Original Study

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Mammalian responses to agricultural cycles in Brazilian Atlantic Forest croplands

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Abstract: This study investigated how mammal communities responded to crop type, crop development stage, and distance from forest fragments in the Brazilian Atlantic Forest. We examined mammal diversity in annual crops (corn and soybeans) in Southern Brazil, testing three hypotheses: (a) crop types support distinct mammal communities, (b) diversity decreases with distance from forest fragments, and (c) mammal presence varies across crop development stages. Camera traps and pitfall traps were deployed across seven sites during 2020–2021 to monitor small and medium-large mammals. Crop type significantly influenced mammal communities, with corn fields showing higher trapping efficiency than soybeans, particularly for medium-large mammals. Species richness and capture efficiency declined as distance from forest fragments increased, regardless of crop type. Temporal patterns differed between groups: small mammals were more prevalent during later crop stages, while medium-large mammals were more active during early development, especially in corn. These findings highlight the importance of maintaining vegetative fragments within agricultural matrices and accounting for temporal wildlife activity patterns. Results contribute to developing wildlife-friendly farming practices and conservation strategies in agricultural landscapes of the Brazilian Atlantic Forest.

Keywords: agroecosystems; mammal diversity; landscape fragmentation; Atlantic Forest biodiversity

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1 Introduction

The expansion of agricultural landscapes significantly impacts native wildlife and biodiversity conservation. Understanding how wildlife utilizes these areas is essential for assessing the consequences of agricultural growth and for developing sustainable practices that harmonize food production with ecosystem preservation (Carter et al. 2020; Maxwell et al. 2016). Recent studies emphasize the need for comprehensive data collection to inform these practices effectively (Machado et al. 2021; Pedroso et al. 2024; Santos et al. 2024). Agricultural landscapes are essential for food supply and play an important role in biodiversity conservation, as they often occupy large land areas adjacent to wildlife habitats and rely on ecosystem services for their productivity (Viers et al. 2013). While the agricultural matrix can provide habitat and connectivity for some species (Braga et al. 2015), it also contributes to habitat fragmentation and ecological pressure on native fauna (Rodrigues et al. 2019). Balancing agricultural productivity with biodiversity conservation remains a major challenge, particularly in biodiversity hotspots such as the Brazilian Atlantic Forest, where agricultural expansion has been a major driver of habitat loss (Ribeiro et al. 2009).

The relationship between wildlife and agricultural fields is intricate and multifaceted (Fehlmann et al. 2020). Different species exhibit varying levels of adaptation to and utilization of agricultural landscapes. Some species have adapted to thrive primarily in agricultural environments, using crop fields for foraging, shelter, and reproduction (Santos-Filho et al. 2024); these are considered farmland specialists. Other species, known as generalists, can utilize both natural and agricultural habitats, often moving between them based on resource availability (Umetsu and Pardini 2007).

Crop structure is a key element that shapes how wildlife interacts with agricultural landscapes (Boesing et al. 2018a, 2021). The physical characteristics of crops can either facilitate or hinder wildlife movement and occupation. The similarity between crop structures and adjacent native

habitats significantly affects how different species interact with agricultural areas (Boesing et al. 2018a, 2021). For instance, species adapted to open habitats may find newly sown fields hospitable, while struggling to occupy the same area once crops have matured and created denser cover. Predation risk also varies among different crop types and growth stages, significantly impacting wildlife movement and occupation patterns. Some crops may provide better cover from predators, while others might leave animals more exposed (Coppola et al. 2021). Understanding these dynamics is essential for managing wildlife populations in agricultural settings. Small mammal populations may fluctuate based on changing crop conditions and associated predation risks throughout the growing season (Bonecker et al. 2009). By considering crop structure, we can better predict and manage wildlife occupancy in agricultural landscapes, supporting both biodiversity conservation and agricultural productivity.

The spectrum of responses to agricultural landscapes reflects the diverse ecological strategies of different species (Blitzer et al. 2012). While some animals may indeed "spill over" from natural habitats into croplands (Blitzer et al. 2012; Boesing et al. 2018a, 2021), others have developed more permanent associations with agricultural environments. Understanding these varied relationships is crucial for effective wildlife management and conservation in human-modified landscapes.

Annual crops introduce unique challenges for wildlife due to their dynamic nature. The rapid life cycles of these crops result in substantial seasonal variations in physical structure and resource availability, influencing the capacity of various species to utilize these fields at different growth stages. Consequently, both the seasonality of crop cycles and the surrounding landscape context emerge as pivotal factors driving species occupancy or exclusion in agricultural settings (Jackson and Fahrig 2015; Pickett and Siriwardena 2011).

The Brazilian Atlantic Forest (BAF) is recognized for its rich biodiversity and serves as a compelling case study for examining wildlife-agriculture interactions (Brooks et al. 2002; Joly et al. 2014). This biome covers 15 % of Brazilian territory and is home to a diverse variety of unique species, yet this biodiversity hotspot faces significant threats from anthropogenic activities, particularly agricultural expansion (Myers et al. 2000; SOS Mata Atlântica Foundation 2025). Although this biome hosts 27 % of the country's agricultural lands (Pinto et al. 2022), research on biodiversity occupation in crop fields remains limited. This scarcity of studies in agricultural landscapes underscores the urgent need for more comprehensive investigations to understand the patterns and requirements of cropland occupation by biodiversity in Brazilian agricultural contexts.

The development of strategies that effectively reduce the impact of agricultural inputs on wildlife while maintaining productive farming practices requires a deeper understanding of how biodiversity utilizes agricultural lands. To address this need, we monitored mammal biodiversity in annual crops in Southern Brazil over a year. We focused on mammals (both small and medium-large species) in crop fields of two major annual crops cultivated (corn and soybean) and throughout various stages of crop development. Three main hypotheses were tested: (a) different crop types (corn vs. soybean) support different mammal communities due to variations in crop structure and resource availability; (b) mammal occurrence and sample efficiency decreases with increasing distance from forest fragments due to habitat requirements and movement patterns; and (c) mammal presence varies across crop development stages (sowing, reproductive, and maturation phases) due to changes in cover and resource availability. Regarding hypothesis (a), for small mammals we expected higher species richness and trapping efficiencies in corn than in soybean fields due to increased cover and resource availability, while medium-large mammals were also anticipated to exhibit higher occurrence in corn fields, likely utilizing the crop for foraging and temporary shelter. For hypothesis (b), we hypothesized a sharper decline in diversity of species and trapping efficiency for small mammals further from forest fragments, given their more restricted movement patterns and reliance on forest habitats. In contrast, medium-large mammals, with larger home ranges, were expected to utilize crop areas further from forests, but with overall decreasing trends in diversity and occurrence as distance increased, though potentially showing higher observation number at field borders. For hypothesis (c), we predicted that small mammal presence, diversity, and trapping efficiency would increase in later crop development stages (reproductive and maturation) as vegetation provides more cover and food resources. Conversely, medium-large mammals were expected to show higher activity or presence in earlier crop stages (sowing, early growth) for foraging or, they may utilize later stages for cover depending on species-specific needs and the availability of thermal refuges in forests. The hypotheses were tested by: (i) comparing species richness, trapping efficiency, and species composition between corn and soybean fields, (ii) analyzing how species' richness and occurrence changed along the distance gradient from forest fragments, and (iii) analyzing the effect of crop development stages in different crop types to determine if temporal patterns of species richness and trapping efficiency differed

between corn and soybean fields. Through testing these hypotheses, we aimed to evaluate temporal and spatial variation in crop use by small, medium, and large mammals, providing insights into how species interact with agricultural landscapes over time.

2 Materials and methods

2.1 Study region

The study was conducted in northern Paraná, Brazil (Figure 1). This region has a seasonal climate, with a dry season from April to September and a wet season from October to March. During the wet months, temperatures average 22–28 °C with high rainfall and humidity. The area was originally covered by Atlantic Semi-deciduous forest, adapted to this seasonal climate (Roderjan et al. 1993). According to the Köppen classification, this region has a Cfa climate with an annual mean air temperature of 20.1–20.8 °C and a total annual rainfall of 1,200–1,400 mm (Aparecido et al. 2016). This region is one of Brazil's most crucial agricultural zones, characterized by its production of soybean, corn, sugarcane, dry bean, and winter cereals (Pinto et al. 2022).

2.2 Sampling design

We selected seven independent sampling sites distributed across northern Paraná, Brazil (Figure 1). Site selection was based on parameters such as the amount of native forest at the landscape scale, crop standardization (farms growing both soybeans and corn), and a minimum distance of 5–6 km between sites (Boesing et al. 2018b). Therefore, each site consisted of a farm of approximately 40 ha containing annual crop fields (corn and soybean), adjacent forest remnants, and one fallow area. The selection of these sites was based on a preliminary landscape analysis to control for potential confounding effects of landscape composition on local biodiversity patterns (Figure 2).

Prior to site selection, we conducted a landscape analysis using QGIS 3.40 software to quantify the percentage of forest cover within a study area by selecting a reference point corresponding to a farm location and creating a 2-km radius buffer around this point. This circular area (1,256.64 ha theoretical area) represents the local landscape context surrounding the farm, providing insights into land use patterns within the immediate agricultural environment. Land use and land cover data were obtained from MapBiomas Collection 10 for the year 2020. MapBiomas provides annual land use classifications for Brazilian territory at 30-m spatial resolution using Landsat satellite imagery and machine learning algorithms (MapBiomas Project 2024). Land use and land cover for each property are indicated on the Supplementary Material (Supplementary Tables S1 to S5). The successional stage for each forest fragment is not available.

To isolate the effects of local factors (crop type, distance from forest, and crop development stage) from landscape-level influences, we selected seven farms where the percentage of forest cover within the 2-km buffer ranged from 20.6 to 32.8 % (Supplementary Tables S1–S7; Supplementary Figures S1–S7; mean = 26 %, SD = 4.9 %). This narrow range allowed us to control landscape-level effects while focusing on local-scale factors. This standardization was particularly important because in the BAF biome, private properties in rural areas must legally maintain at least 20 % of their area as native vegetation (Legal Reserve) according to the Brazilian Forest Code (Brasil 2012). At each of the seven sites, we established a standardized sampling design to investigate three main factors. First, crop type: each site was sampled during both corn and soybean growing seasons within the same agricultural year (2020–2021). Second, distance gradient: at each site, we established three sampling positions – forest interior (50 m inside the forest fragment), field border (within 10 m of the forest-crop edge), and field interior (approximately 150 m from the forest edge into the crop). These distances were specifically chosen to capture the ecological gradient of biodiversity use, from the forest interior (representing a potential source habitat) across the forest-crop interface (field border) and into the crop interior. This non-symmetrical design was adopted to investigate 'spillover' effects and the varying degrees of species penetration into the agricultural matrix, rather than a uniform sampling across arbitrary distances. Third, crop development stages: each site was sampled during three distinct phases of crop development – T1 (early stage), during sowing period through early pre-emergence, characterized by mostly exposed soil with minimal plant cover (0–15 days after planting); T2 (reproductive stage), during pre-tasselling and tasselling in corn, or blooming and pod development in soybeans, characterized by maximum plant height and complete soil coverage (45–60 days after planting); and T3 (maturation stage), during crop maturation and senescence, characterized by drying plants and seed/grain development (80–100 days after planting).

These development stages were selected to tackle critical phases of crop growth with different structural characteristics and potential for wildlife habitat, as well as different management practices and agricultural inputs (González et al. 2016). Each site was sampled during all three development stages for both crop types, resulting in six sampling events per site over the course of the agricultural year. To

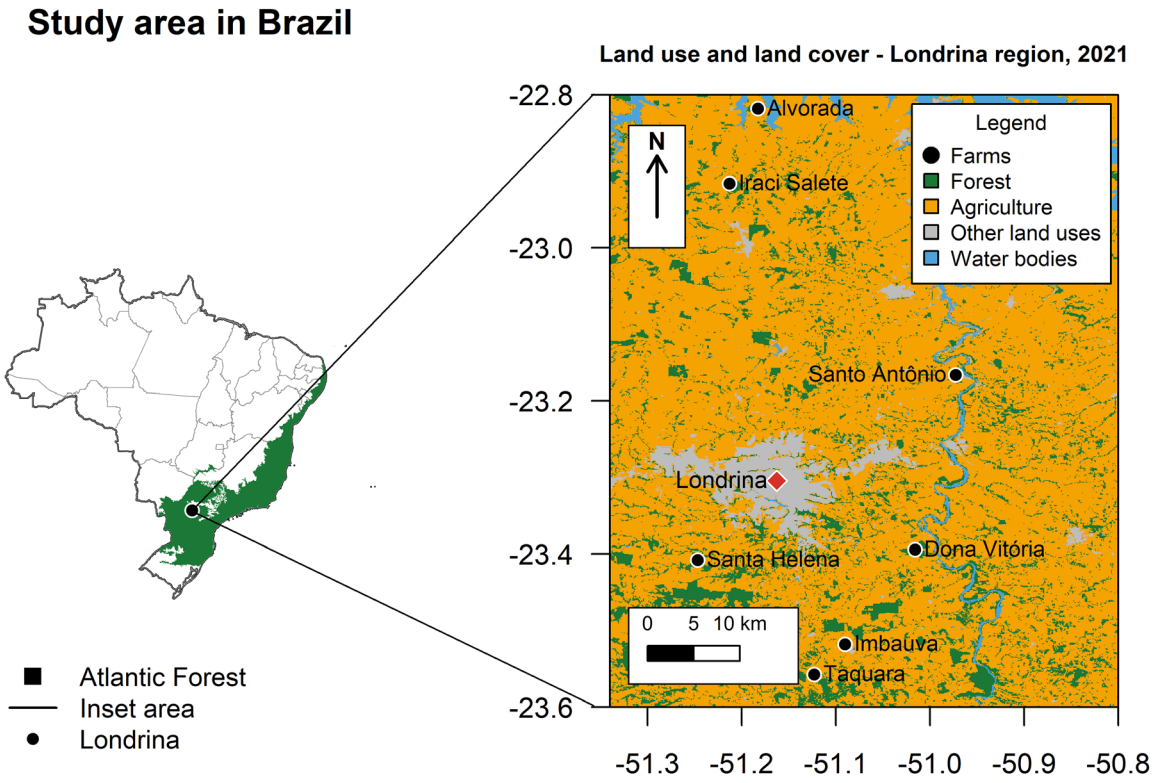

Figure 1: Land-use map of a region in Brazil with a detailed inset around Londrina. The map illustrates the spatial distribution of major land-cover classes: Farms (black dots), Forest (dark green), Agriculture (orange), Other land uses (light gray), and Water bodies (blue).

ensure comparability across sites, we selected farms that followed similar crop rotation patterns, with corn typically grown during the dry season (April–September) and soybeans during the wet season (October–March). All selected farms employed conventional tillage practices and similar pest management regimes.

2.3 Mammal surveys

In each sampling site (composed of a forest fragment and a crop adjacent to it), an established standardized protocol to survey mammals during both corn and soybean seasons was applied. In each sampling site, mammals were surveyed in three temporal windows following crop development (i.e., T1, T2, T3). Each temporal window consisted of a period of 7 days and six nights of surveys during which all groups were surveyed simultaneously. Mammals were surveyed along a spatial gradient from the interior of the forest into the interior of the crop: in the forest patch (which potentially serves as a source of individuals moving into crops) and two distances from crop edges into the crop: at crop edges (until max 10 m in the crop) and far from edges (~150 m in the crop). Efforts were made to adhere to the 7-day window as closely as possible, but there were exceptions when climate or other factors impacted the survey.

2.3.1 Small mammals

Dry pitfall traps were used to collect data on the species richness and occurrence of small mammals (Barros et al. 2015; Bovendorp et al. 2017; Boyle et al. 2021; de la Sancha 2014; de la Sancha et al. 2023; Umetsu et al. 2006). Pitfall traps were the main method for surveying small mammals. Sampling data by other methods (camera traps) were not included in the final analysis for standardization purposes. Dry pitfall traps consist of a sequence of containers (i.e., buckets) buried in the ground with rims at surface level connected by fences of plastic canvas and of 70 cm height; the fences intercept the small mammals during their movement on the ground and guide them to fall into the containers (Voss and Emmons 1996). In each environment (forest remnants, field border and field crop) of the seven sampled farms, we set a 56 m sequence of seven 60 L pitfall traps, yielding a mean interval of 8 m. Pitfalls were examined daily in the morning for six consecutive days at each of the three stages of corn and soybean development

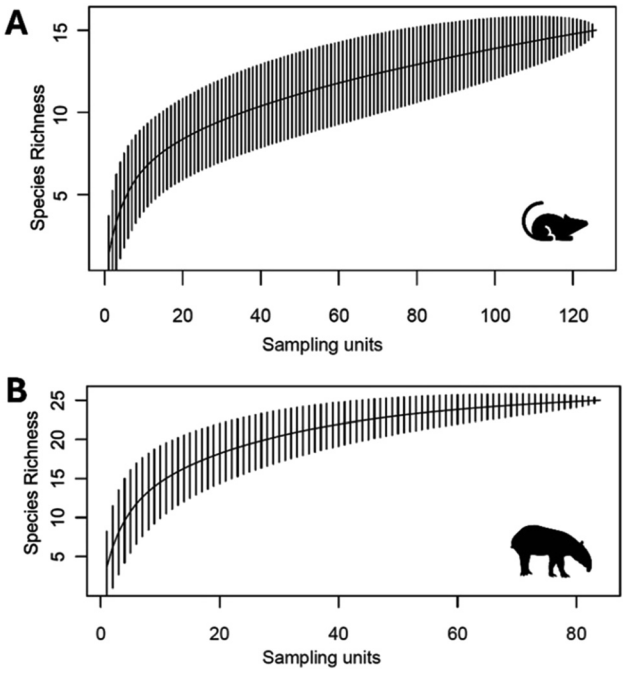

Figure 2: Sample-based species accumulation curve to assess the sampling effort applied to different groups across the study. (A) Sample-based species accumulation curve for small mammals, (B) sample-based species accumulation curve for medium and large-sized mammals.

(T1, T2, T3). The captured small mammals were measured, weighted, and photographed for identification, and some of them were collected to confirm the identifications performed in the field. Due to occasionally damaged pitfalls (e.g., after storms) and logistic problems related to farm access, the final sampling effort was 5,112 trap nights (only 3.4 % less than the planned 5,292 trap nights).

2.3.2 Medium and large-sized mammals

Observational methods were performed in each sampling site to detect medium-large sized mammals. Initially two methodologies were employed: (1) active search of evidence and (2) camera trapping. Since these two sampling designs would result in unequal sampling effort across the distance categories only the camera trap data was considered for all the assessments performed in this work. This selection was mainly because the crop fields were sampled only by camera traps while the field border was initially sampled by both active search and camera traps. Therefore, to normalize the sampling effort for medium-large sized mammals for the analysis of both trapping efficiency and species richness, only the camera trap data were considered in the estimation.

The camera trap sampling methodology involved the use of passive infrared camera traps (Bushnell Trophy Cam HD models), configured with a high-sensitivity motion trigger and a 10-s interval between consecutive recordings to minimize redundant captures. Each camera was set to operate in photo mode with time and date stamps enabled, and infrared flash was used to ensure night-time detection without disturbing wildlife. Camera traps were deployed in two locations per farm: one within the forest fragment (capturing data for the field border) and one at the crop edge directed towards the field crop (capturing data for the field). Cameras remained active continuously throughout all crop development stages (T1–T3), however for the trapping efficiency analysis only the sampling data produced for six trap nights was considered, so it can be comparable with the pitfall data for small mammals. We did not use camera trap images when estimating small mammal trapping efficiency.

To standardize the mammal occurrence analysis, we estimated the trap efficiency of each method, crop cycle and distance fragment by each trap night. The estimate was performed separately for both sampling methodologies – pitfall and camera traps – considering the distance fragments of forest (only for pitfall traps), field border and field. Trap efficiency was estimated by dividing the number of captured specimens by the number of traps available, for each trapping events (6 trap nights considered for both sampling methods) for each crop, farm and crop cycle and then we calculated the average efficiency of all sites for each treatment period (T1, T2, and T3) and crop (corn and soybean). For small mammals, we considered only the dataset from pitfall traps, while for medium and large mammals we considered only the data retrieved from camera traps (Table 1).

2.4 Statistical analysis

We considered each transect or pitfall trap line as a sampling unit, pooling the data from each taxonomic group (small mammals and medium-large mammals) collected on different days and during the same stage of each crop development (T1, T2, T3). To evaluate the adequacy of our sampling effort, we constructed sample-based species accumulation curves using the *specaccum* function from the *vegan* package in R. These curves were generated with 1,000 randomizations of sample order, allowing us to visualize the rate of species detection and assess whether the sampling approached an asymptote, as recommended by Gotelli and Colwell (2001). We adopted a sample-based approach rather than individual-based rarefaction to maintain consistency with our sampling design and to account for natural heterogeneity among sampling units. This method is particularly suitable for ecological studies where sampling effort is distributed across spatially distinct plots or transects. To

Table 1: Mean sampling efficiency considering all farms assessed for each crop type, crop cycle and distance fragment.

Crop	Crop cycle	Distance fragment	Pitfall trap mean trapping efficiency	Camera trap mean trapping efficiency
Corn	T1	Field	0.010	1.07
		Field border	**0.04**	**2.64**
		Forest	**0.04**	NA
	T2	Field	0.07	0.57
		Field border	**0.098**	**0.9**
		Forest	0.087	NA
	T3	Field	0.11	0.66
		Field border	**0.14**	**0.92**
		Forest	0.074	NA
Soybean	T1	Field	0.02	0.57
		Field border	0.057	**1.11**
		Forest	**0.12**	NA
	T2	Field	0.031	0.38
		Field border	0.075	**0.88**
		Forest	**0.2**	NA
	T3	Field	0.027	0.3
		Field border	0.081	**1.04**
		Forest	**0.095**	NA

In bold are the higher trapping efficiency values for each crop cycle and distance fragment. NA, not available.

estimate total species richness and assess sampling completeness, we applied non-parametric richness estimators, including Chao2 and Jackknife2 (Gotelli and Chao 2013).

Trapping efficiency inside the crop field and in the field border was calculated to understand if there was a higher occurrence of animals trapped in the field border compared to the crop field, which was one of the hypotheses tested in this study. As trapped individuals were not marked, no abundance estimates could be performed. To assess differences in species richness and trapping efficiency between the field interior and the combined off-field areas (field border and forest fragment), we applied Mann–Whitney U tests, which compare two independent groups. Each test was conducted as a pairwise comparison: field interior versus off-field (field border and forest fragment), separately for each crop type (corn and soybean). A more detailed description of each pairwise comparison made can be found in Table 2.

To test our three hypotheses, we conducted pairwise Mann–Whitney U tests comparing species richness and trapping efficiency between two independent groups at a time:

(a) Crop type effects: We applied a Mann–Whitney U test to compare the significance of the differences observed in species richness, trapping efficiency, and species community structure between corn and soybean fields.

(b) Distance effects: The number of species observed and the mean trapping efficiency for six trap nights were used to analyze how species richness and mammal occurrence changed along the distance gradient from forest fragments towards the crop field. To understand the statistical relevance of differences in species richness and trapping efficiency, we used a Mann–Whitney U test to compare two independent groups: the crop field (in-field) and the off-field areas (comprising forest interior and field border).

(c) Temporal effects: The effect of crop development stages was analyzed by using the number of species observed and the mean trapping efficiency for six trap nights considering each development stage (T1, T2, T3) determine if temporal patterns differed significantly between corn and soybean fields.

For the statistical analysis of small mammals since we had data for three different distance gradients (field, field border and forest) we performed two types of analysis, one considering a classical Mann–Whitney U-test with the values for the off-field pooled by two distance fragments: field border and forest and a Kruskal–Wallis test followed by a pairwise Mann–Whitney U-tests for all possible group combinations to identify which specific pairs differed. In order to simplify the results and because we were interested primarily in understanding the differences between inside the crop field and outside of the crop field we provided the results in Table 2 for the first analysis performed, however, we understand that doing it so, we would lose the visibility for the analysis and the impact of the distance from the field as gradient in increasing the diversity (one of the hypotheses considered in the manuscript).

Therefore, we corrected Table 2 to reflect the two distinct analysis we performed, for small mammals considering the second analysis based on the Kruskal–Wallis test followed by a pairwise Mann–Whitney U-tests for all possible group combinations and for large/medium mammals a classical Mann–Whitney U-test since we had only two distance gradient to compare (field and field border).

For small mammals in corn and soybean fields, sampling efficiency and species richness was compared across three distance gradients: Field, Field border and Forest. Because more than two groups were compared simultaneously, a one-way Kruskal–Wallis test was applied as the non-parametric equivalent of a one-way ANOVA (Kruskal and Wallis 1952). This test evaluates whether at least one group differs from the others in terms of rank distributions, without assuming normality or homogeneity of variance.

Table 2: Mann Whitney U test results for richness of species observed and trapping efficiency across crop type and distance gradient.

Small mammals					
Response variable	**Crop**	**Comparison**	***P*-value**	**Adjusted *p*-value**	**Significance**
Species richness	Corn	Field versus field border	0.027	0.081	Moderate
		Field versus forest	0.269	0.807	Not significant (ns)
		Field border versus forest	0.301	0.903	Not significant (ns)
	Soybean	Field versus field border	0.01	0.016	Moderate
		Field versus forest	0.011	0.032	Moderate
		Field border versus forest	0.869	0.998	Not significant (ns)
Trapping efficiency	Corn	Field versus field border	0.097	0.584	Not significant (ns)
		Field versus forest	0.028	0.167	Small
		Field border versus forest	0.14	0.84	Not significant (ns)
	Soybean	Field versus field border	0.008	0.045	Moderate
		Field versus forest	0.0003	0.002	High
		Field border versus forest	0.051	0.306	Small
Large/medium mammals					
Species richness	Corn	Field versus field border	0.0062	NA	High
	Soybean	Field versus field border	<0.0001	NA	Very high
Trapping efficiency	Corn	Field versus field border	0.0181	NA	Moderate
	Soybean	Field versus field border	<0.0001	NA	Very high

NA, not applicable.

The effect size associated with the Kruskal–Wallis test was estimated using eta-squared (η^2), calculated from the H statistic, which quantifies the proportion of variance in ranks explained by group membership (Tomczak and Tomczak 2014). Following a significant Kruskal–Wallis result, pairwise Mann–Whitney U-tests (Mann and Whitney 1947) were conducted for all possible group combinations to identify which specific pairs differed.

To control for the inflation of Type I error inherent to multiple comparisons, *p*-values were adjusted using a complementary correction method the Bonferroni correction, which is the most conservative approach and controls the family-wise error rate by multiplying each *p*-value by the number of comparisons (Dunn 1961). The effect size for each pairwise comparison was quantified using Rosenthal's r, derived from the Z-statistic of the Wilcoxon test divided by the square root of the total sample size, where values of 0.1, 0.3, and 0.5 correspond to small, medium, and large effects, respectively (Cohen 1988; Rosenthal 1991).

For large and medium mammals in corn and soybean fields, camera trap deployment was restricted to two distance gradients: Field and Field Border. Given that only two independent groups were compared, the Kruskal–Wallis test was not necessary; instead, a direct classical Mann–Whitney U-test was applied as the primary inferential test (Mann and Whitney 1947). This test compares the rank distributions of two independent samples and is the non-parametric equivalent of the independent samples *t*-test. The effect size was estimated using Rosenthal's r.

The Mann–Whitney U test was applied separately for each response variable (trapping efficiency and species richness) with a statistical significance set at $p < 0.1$. Effect sizes were estimated using the rank-biserial correlation performed using R language and the function 'wilcox_test()'. These results were computed with the significance value estimated (*p*-value) for each combination of crop type (corn and soybean), crop development stage and distance gradient (field and off-field areas), enabling a robust assessment of how agricultural practices and landscape structure influence mammalian occurrence and species composition.

3 Results

During the study period, which was throughout the productive year, we recorded 345 detections of small mammals from 14 species, and 515 detections of medium and large-sized mammals from 25 species. Sample-based species accumulation curves showed a clear tendency toward reaching an asymptote, indicating that the sampling effort was sufficient to capture most of the small mammal diversity across the study sites. For small mammals the observed

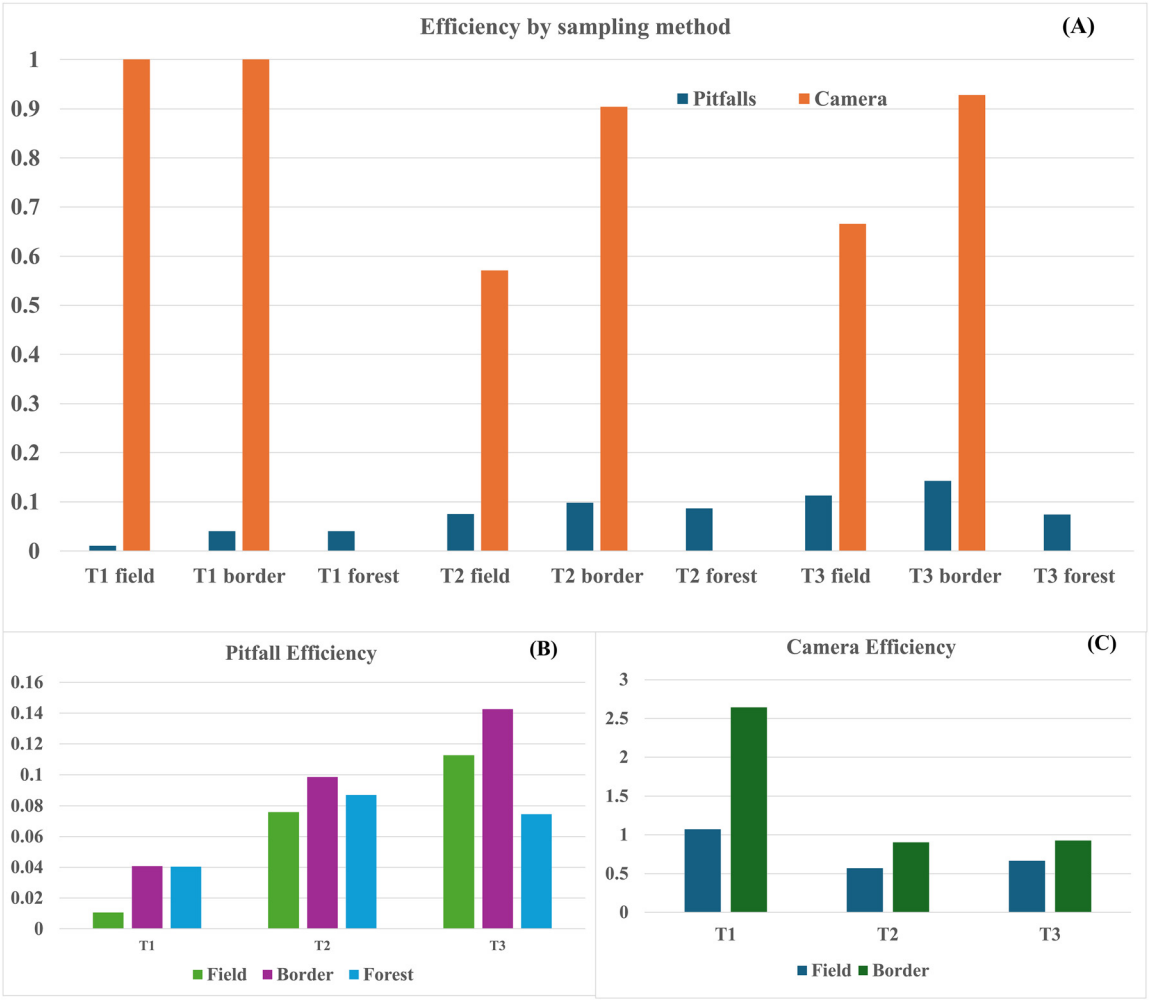

Figure 3: Trap efficiency in corn fields. (A) overall trap efficiency, (B) trap efficiency in pitfall traps and (C) trap efficiency in camera traps.

species richness was 14 species, while non-parametric estimators suggested slightly higher asymptotic values: 18.98 species according to Chao2 (95 % CI: 16.00–25.58) and 22.93 species based on Jackknife2. Sample-based analysis of medium and large mammal diversity revealed an observed species richness of 25 species, with non-parametric estimators suggesting slightly higher asymptotic values: 27.50 (95 % CI: 24.91–30.09) species according to Chao2 and 29.00 species based on Jackknife2. The close alignment between observed and estimated richness values supports the adequacy of the sampling effort and confirms that the inventory provides a robust representation of the mammal community across the study area.

Trap efficiency was estimated for both corn (Figure 3) and soybean fields (Figure 4). In both crops, trap efficiency was higher in the off-field areas (forest and field border) during the entire study. In corn, trapping efficiency of the pitfall traps (applied for small mammals) increased with the crop development stage, while for camera traps, trapping efficiency was higher only during the T1 period. As for soybeans, although the same trend was observed, regarding the camera traps, differences between the crop field and field border areas were smaller, which may be due to different effects like rainfall pattern, crop canopy structure which is smaller for soybeans when compared to corn and therefore facilitate spotting specimens.

The results of the Mann–Whitney U test (Figure 5 and Table 2) showed that corn species richness differed significantly between the two distance gradients. The Field Border presented higher median species richness (Median = 5) compared to the Field (Median = 3). The Mann–Whitney U test indicated that this difference was statistically significant (p = 0.0062, p = 0.081) supporting the conclusion that species richness was consistently lower in the Field than in the Field Border and Forest fragment for this crop in all crop cycles.

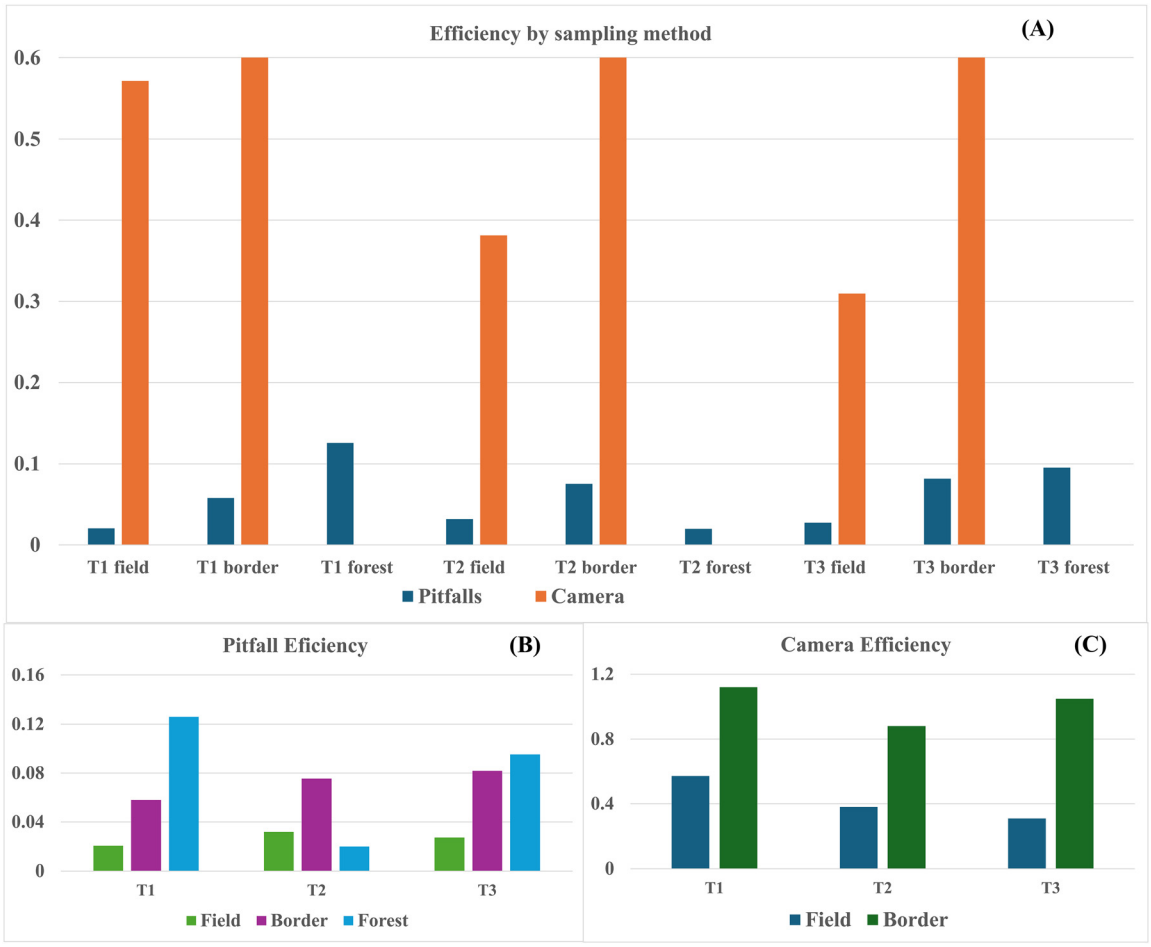

Figure 4: Trap efficiency in soybean fields. (A) overall trap efficiency, (B) trap efficiency in pitfall traps and (C) trap efficiency in camera traps.

In soybean the difference between fragments was markedly stronger. The overall Mann–Whitney U test indicated a highly significant difference ($p < 0.0001$, $p = 0.016$), with a large effect size ($r = 0.70$) and a median difference of three species (Field Border: Median = 6; Field: Median = 3). When stratified by crop stage, the difference remained statistically significant at all three stages (Stage 1: $W = 3.0$, $p = 0.006$, $r = 0.73$; Stage 2: $W = 2.0$, $p = 0.007$, $r = 0.74$; Stage 3: $W = 8.0$, $p = 0.039$, $r = 0.55$), with large effect sizes throughout, indicating a robust and consistent pattern independent of crop stage and sampling period.

Trapping efficiency for both mammal classes varied greatly between sampling locations, with off-field areas (median = 14.29 %) exhibiting up to twelve-fold higher detection rates than cultivated fields (median = 1.19 %). This difference was highly significant (Mann–Whitney U: $W = 69.5$, $p < 0.001$, $r = 0.569$, Cohen's $d = 1.386$), representing a large effect size that provides strong evidence of mammal preference for off-field areas when compared to crop field cultivation zones for both small mammals (Figures 6 and 7) and medium-large mammals (Figures 8 and 9). The observed spatial pattern indicates that agricultural fields may create habitat limitations, with cultivated fields supporting the smallest mammal trapping efficiency (mean = 2.62 % ± 4.22 %) compared to non-agricultural areas (mean = 15.48 % ± 12.42 %). Notably, field borders and forest zones exhibited equivalent efficiency ($p = 0.84$, $p = 0.306$), indicating these fragments function may act as preferred habitats. These findings emphasize that according to the trapping efficiency and richness of species observed, both mammal classes seem to present a clear preference for off field areas (field border and forest fragment) when compared to both field crop areas assessed.

3.1 Small mammals

A total of 345 individuals from 14 small mammal species were recorded, with significant differences in species richness between crop types, where the soybean seasons

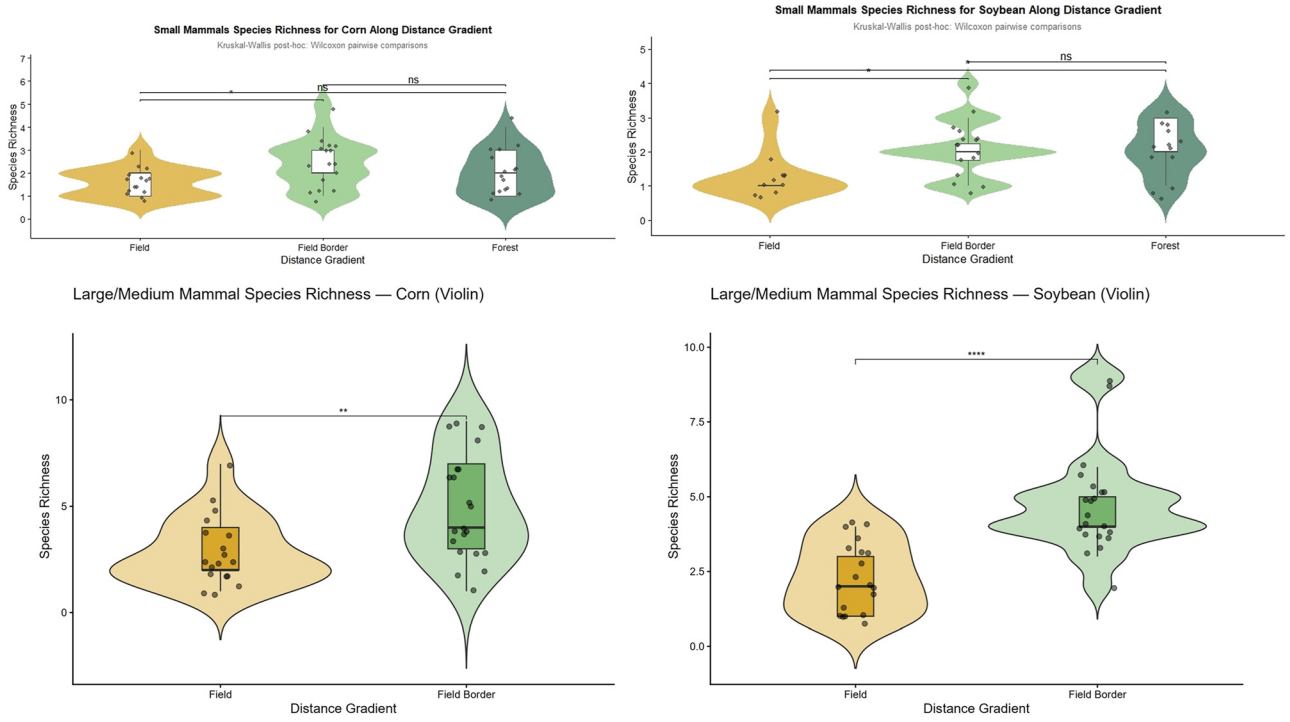

Figure 5: Mann–Whitney U test results to validate the species observation data for each crop and fragment considering both mammal classes.

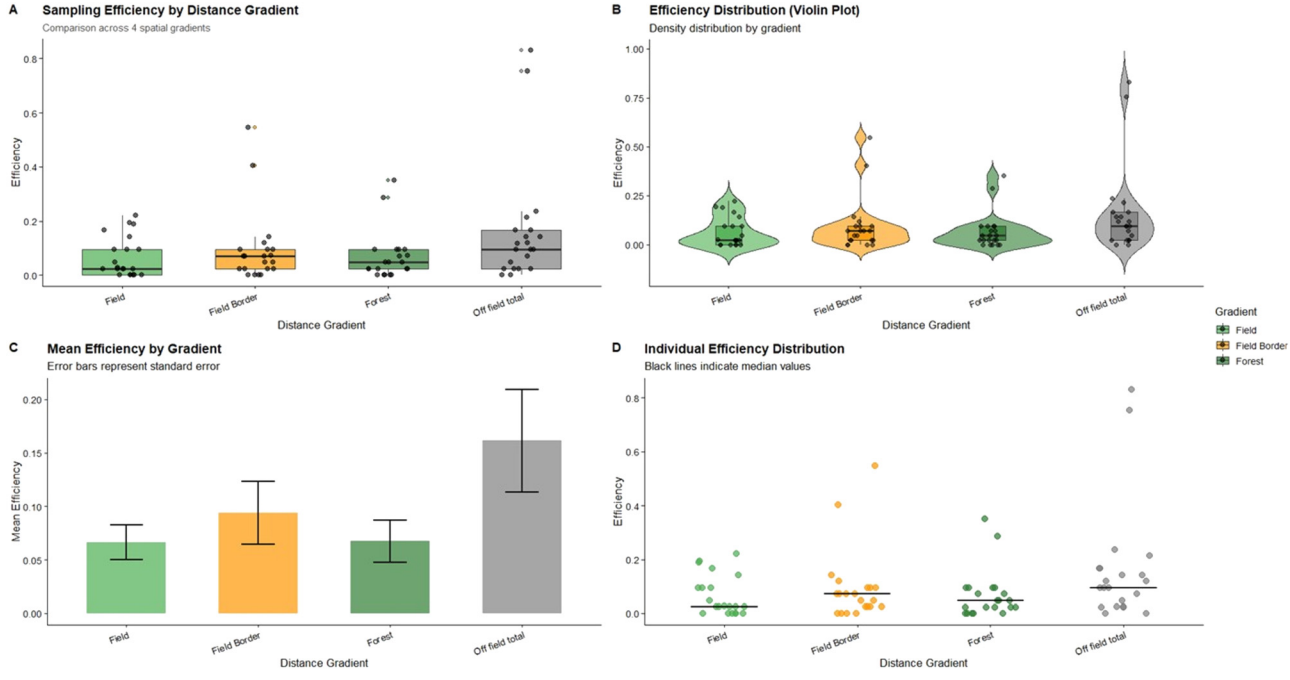

Figure 6: Mann–Whitney U test results to validate the trapping efficiency data for corn considering each crop fragment for small mammals.

exhibited slightly higher species observed with 12 species compared to 11 species during corn seasons. Each crop presented unique species with one exclusive to corn and three exclusives to soybean. Moreover, we also found significant variation in species richness across distance gradients and crop development stages (Table 2).

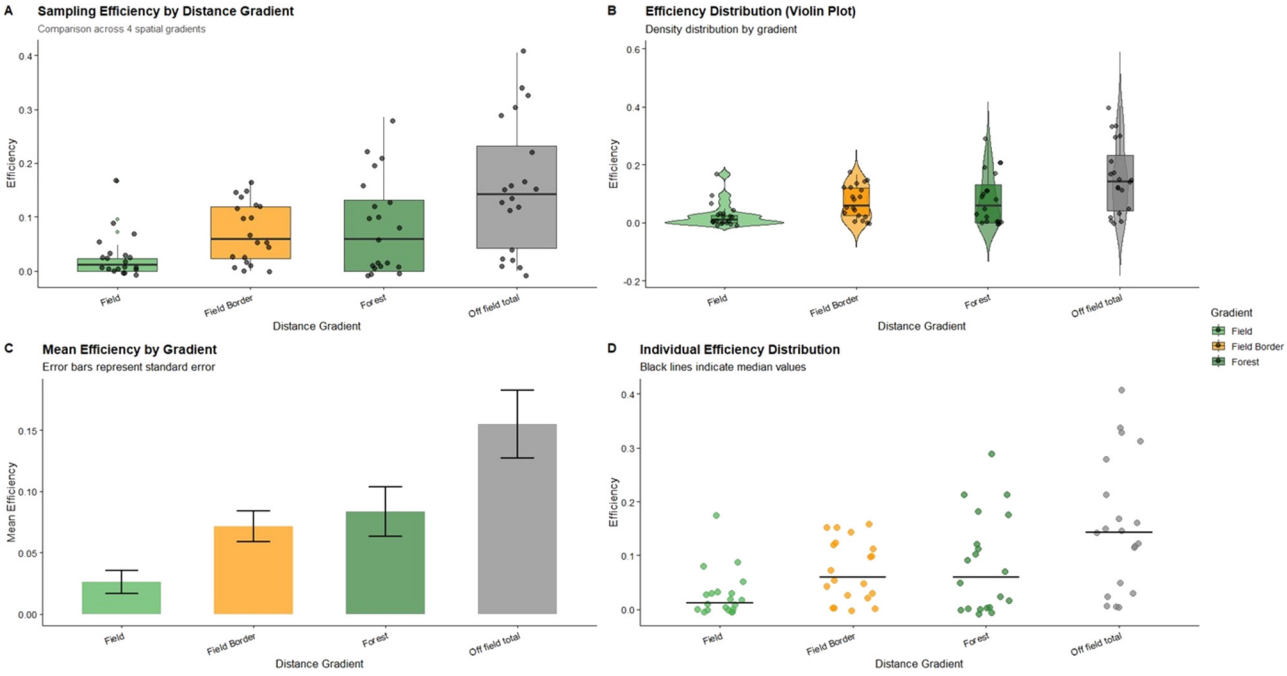

Figure 7: Mann–Whitney U test results to validate the trapping efficiency data for soybean considering each crop fragment for small mammals.

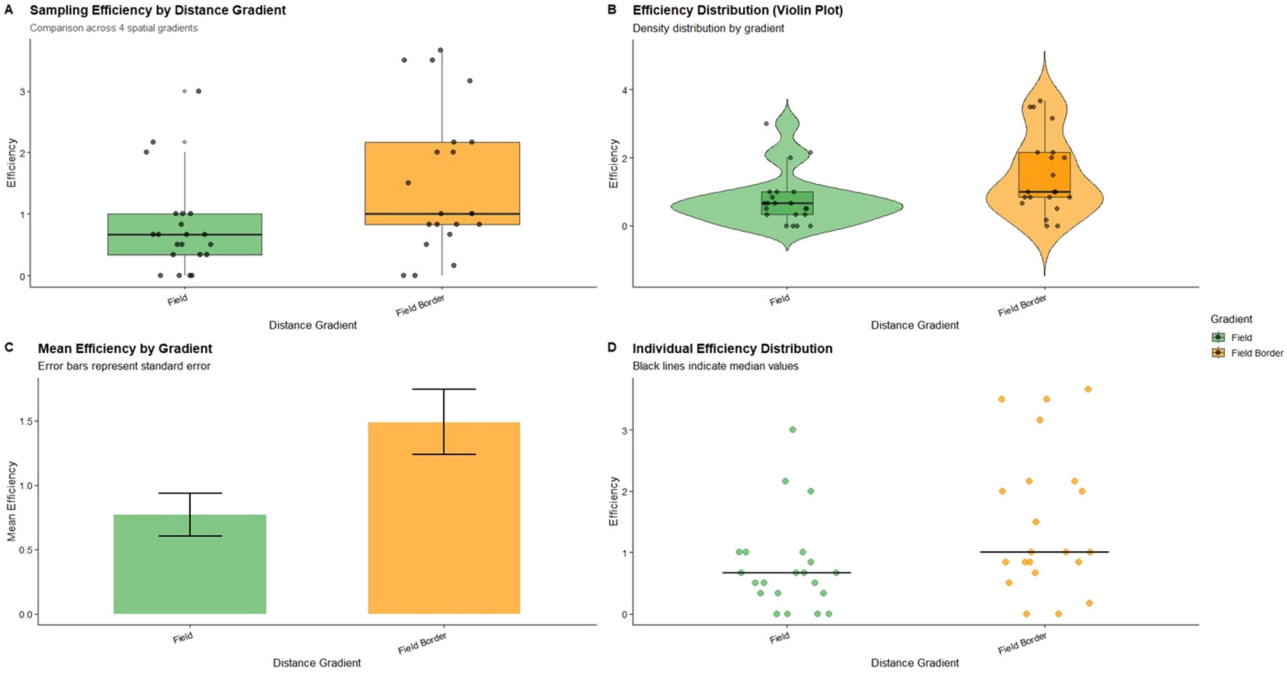

Figure 8: Mann–Whitney U test results to validate the trapping efficiency data for corn considering each crop fragment for medium-large mammals.

Regarding the trapping efficiency and occurrence of animals, there was a significant effect of crop type with soybean presenting a clear statistical difference for both species occurrence and trapping efficiency between the crop field and off-field areas ($p < 0.001$; Table 2). In addition, we found a statistically significant variation in the occurrence of small mammals between all three crop development stages and distance gradient. Our analysis suggests that seasonal factors, potentially rainfall and crop structure, may influence species occurrence in crop fields. However, these

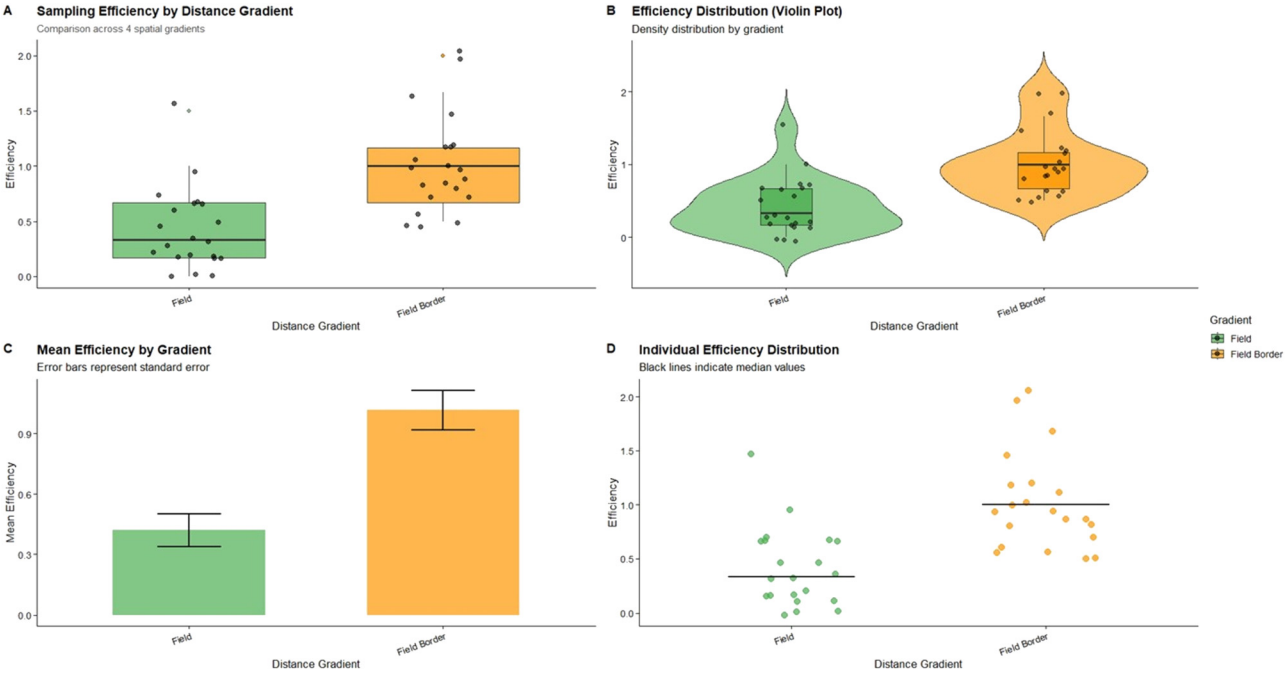

Figure 9: Mann–Whitney U test results to validate the trapping efficiency data for soybean considering each crop fragment for medium-large mammals.

effects are difficult to disentangle from changes in crop growth stages, which are closely linked to seasonal patterns.

In corn fields, *Cryptonanus* sp. (Voss et al., 2005) and *Bibimys labiosus* (Winge, 1887) were recorded both in the forest and in the field border, while *Marmosa paraguayana* (Tate, 1931) was only recorded in the forest. For soybean fields, *B. labiosus* were recorded both in the forest and in the field border, *Gracilinanus* sp. (Gardner and Creighton, 1989) was recorded only in the field, while *Cryptonanus* sp. and *Juliomys* sp. (González, 2000) only in the field border, and *Didelphis albiventris* (Lund, 1840) only in the forest.

3.2 Medium and large-sized mammals

A total number of 515 detections from 25 species of medium- and large-sized mammals were recorded. Regarding species richness, more species were observed during the corn season (23 species) than during the soybean season (21 species); species unique to each crop were also identified (corn: 4; soybean: 2). According to the results, a significant variation in species richness across distance gradients and crop development stages (Table 2) was observed.

Regarding the trapping efficiency, we found a significant effect of crop type on medium and large-sized mammals (Table 1), in general more individuals were recorded during the corn season (N = 319) than in the soybean season (N = 196). In addition, we found significant variation in medium and large sized mammal occurrence across crop development stages and distance gradients. We found a lower number of detections of medium and large mammals at the field in comparison to the field border (Table 1; Figures 3 and 4).

For corn, *Herpailurus yagouaroundi* (É. Geoffroy Saint-Hilaire, 1803), *Lycalopex gymnocercus* (G. Fischer, 1814), *Hydrochoerus hydrochaeris* (Linnaeus, 1766), *Leopardus pardalis* (Linnaeus, 1758), and *Conepatus chinga* (Molina, 1782) were only recorded in the field border, *Euphractus sexcinctus* (Linnaeus, 1758) and *Cavia aperea* (Pallas, 1766) were only recorded in the field. For soybean, *Sapajus nigritus* (Goldfuss, 1809), *Dicotyles tajacu* (Linnaeus, 1758), *Didelphis* sp. (Linnaeus, 1758), *L. pardalis*, *E. sexcinctus*, *Leopardus* sp. (Gray, 1842), *Myocastor coypus* (Molina, 1782), and *Eira barbara* (Linnaeus, 1758) were recorded only in the field border. As for *Sylvilagus* sp. (Gray, 1867), *C. chinga* and *H. yagouaroundi* were recorded only in the field. *Mazama* sp. (Rafinesque, 1817), *Galictis cuja* (Molina, 1782), *L. gymnocercus*, and *C. aperea* were only recorded in corn fields, while *M. coypus* and *E. barbara* were only recorded in soybean fields.

4 Discussion

The knowledge concerning how biodiversity occupies and responds to crop dynamics in the Atlantic Forest biome is

nearly absent. Therefore, this may represent a comprehensive assessment of spatiotemporal occupation of biodiversity in annual crops in the Atlantic Forest throughout their development. First, the contrasting effects of crop type (corn vs. soybeans) according to the taxonomic group evaluated represents a key result from this research. Considering both groups of mammals, trapping efficiency and richness were higher during the corn season. Second, there was a general trend of decline in species richness and mammal occurrence close to the crop fields, with both groups having a preference to occupy areas off-field (forest fragment and field border). Finally, temporal responses to crop development were also taxonomic-group dependent, with medium to large-sized mammals, occupying crops more intensively during early stages of crop development (at sowing), while small mammals occupied crops more intensively at later stages of development (blooming and maturation).

4.1 Spatial changes of biodiversity occupation in annual crops

4.1.1 Small mammals

It was observed that the community species structure changed significantly along the distance gradient from forest edge to crop interior in both crop types. This suggests that proximity to forest fragments is a crucial factor influencing small mammal diversity in agricultural areas.

Small mammals have small home ranges, typically up to 1 ha (Püttker et al. 2012), and their movements are restricted to a small spatial range (Bowman et al. 2002; Püttker et al. 2006). This suggests that at least the most common species observed in the fields *Calomys* sp. (Waterhouse, 1837), *Mus musculus* (Linnaeus, 1758) and *Oligoryzomys* spp. (Bangs, 1900) may use croplands as foraging habitat. During the study, we found several rodent nests in corn straw on the ground of crop fields, reinforcing this statement. As for all studied groups, the small mammal species able to colonize crop fields are specialized in open ecosystems, such as species from the genus *Calomys*, or are habitat generalists that occur in all major habitat types in fragmented landscapes, such as *Oligoryzomys* spp. (Umetsu and Pardini 2007). Except for *M. musculus*, an introduced European species strongly associated with anthropogenic habitats (Umetsu and Pardini 2007), small mammals can colonize crops from the remaining natural areas, including forest fragments acting as a source of individuals.

Both species richness and trapping efficiency of small mammals were significantly impacted by the distance gradient, with lower values observed in crop fields compared to forests and field borders. It is well known that secondary forest fragments, such as those in our study area, are important habitats for small rodent and marsupial species (Pardini et al. 2005; Pinotti et al. 2015), including unique forest-species for instance, (*M. paraguayana* and *Cryptonanus* sp.). The vertical structural complexity of trees and shrubs in forests provides specific microhabitats for many species, especially arboreal mammal species, as *Juliomys* sp. recorded in our surveys.

Three genera of native rodents *Akodon* sp. (Meyen, 1833), *Calomys* and *Oligoryzomy*, along with the introduced house mouse *M. musculus*, presented the highest occurrences along the survey. All of them are well known for their generalist habits and preference for open areas, with some variation in the presence of bushes, herbaceous vegetation, and anthropogenic interference (Patton et al. 2015; Wilson et al. 2017). For example, *Calomys* is a rodent genus that takes advantage of areas where the vegetation cover was completely transformed into open landscapes, like agricultural fields (Pardiñas et al. 2010). Concerning the differences among environments, only *Calomys* and *Mus* seemed restricted to fields and field borders, while *Akodon* and *Oligoryzomys* also occurred in the forest fragments.

We observed clear spatial variation in small mammal diversity along the distance gradient, with off-field areas consistently showing higher species richness and trapping efficiency. This pattern supports previous evidence that forest remnants provide structurally complex and stable habitats, which are essential for forest-dependent species (Püttker et al. 2008). For most crop periods field borders exhibited intermediate species richness and trapping efficiency values, indicating their role as transitional habitats that may facilitate movement and resource access for generalist species (Pardini 2004). In contrast, field interiors generally showed the lowest diversity, especially during early crop stages, likely due to reduced vegetation cover and habitat complexity (Mattos et al. 2021).

4.1.2 Medium and large-sized mammals

In contrast, medium to large mammals showed a different pattern. While their community species composition also varied significantly along the forest-to-crop gradient, we additionally found differences between corn and soybean fields. Medium and large mammals have larger home ranges since they can move across different land uses and travel

long distances daily (Garland 1983; Reis et al. 2011). Some species, such as *E. sexcinctus* and *Leopardus guttulus*, were never detected in the fields. Other species, such as the native *Cerdocyon thous* and *Tapirus terrestris*, and the invasive species *Lepus europaeus* and *Sus scrofa*, seem to tolerate better the agricultural matrix, as we found several traces of them in the fields. Even though most medium and large-sized mammals cannot live in landscapes composed of annual crops only since they require forested areas for resting, shelter, and feeding resources (Pereira et al. 2021), many species can move and forage in crop fields.

The ability of medium-sized and large mammals to occupy annual crops is also related to the amount of landscape-level habitat that provides stable year-round resources and habitat for this group (Andrade-Núñez and Aide 2010). However, it also depends on the degree of habitat dependence of different species (Püttker et al. 2020). Forest specialist species are more likely to respond negatively to habitat loss and conversion than generalist species (Devictor et al. 2008; Núñez-Regueiro et al. 2015; Zimbres et al. 2017).

A spatial variation in species richness and mammal occurrence along the distance gradient, with field borders consistently presenting higher number of different species was observed and higher mean trapping efficiency compared to field interiors. This pattern was consistent across both corn and soybean crops and aligns with previous findings that edge habitats often provide increased structural complexity, resource availability, and connectivity to adjacent natural areas, facilitating the movement and foraging of medium- and large-sized mammals, such as carnivores and ungulates, within agricultural matrices (Dorph et al. 2021). Field interiors exhibited the lowest trapping efficiency values, likely reflecting reduced habitat suitability due to limited cover and increased human disturbance, as commonly reported under land-use intensification (Santos et al. 2024; Santos et al. 2025). While our analyses indicate that field borders consistently presented higher occurrence of mammals compared to field interiors for medium and large-sized mammals, it is important to acknowledge potential methodological influences on these findings. Since two different sampling methods were applied to medium-large mammals, we decided to only consider the data available from the camera traps (considering a sampling period of six trap nights) to perform the statistical analysis presented in this work, however, methodological difficulties such as camera malfunctions and the different canopy structure of both crops assessed may influence in the trapping efficiency results throughout all crop cycles considered.

Therefore, we must interpret these occurrence patterns with caution, recognizing that while ecological factors such as increased structural complexity, resource availability, and connectivity at edges likely play a significant role, methodological considerations may also influence the observed magnitude of difference. Our focus remains on the *relative patterns* of habitat use across the gradient, acknowledging that absolute diversity comparisons between unequally sampled zones should be made with these limitations in mind.

4.2 Temporal changes in biodiversity occupation in annual crops

Regarding crop phenology, the patterns are not as straightforward as those detected only when looking for spatial patterns. We found a variety of responses changing across groups and different responses in different crops. Crop development stages have significantly affected the general species composition of small or medium to large mammal communities, especially considering soybean areas (Table 2).

4.2.1 Small mammals

The trapping efficiency of small mammals increased at later stages of development for both crop types (Table 1). Once the crop grows, the physical structure provides a habitat for different species. Several studies show that rodents inhabiting open areas increase their abundance with the complexity level of the environment (Mena and Medellín 2017). Several factors may contribute to this, including an increase in leaf cover, litter accumulation, soil cracking, increase in arthropods, increase in humidity, increase in the herbaceous vegetation at the borders, among other factors. These factors affect the availability of shelters, food, water, and reproductive sites.

Another factor that could explain the lower trapping efficiency of small mammals in the early stages of crop development is the heavy impact of farm machinery during plowing and sowing (T1) and harvesting (T3), which might lead many individuals to death or dislocation of their populations to other areas. Both stages might be stressful for the rodent population, generating several disturbances (Jacob 2003). Cavia et al. (2005) observed harvesting dislocated rodent populations living in the crop to forest edges (pattern observed for *Akodon* sp. in the mentioned study). At the T3 stage, corn and soybeans present low grain availability for rodents because most seeds remain attached to the plant until the harvest – especially the soybeans. Thus, we consider that crop seeds may contribute little to the increase in the trapping efficiency of small mammal species. Because the number of captures was related to the movement around

traps, we interpreted the trapping efficiency data as the intensity of use and mammal occurrence of these areas. Despite the lower efficiencies inside the field crops compared to other environments, our results suggest that fields could be used by some species of small mammals, especially during the corn season. Notably, small mammals showed a preference for corn fields rather than soybean fields. Rainfall appeared to have a direct effect on small mammal detection. The corn crops were remarkably dry in the region studied, while the soybean crop received more rain in the sampled period.

We observed temporal variation in small mammal trapping efficiency, with efficiencies generally lower during stage T1 and increasing in later stages, particularly at field borders. This pattern likely reflects seasonal shifts in resource availability and vegetation structure, which influence habitat suitability and foraging behavior (Püttker et al. 2008). Previous studies have shown that small mammals respond to crop phenology and microhabitat changes, with some species increasing activity and occurrence as vegetation matures (Pardini 2004). The observed increase in trapping efficiency during later stages suggests that crop development can temporarily enhance habitat conditions for certain species, especially in edge environments.

4.2.2 Medium and large-sized mammals

Large mammals showed lower occupation of crops in the later stages of development, with a more substantial effect during the soybean season (Table 2). One crucial factor in understanding the response of medium and large-sized mammals to crop seasonality and occupation of crops is that all of them are to some degree associated with forest habitats (except *L. europaeus* and *Sus scrofa*). Even the genus *Didelphis*, often observed in disturbed environments and common in rural areas, is associated somewhat with forest environments. In general, there is a relationship between home range size and resource availability, with higher resource availability leading to smaller home ranges (Anderson et al. 2005; Newsome et al. 2013). We could expect that the higher abundance of resources in the forest occurs during the wet season (soybean season) – which could explain the lower propensity of medium and large-sized mammals to cross soybean fields during the growing seasons since they might move less to achieve resources since the forest presents higher rates of resource availability.

Finally, the predominantly nocturnal activities of medium- and large-sized mammals may influence their response to crop phenology, as their primary interactions with the environment, including agricultural fields, occur during the night. While increased daytime temperatures (Kay et al. 2017; Rivrud et al. 2010) lead to lower diurnal activity and increased reliance on forest patches as thermal shelters during scorching days (Attias et al. 2018; Mourão and Medri 2007), nocturnal activity in crops might be influenced by different factors. For instance, the physical structure of crops at night could offer varying levels of cover from nocturnal predators or facilitate access to food resources. The higher abundance of resources in the forest during the wet (soybean) season, combined with potentially higher nighttime temperatures in open fields, might reduce the necessity for nocturnal mammals to extensively forage in crops, leading to the observed avoidance and lower trapping efficiency inside the fields during this period. As indicated in the Methods section, our study utilized camera traps configured for night-time detection, which helped capture these nocturnal movements. However, future research specifically focusing on the nocturnal ecology of these species within agricultural landscapes could potentially provide deeper insights into these complex interactions.

5 Conclusions

This study investigated mammal responses to agricultural landscapes in the Brazilian Atlantic Forest, examining effects of crop types, distance from forest fragments, and temporal patterns in crop development. We found that medium and large sized mammals showed different species compositions between corn and soybean fields, while small mammals presented a similar pattern across crops. Mammal species diversity and occurrence decreased with distance from forest fragments across all groups, highlighting the importance of field border fragments and forest patches. Temporal responses varied by group with small mammals increasing in trapping efficiency during later crop stages, while medium-large mammals were more frequently observed in early stages, particularly in corn fields. Off-field areas (forest and field border) maintained relatively high species richness and trapping efficiency throughout all crop stages, reinforcing their consistent role as key habitat features in modified landscapes. These findings contribute to understanding wildlife-crop interactions and inform management practices that balance agricultural productivity with biodiversity conservation.

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Informed consent: Not applicable.

Author contributions: All authors have accepted responsibility for the entire content of this manuscript and approved its submission. GSS: manuscript and data review; FC: manuscript and data review; AC: project coordination and manuscript review; MA: manuscript and data review; MP: project coordination; DS: manuscript and data review; SK: manuscript and data review.

Use of Large Language Models, AI and Machine Learning Tools: Not applicable.

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