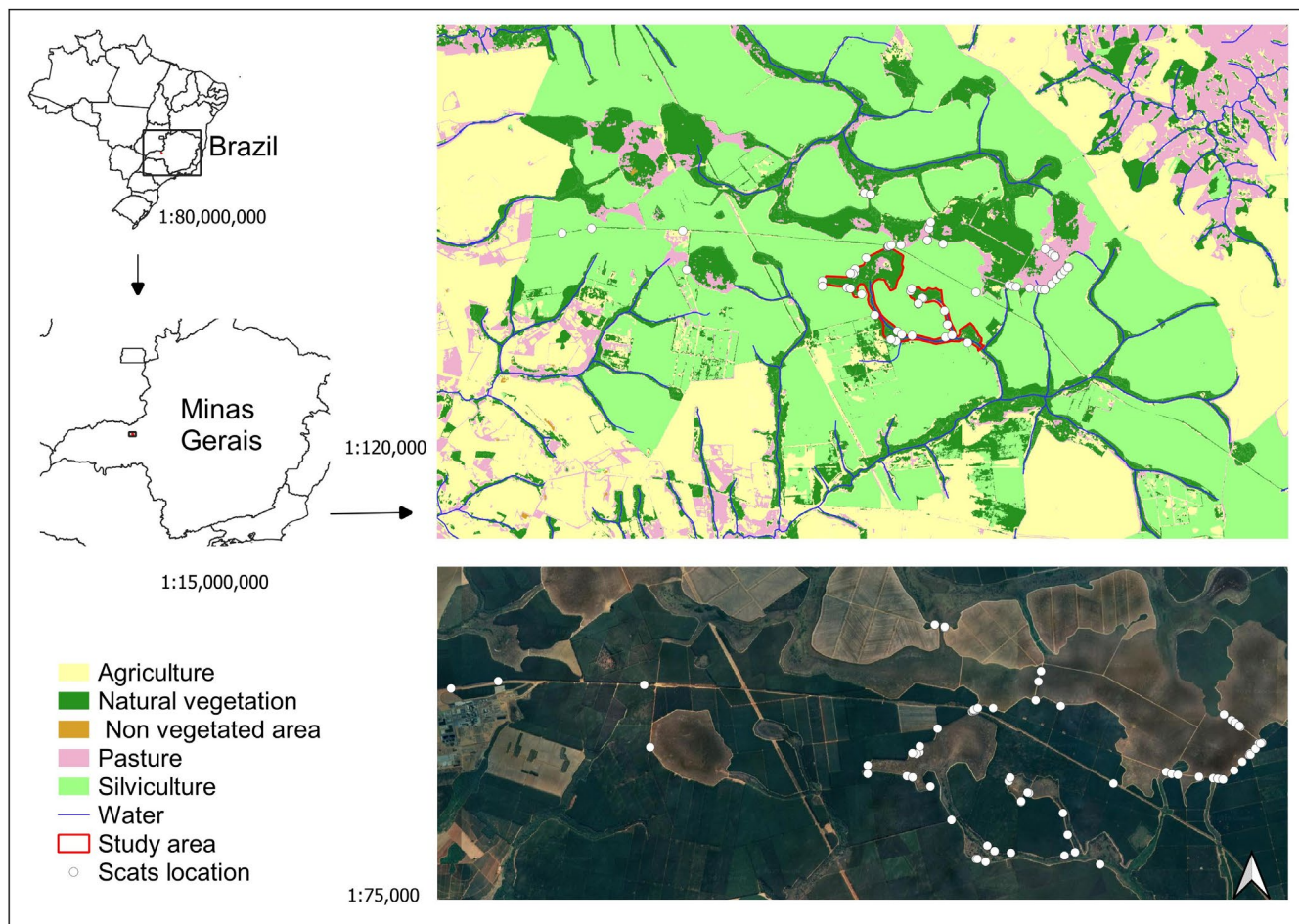


FIGURE 1 | Study area, highlighting the landscape matrix and the location where the scats were collected.

scats around a Cerrado fragment amounting to 363 ha within the property's core area, which is surrounded by silviculture and other Cerrado fragments.

The flora of FNMC comprises 155 plant species, distributed across 69 genera and 38 families, with Myrtaceae (27 spp.), Malpighiaceae (25 spp.), and Melastomataceae (15 spp.) being the richest families (Santos 2018). The avifauna totals 133 species, mostly belonging to the order Passeriformes (Campos 2016). Regarding medium and large-sized mammals, 19 species have been recorded (from 14 Families), with the order Carnivora being the most diverse, followed by Rodentia and Cingulata (Veloso et al. 2025). Finally, the herpetofauna includes 16 amphibian and six reptile species (LD Celulose S/A and Pory 2018).

According to Köppen classification, the region's climate is characterized as Cwc, with hot, rainy summers and cold, dry winters. The average annual precipitation is 1300 mm, and the average temperatures range from 20°C to 22°C (Alvares et al. 2013).

2.2 | Collection of Scats

We collected maned wolf scats monthly from August 2017 to September 2018 by walking along the unpaved roads surrounding the study area during daylight hours and on other unpaved roads near the study area. We conducted 16 surveys, each covering at least 22 km. Each scat was georeferenced, dated, photographed, and placed in labeled plastic bags. The scats were identified according to morphological characteristics, location, deposition, and association with footprints (Figure S1) (Dietz 1984).

All scats underwent a washing process using running water over sieves with varying particle sizes. Sorting and separation of materials were conducted using a stereoscopic microscope. All items were identified at the lowest taxonomic level and categorized as follows: animal items (vertebrates or arthropods), native plant items, and exotic plant items. In cases requiring specialized expertise, samples were sent to specialists. Animal items were preserved in 70% ethyl alcohol, while seeds were air-dried at room temperature and stored in paper bags.

2.3 | Feeding Ecology Statistical Analysis

To determine the frequency of occurrence of each item consumed by the maned wolf, we divided the number of scats containing the item by the total number of scats ($n = 84$). To visually estimate if the sampling effort was sufficient to identify the number of items consumed by the maned wolf, we ran a species accumulation curve. We also calculated the estimated richness using the first order Jackknife and Bootstrap estimators, which require only species incidence data (Smith and Van Belle 1984). We performed all these tests in EstimateS program version 9.1. (Colwell 2013).

We calculated the trophic niche breadth using Levins' index (Levins 1968), standardized by Hurlbert (1978), which measures the uniformity of the distribution of individuals of each food

item among resource categories. We defined five broad resource categories based on the highest taxonomic resolution achievable for each item type: plants (identified to species), mammals (Family), arthropods (Order), reptiles (Suborder), and birds (Class). The Levins' index formula is: $Ba = \frac{B-1}{n-1}$ where Ba is Levins' index, B is expressed by $\frac{1}{\sum p_j^2}$, p_j is the fraction of items in the diet that are in food category j , n is the number of items present in the diet. Niche breadth is expressed on a scale from 0 to 1; indices with values close to or equal to 1 indicate an equal distribution of resources, and values close to 0 indicate that few items are consumed at high frequencies (Krebs 2014).

To identify whether the maned wolf consumed items at different frequencies and to assess the influence of seasonality (rainy and dry seasons), we used logistic regression models with a binomial distribution and logit link function. The response variable was the presence/absence of a specific category within each scat sample. The predictor variables included season and the type of item consumed (levels of a factor, e.g., animal, native plant, exotic plant), with an interaction term included between them in all models. Analyses were structured across different levels of taxonomic resolution to evaluate consumption patterns, totaling four models: (i) Broad level: comparing animals, exotic plants, and native plants; (ii) Animal level: comparing arthropods, birds, mammals, and reptiles; (iii) Native plants level: comparing the families Euphorbiaceae, Fabaceae, Malvaceae, Poaceae, and Solanaceae; and (iv) Exotic plants level: comparing the families Asteraceae, Moraceae, and Poaceae. To test whether our predictors significantly improved the model's fit, we performed a Likelihood Ratio Test on the logistic regression models using the `anova()` function. Significant differences between specific item types were identified through pairwise post hoc comparisons using the `glht()` function in the `multcomp` package. All analyses were conducted in R software, version 4.5.2 (R Core Team 2025). The months of May to September were considered the dry season, and the months of October to April the rainy season (Rosa et al. 1991).

2.4 | Literature Review

We performed a literature review to compare our results, specifically focusing on the niche breadth and the number of items consumed by the maned wolf. We extracted data on the maned wolf diet from grey literature (including technical reports, conference proceedings, master's and PhD's theses), and scientific manuscripts. We included grey literature to increase the chances of finding relevant studies and facilitate more robust comparisons. We used the following keywords in English and their Portuguese translations: "*Chrysocyon brachyurus*" OR "maned wolf" AND "diet" OR "food habit" OR "feeding ecology", in the "Portal de Periódicos da Capes" (<https://www-periodicos-capes.gov.br.ez34.periodicos.capes.gov.br/>) and Google Scholar.

We considered studies that collected maned wolf scats, performed screening, and provided a subsequent description of all items consumed using frequency of occurrence. Only studies conducted in the Cerrado domain that calculated standardized Levins' niche breadth performed until the year 2020 were included. We excluded duplicate studies and those analysing the same data. We extracted information on niche breadth, the

name of the study area, the size of the area, the number of scats analysed, the number of items identified, and the most consumed items.

The only reliable method for comparing standardized Levin's niche breadth across studies is to ensure a consistent taxonomic resolution among them, as the level of identification influences whether an animal or population is classified as a specialist or a generalist (Metz et al. 2024). Unfortunately, we lacked access to the raw data from most external studies. To mitigate this methodological bias, we compared our value of niche breadth to those that met two criteria: (1) presented an approximately similar taxonomic resolution (i.e., plants classified to species, reptiles to Suborder, birds to Class, mammals to Family, and arthropods to Order); and (2) identified a similar total number of consumed items (19–33).

2.5 | Wolf's Fruit Germination Tests

For germination tests of wolf's fruit (*Solanum lycocarpum*) from scats, we separated the seeds of the wolf's fruit from the other consumed items and dried them on absorbent paper at room temperature (Figure 2). We visually classified them as whole, damaged, or germinated. Only whole seeds were considered for germination tests, while broken and/or parasitized seeds

(containing larvae or insects) were discarded. The seeds were then packed in paper bags and stored in a ventilated environment to prevent pathogen growth until the beginning of the experiment.

In June 2018, we collected ripe wolf's fruits from the ground beneath the mother trees. After completing the maturation cycle, the fruits were depulped and sorted into sieves under running water, and the seeds were then dried on absorbent paper at room temperature. Seeds showing mechanical damage or malformation were removed to obtain a homogeneous batch. Subsequently, the seeds were stored in paper bags and properly sealed.

The germination experiment followed a factorial design ($2 \times 2 \times 3$), resulting in 12 treatments. The factors considered were seed origin (scats or ripe fruits), asepsis (sodium hypochlorite or water), and substrate (paper, vermiculite, or sand). These factors were selected based on standardized laboratory protocols that aim to maximize germination success and reduce pathogen interference, particularly from fungal attacks (Brasil. Ministério da Agricultura 2009).

Each treatment had four replicates of 50 seeds, organized in a randomized block design. Before setting up the experiment, all seeds underwent a disinfection process using a 2% sodium

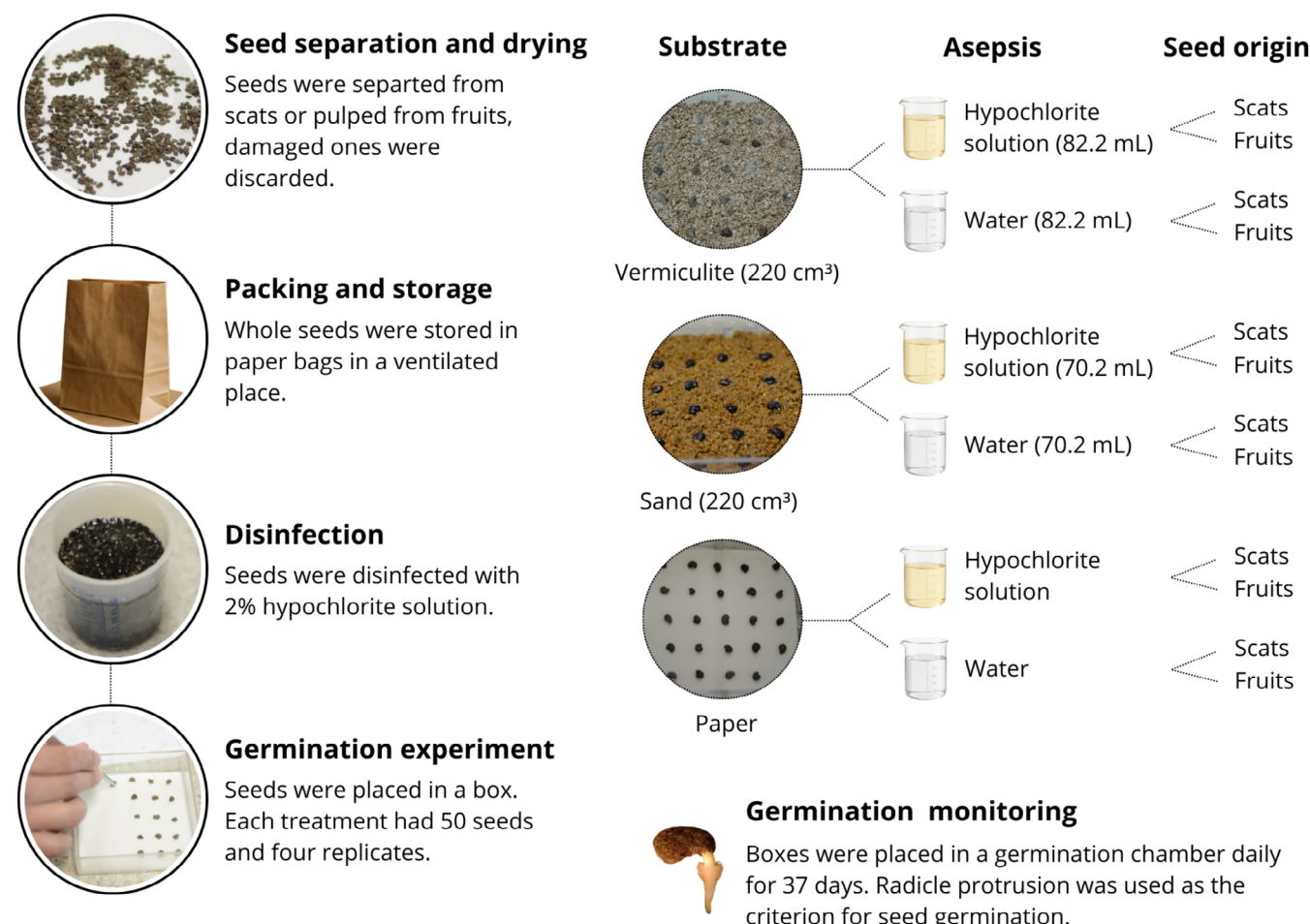


FIGURE 2 | Scheme used to represent the steps used in the germination experiment of wolf's fruit seeds from scats and ripe fruits in three different substrates (sand, vermiculite, and paper) and two different asepsis procedures (hypochlorite solution and water).

hypochlorite solution for 2 min, followed by washing in running water and then distilled water for the same duration. Seeds were then placed on sterilized filter paper for quick drying.

Seeds were placed in plastic “gerbox” boxes containing one of the three substrates. We used 220 cm³ of vermiculite or sand, and paper was used in sufficient quantity to fully cover the bottom of the container. The substrates were moistened with either a 0.5% sodium hypochlorite solution (treatment) or water (control). For moisture standardization, 82.2 mL was added to vermiculite, 70.2 mL to sand, and in the case of paper, the substrate was saturated, and any excess solution was removed.

The experiment was carried out in a germination chamber under alternating light and temperature conditions (20°C/30°C every 12 h), following Pinto (2007). Germination was monitored daily for 37 days. After this, all seeds showed signs of fungal proliferation. Radicle protrusion was used as the criterion for seed germination.

2.6 | Wolf's Fruit Germination Statistical Analysis

We applied an analysis of variance (ANOVA) to assess if the seed origin (scats or fruits), substrate (sand, vermiculite, or paper), and asepsis procedure (hypochlorite solution and water) influenced the number of seeds that germinated. To assess data normality of ANOVA residuals, we used the Shapiro test, and to examine variance homogeneity, we applied Levene's test. Additionally, a proportion test was conducted for two samples, where germination was coded as 1 and absence of germination as 0 ($\alpha = 0.05$). To assess the impact of the maned wolf's digestive tract on ingested seeds, we evaluated the proportions of whole, broken, and germinated seeds using the chi-square (χ^2) test. We used the R software environment (R Core Team 2025) to perform these analyses.

3 | Results

3.1 | Feeding Ecology

We collected 84 scats of maned wolves, comprising 20 (23.8%) from the rainy season and 64 (76.19%) from the dry season (check Table S1 for scats location). We identified at least 27 distinct food items: 10 of animal origin, nine of native plants, and eight exotic plants (Table 1).

The species accumulation curve did not reach the asymptote (Figure 3). The non-parametric first order Jackknife and Bootstrap estimators yielded values of 38.86 (± 3.76) and 32.13 (± 0.86) species, respectively, suggesting that increasing the number of scats could potentially reveal up to five additional items consumed by the maned wolf.

The niche breadth was 0.122, with slight variation between the dry (0.117) and rainy season (0.132). Most items were consumed in low frequency; only the wolf's fruit, items from the family Poaceae, small mammals (Didelphimorphia and Rodentia), birds, and items from the order Hymenoptera were present in more than 15% of the scats (Table 1, Table S2).

The overall diet composition was significantly non-uniform ($\chi^2 = 166.7$, $p < 0.00$). Native plants (100%) and animal items (85%) were the most frequently consumed items in the maned wolf's diet, while exotic plants were identified in only 18% of the scats (Figure 4). Diet composition did not vary with the season ($\chi^2 = 0.06$, $p = 0.79$), and no interaction was detected between the type of item consumed and season ($\chi^2 = 1.19$, $p = 0.55$). Among animal items, birds were the most common (73.8%), showing a significant difference in relation to mammals (25.0%), arthropods (17.9%), and reptiles (14.3%) ($\chi^2 = 86.1$, $p < 0.00$) (Figure 4). Animal items were more frequently consumed in the dry season (65% vs. 20% in the rainy season) ($\chi^2 = 4.0$, $p = 0.04$), but there was no interaction between animal item and season ($\chi^2 = 1.13$, $p = 0.77$). Native plants were largely characterized by items from the Solanaceae family, which were found in all scats (100% occurrence) ($\chi^2 = 354$, $p < 0.00$) (Figure 4). Native plant items were more commonly consumed during the rainy season (27% vs. 1% in the dry season, excluding Solanaceae, that was present in all scats) ($\chi^2 = 6$, $p = 0.01$). No significant interaction was observed between native plant items and season ($\chi^2 = 4$, $p = 0.42$). Exotic plants were predominantly represented by the Poaceae family (14.3%) ($\chi^2 = 13.5$, $p = 0.001$), with no significant influence of seasonality ($\chi^2 = 1.7$, $p = 0.19$), nor interaction between item type and season ($\chi^2 = 5.1$, $p = 0.08$) (Figure 4).

3.2 | Literature Review

We identified 21 unique studies about the maned wolf's feeding ecology that calculated the niche breadth for 24 different places (Table S3). Niche breadth varied from 0.09 to 0.57. Among the studies with comparable taxonomic resolution and a similar number of consumed items (10 studies, including ours), the mean niche breadth was 0.37 (± 0.15 , ranging: 0.09–0.52) (Figure 5). Regarding the number of species/items consumed by the maned wolf, our study was below the mean of 40.96 (± 18.63), which ranged from 11 to 77 (Figure 5). The mean number of scats we analysed was also under the mean of 247.71 (± 359.07); these values ranged from 17 to 1673 (Figure 5). The most consumed items by maned wolves were the wolf's fruit and small mammals, accounting for 80% and 76% of the studies each (Figure 5). Birds, arthropods, and miscellaneous fruits were consumed more frequently in only 16%–20% of the studies, and plant items from the Poaceae family in 8%.

3.3 | Wolf's Fruit Germination

Wolf's fruit seeds from scats exhibited higher germination rates than those from ripe fruits ($F = 1127.27$, $df = 1$, $p < 0.000$) (Figure 6), 52% and 2%, respectively. Germination was lower on sand (22%) than on paper (31%) and vermiculite (27%) ($F = 10.73$, $df = 2$, $p < 0.000$) (Figure 6), and did not vary according to the aseptic procedure ($F = 1.11$, $df = 1$, $p = 0.298$) (Figure 6). Seeds from scats showed lower germination on sand compared to the other treatments ($F = 7.11$, $df = 2$, $p = 0.002$) (Figure 6) (44%, vs. 53% on vermiculite and 59% on paper), although there was no interaction for ripe fruit seeds and substrate. Aseptic procedures showed no significant difference in germination averages between scats and ripe fruit seeds ($F = 0.08$, $df = 1$, $p = 0.782$) (Figure 6).

TABLE 1 | Items consumed by the maned wolf (*Chrysocyon brachyurus*) in a Cerrado fragment surrounded by silviculture in Southeast Brazil (2017–2018).

Taxa	Common name	Season		Total	Frequency
		Rainy	Dry		
Number of faecal samples		20	64	84	
Native vegetable items					
Euphorbiaceae					
Croton glandulosus L.	Tooth-leaved croton	2	1	3	3.6
Euphorbia heterophylla L.	Painted euphorbia		1	1	1.2
Fabaceae					
Stylosanthes sp.	Pencilflower		1	1	1.2
Malvaceae					
Guazuma ulmifolia Lam.	Bay cedar		1	1	1.2
Poaceae not identified		6	20	26	30.9
Panicum spp.	Panicgrass	2	2	4	4.8
Paspalum spp.	Paspalum	3		3	3.6
Setaria sp.	Bristle grass		1	1	1.2
Solanaceae					
Solanum lycocarpum A.St.-Hil.	Wolf's fruit	20	64	84	100
Solanum americanum Mill.	American black nightshade		1	1	1.2
Solanum sp.		1		1	1.2
Native vegetables not identified		2	6	8	9.5
Exotic vegetable items					
Asteraceae					
Helianthus annuus L.	Common sunflower		3	3	3.6
Moraceae					
Artocarpus heterophyllus Lam.	Jackfruit		1	1	1.2
Poaceae					
Sorghum bicolor (L.) Moench	Sorghum		1	1	1.2
Triticum aestivum L.	Common wheat		2	2	2.4
Urochloa brizantha (Hochst. ex A. Rich.) R.D. Webster	Palisade grass	3		3	3.6
Urochloa decumbens (Stapf) R. D. Webster	Congo grass	2	3	5	5.9
Urochloa ruziziensis (R. Germ. & Evrard) Crins	Congo grass	1		1	1.2
Zea mays L.	Corn		2	2	2.4
Animal items					
MAMMALIA not identified		1	9	10	11.9
Didelphimorphia					
Didelphidae		1	4	5	5.9
Rodentia		2	8	10	11.9

(Continues)

TABLE 1 | (Continued)

Taxa	Common name	Season		Total	Frequency
		Rainy	Dry		
BIRDS not identified		14	48	62	73.8
LEPIDOSAURIA					
<u>Squamata</u>			3	3	3.6
Sauria			2	2	2.4
Teiidae					
<i>Ameiva ameiva</i> (Linnaeus 1758)	Jungle-runners		1	1	1.2
Colubridae not identified		1	2	3	3.6
<i>Phalotris mertensi</i> (Hoge 1955)	Falsa-coral		1	1	1.2
Viperidae					
<i>Bothrops</i> sp.	Jararaca		1	1	1.2
<i>Crotalus durissus</i> (Linnaeus 1758)	Rattlesnake		2	2	2.4
INSECTA					
<u>Coleoptera</u>		1	1	2	2.4
<u>Diptera</u>			1	1	1.2
<u>Hymenoptera</u>		1	12	13	15.5
Vespidae					
<i>Polybia</i> sp. (Lepeletier 1836)	Wasp		1	1	1.2
Total		63	206	269	
Niche breadth		0.132	0.117	0.122	

The proportion of germination differed between seeds from scats and ripe fruits ($p=0.000$), with 100% of scat treatments showing at least one seed germinating, compared to only 50% for ripe fruit seeds. Most seeds that passed through the maned wolf's digestive tract were found whole (94%), only 5.4% were damaged, and a small fraction was already germinated (0.2%) ($p<0.000$).

4 | Discussion

Our study reveals that the maned wolf exhibits a relatively narrow niche breadth while maintaining a diverse diet, and plays an important role in seed dispersal by increasing germination probability. We identified 27 different food items in the maned wolf's diet, mostly native plants and animals. Notably, we found a distinct seasonal shift in foraging strategy: animal prey consumption peaked during the dry season, while native plant intake increased significantly during the rainy season. Furthermore, our results highlight the maned wolf as an effective seed disperser; seeds of *Solanum lycocarpum* that passed through the digestive tract exhibited a 50% increase in germination success compared to those from ripe fruits.

The maned wolf's niche breadth in our study was very narrow, indicating less equidistribution of the resources used, with few items consumed at high frequencies, as wolf's fruit, Poaceae

species, and small vertebrates, and most at low frequencies. While a narrow niche breadth is often interpreted as evidence of specialization, this metric primarily reflects the dominance structure of the diet rather than the total diversity of items consumed (Levins 1968). This pattern raises the question of whether the observed dominance reflects true dietary preference or simply the high availability of these resources within the silvicultural matrix. Resource use may vary across temporal and spatial scales, whereas true specialization is expected to be more consistent (Carlo et al. 2025). Therefore, if the maned wolf acts as a specialist, it likely prioritizes certain resources due to their high nutritional quality (e.g., high in energy or protein), selecting the most profitable food resources to maximize energy gain (MacArthur and Pianka 1966; Charnov 1976). Even if partly driven by resource availability, this pattern may characterize the species as exhibiting a dominant-core feeding strategy, in which a few key resources structure the diet. We must acknowledge, however, that the niche breadth value may also be influenced by our relatively low sample size, which will be discussed further below.

Our literature review revealed that, although the maned wolf is commonly classified as a generalist species (Dietz 1984; Jácomo et al. 2004; Santos et al. 2003; Queirolo and Motta-Junior 2007; Bueno and Motta-Junior 2009; Emmert 2012; Michalski et al. 2013; Soares 2018; Franceschini 2020), the mean niche breadth of 0.37 (considering only studies that

presented similar taxonomic resolution and similar number of consumed items) suggests that resource use is often uneven across studies. Rather than contradicting its generalist

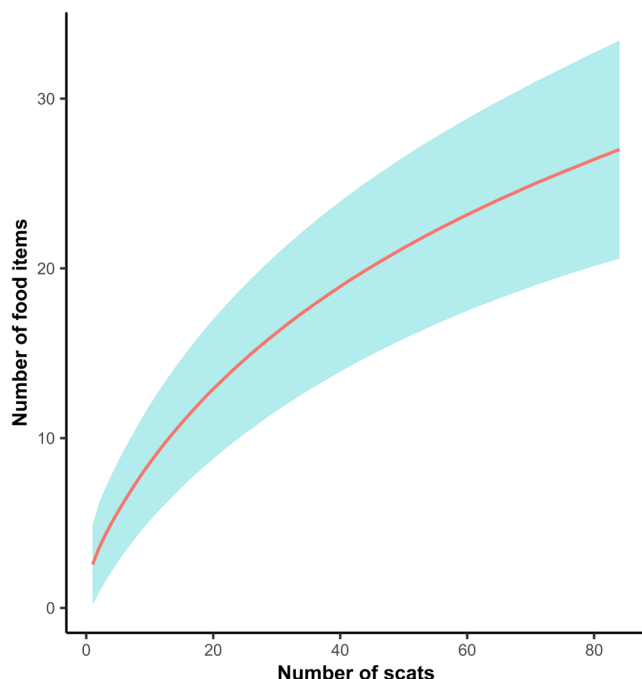


FIGURE 3 | Species accumulation curve of food items consumed by the maned wolf (*Chrysocyon brachyurus*) in a Cerrado fragment surrounded by silviculture in Southeast Brazil (2017–2018).

classification, this pattern indicates that the species typically consumes a wide variety of food items, but with a strong dominance of a few key resources. This apparent discrepancy arises because niche breadth indices based on Levins' index are more sensitive to evenness than to the total number of consumed items. Thus, even species that exploit many resource types may exhibit low to moderate niche breadth values if their diet is structured around a few dominant components. In this context, the maned wolf can be better described as an opportunistic generalist with a structured diet, rather than a strict specialist. Notably, despite variation in specific items across studies, functional categories, such as Solanaceae fruits and small vertebrates, remain remarkably consistent. This suggests a degree of functional specialization toward resource types, rather than toward specific species.

Animals and native plants were similarly distributed in the animal's diet, as also observed in a review of 18 studies (Motta-Junior et al. 2014), and overall diet composition did not vary seasonally. However, when we analysed the groups separately, maned wolves consumed more native plants during the rainy season when compared to the dry season. For animals, the pattern was the opposite. The availability of plants is usually higher during the rainy season (Marinho-Filho et al. 2002). In the dry season, when fruit production declines, these canids shift their diet toward small vertebrates. Thus, the seasonal patterns in feeding ecology appear to reflect the natural cycles of abundance in the Cerrado domain, consequently showing a temporal trophic adaptation of the maned wolf (Motta-Junior et al. 2014).

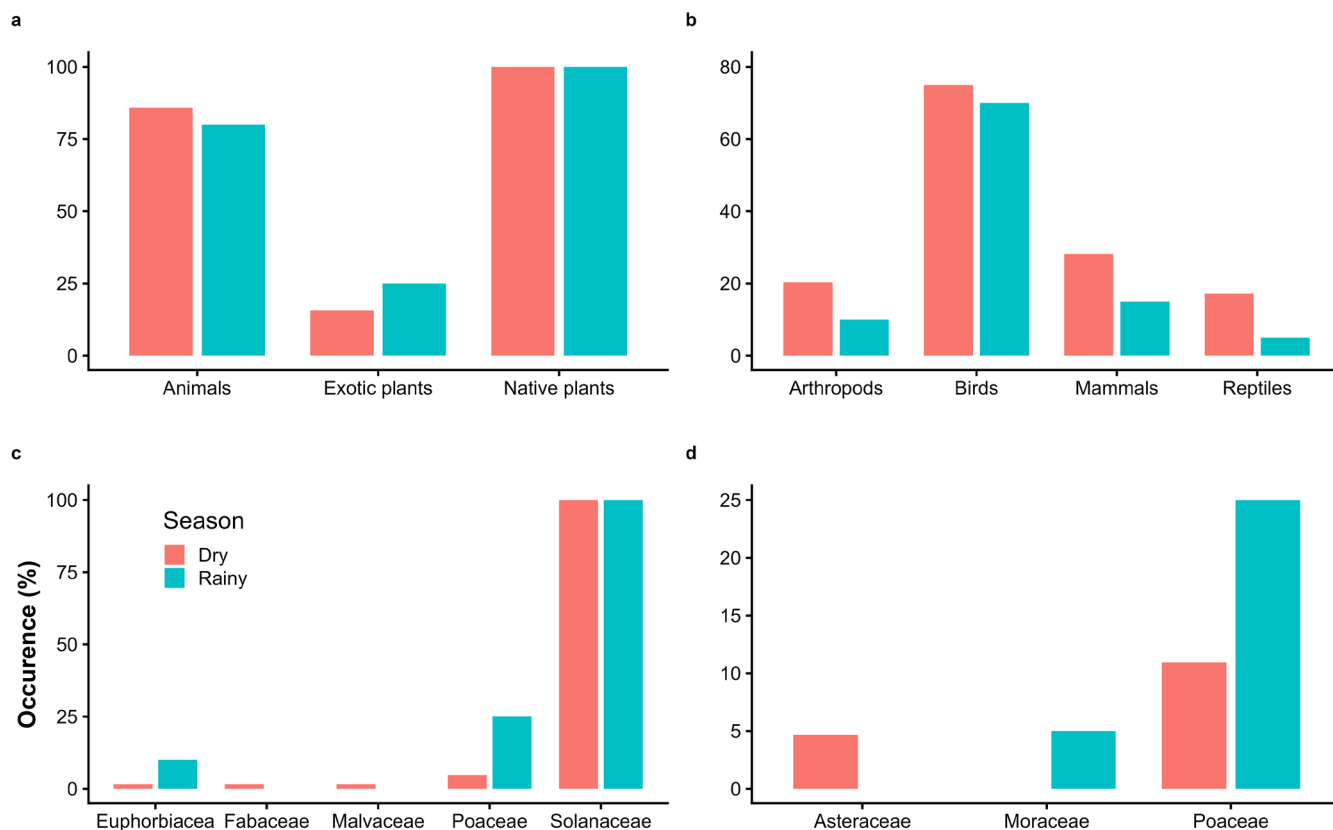
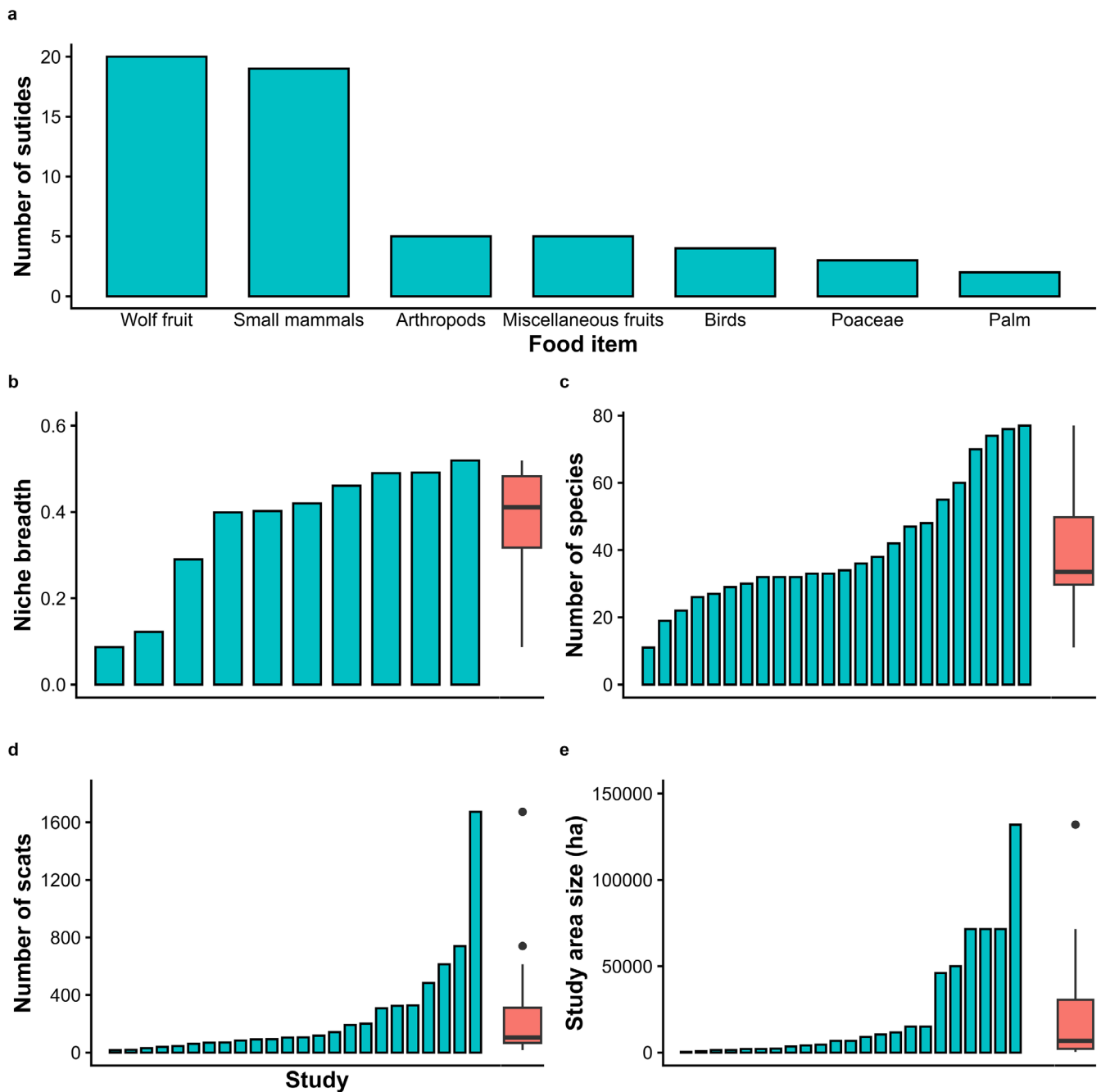


FIGURE 4 | Food items consumed by the maned wolf (*Chrysocyon brachyurus*) in a Cerrado fragment surrounded by silviculture in Southeast Brazil (2017–2018), categorized by season and: (a) broad taxonomic level, (b) animal level, (c) native plants level, (d) exotic plants level.



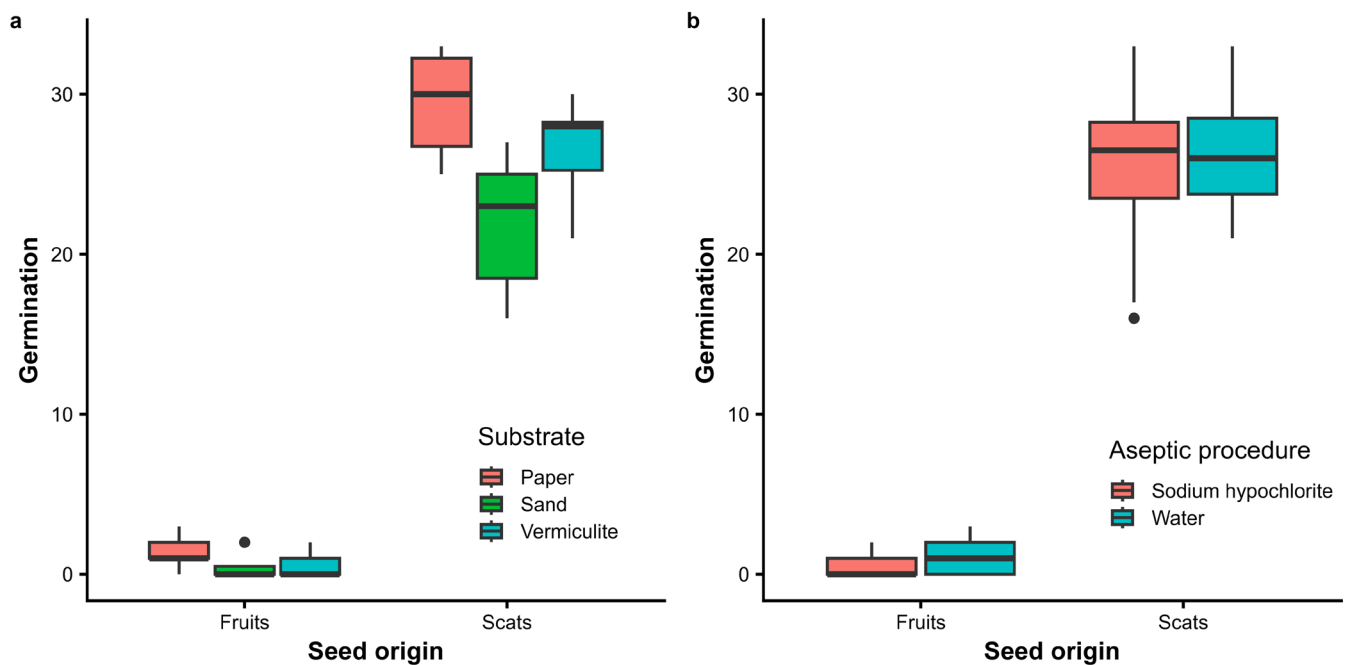


FIGURE 6 | Mean germination rates of wolf's fruit (*Solanum lycocarpum*) seeds from maned wolf (*Chrysocyon brachyurus*) scats and from ripe fruits in (a) three different substrates, vermiculite, sand, and paper; and (b) two aseptic procedures, 0.5% sodium hypochlorite solution and water.

7.3%–35% of scats in other studies) (Aragona and Setz 2001; Bueno and Motta-Junior 2009; Ciocheti 2007; Dietz 1984; Franceschini 2020; Jácomo et al. 2004; Rodrigues et al. 2007).

The consumption of exotic plants was infrequent in our study, being detected in 18% of the faecal samples (Motta-Junior et al. 2014). This low frequency suggests that exotic plants do not constitute an essential food resource for the studied population. Understanding the role of exotic plants in the maned wolves' feeding ecology is an important step toward understanding how these animals can adapt their diet in human-modified landscapes (Magioli et al. 2019). Specifically, it clarifies whether these predators are incorporating novel resources provided by the matrix or remaining functionally dependent on native remnants. Our results indicate that despite the structural modification of the habitat, the species remains functionally tethered to native dietary components.

Seeds dispersed via scats were 26 times more efficient in germination than those from ripe fruits. This increase suggests that the maned wolf's digestive process not only preserves seed integrity (94% whole) but also likely removes germination inhibitors or scarifies the seed coat, enhancing germination potential. This facilitative effect is consistent across the maned wolf's broad diet; previous studies have shown that gut passage maintains the germination of at least 14 out of 16 tested species (Motta-Junior and Martins 2002). Furthermore, these canids can be efficient dispersers as they defecate on sites suitable for seed germination and plant establishment (Motta-Junior et al. 2014), such as trails, dirt roads, and the tops of termite mounds. Coupled with their large home range, varying from 20 to 310 km² (Lemos et al. 2023), and the long distances they travel, an average of 6–9 km/day (Melo et al. 2007), this canid may prevent seed aggregation near the mother plant, thereby

reducing density-dependent mortality and maintaining genetic flow across fragmented matrices. Considering the maned wolf's ability to process seeds of diverse sizes, particularly those exceeding 15 mm in diameter (e.g., *Annona* spp. and various palms) (Lorenzi 2016), in anthropized landscapes where other large-bodied frugivores like tapirs are absent (Medici et al. 2023), the maned wolf becomes an important vector capable of providing long-distance dispersal for large-seeded plants.

While our study is subject to certain limitations, we believe these do not substantially compromise the validity or relevance of our findings. The relatively small scat sample size and the species accumulation curve not reaching an asymptote indicate under-sampling, meaning some food items may have been missed, especially rare food items. However, this reflects a broader challenge in Neotropical carnivore research, where dietary accumulation curves at the species level rarely reach stabilization, even in studies with significantly higher sampling efforts (Cruz et al. 2022). Furthermore, the taxonomic resolution, which often did not reach genus or species level for animal items, could have resulted in an underestimation of the true richness of these items in the maned wolf's diet and inherently has effects on the niche breadth values. While we attempted to control for this in our literature review by selecting studies with similar taxonomic detail, this intrinsic limitation of resolution should be considered when interpreting the niche breadth we found. Crucially, niche breadth indices (Levins 1968) are primarily influenced by the dominance and evenness of core dietary components, whereas rare, incidental items contribute little to the metric. Supporting this, even studies with extensive sampling efforts (e.g., >480 samples) have reported niche breadth values for maned wolves ranging from 0.15 to 0.46 (Bueno and Motta-Junior 2004, 2009; Dietz 1984; Jácomo et al. 2004), which aligns with the moderate value observed in our study.

Another limitation is related to a common methodological constraint in this kind of study; the individual identity of the maned wolf's scat was not confirmed genetically. This means the assumption of data independence for the logistic regression model may have been violated. If possible, future studies should genetically confirm which scats belong to which individuals. Although our inferences are based solely on scat analysis and could underrepresent soft body or fully digested items, this non-invasive method remains a widely used and effective tool for studying feeding ecology. Finally, we did not assess the availability of food items in the environment, limiting our ability to quantify food preferences. Nonetheless, the diversity and frequency of the identified items still offer valuable insights into the maned wolf's feeding ecology in human-modified landscapes.

Taken together, these limitations point to opportunities for future research such as: (1) expand the sample size to clarify the degree of dietary specialization in silviculture matrices (Cruz et al. 2022); (2) to compare studies across a gradient of land-use types, from intact Cerrado to human-modified landscapes, such as silviculture and pasture, helping determine how matrix composition influences dietary diversity and plasticity; (3) to better understand the maned wolf's ecological role, and other canids; future studies should also quantify seed dispersal effectiveness in the field, evaluating not just germination but seedling establishment and plant recruitment (Calixto et al. 2025); (4) to assess the role of exotic plants in the diet, particularly in human-modified landscapes, and determine if their use is increasing over time or varies seasonally; (5) to evaluate the energetic importance of the diet by including estimates of the biomass contribution of food items.

Overall, our findings support the view that the maned wolf is not a strict dietary specialist, but rather a generalist species whose diet is consistently structured around a few dominant resources, reflecting both ecological flexibility and dependence on key food items. A major strength of this study lies in the evaluation of the maned wolf's diet within a silviculture matrix, a landscape type that now dominates large parts of Cerrado and other Southern hemisphere savannas, offering a potential contribution to the understanding of how carnivores respond to these changes. Since the maned wolf relies heavily on native plants like the wolf's fruit and small vertebrates, protecting intact Cerrado areas, especially open and semi-open areas, is crucial for maintaining both habitat availability and dietary resources (Lemos et al. 2023). Restoring degraded areas and creating habitat corridors would help maintain biodiversity and food availability. Furthermore, since maned wolves, and other carnivores, frequently use human-modified landscapes, promoting wildlife-friendly farming practices is essential. This can include preserving natural fragments within farmlands, maintaining scattered trees, and reducing pesticide use to protect native plant species and prey. The maned wolf's significant role in seed germination, especially for wolf's fruit, suggests it may act as a disperser for this species. Consequently, conservation efforts should integrate strategies to protect both the species and the ecological resources on which it depends.

Author Contributions

Aline Carneiro Veloso: methodology, conceptualization, investigation, writing – original draft, data curation, writing – review and

editing. **Ednaldo Carvalho Guimarães:** formal analysis, writing – review and editing, methodology. **Ana Elizabeth Iannini Custódio:** conceptualization, investigation, funding acquisition, methodology, writing – review and editing, supervision, resources, project administration. **Carine Firmino Carvalho-Roel:** conceptualization, writing – original draft, methodology, validation, visualization, writing – review and editing, formal analysis, data curation, supervision. **Arthur Celestino Soares:** conceptualization, investigation, methodology, writing – review and editing.

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Ethics Statement

The authors have nothing to report.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data are available in Tables S1–S3.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** A sample of maned wolf (*Chrysocyon brachyurus*) scat. **Table S1:** Maned wolf (*Chrysocyon brachyurus*) scats location in a Cerrado fragment surrounded by silviculture in Southeast Brazil (2017–2018). **Table S2:** Food items consumed by the maned wolf (*Chrysocyon brachyurus*) in a Cerrado fragment surrounded by silviculture in Southeast Brazil (2017–2018). **Table S3:** Studies about maned wolf (*Chrysocyon brachyurus*) feeding ecology that calculated its niche breadth in Cerrado biome (1984–2020).