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Landscape Composition Matters for Mammals in Agricultural Ecosystems: A Multiscale Study in Southeastern Brazil

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Abstract: The conversion of native habitats into anthropogenic ones compromises the original composition and configuration of the landscapes, influencing ecological dynamics and affecting biodiversity. Increasingly, landscape ecology has shown that these effects can only be understood if they are accessed at adequate spatial scales, as the scale at which landscape structure is evaluated influences species responses. Here, we investigated how three variables of landscape composition (proportion of forest, coffee crop, and pasture) and two of configuration (number of fragments and mean nearest neighbor distance) interfere with the richness and composition of medium- and large-sized mammals, considering a multiscale approach. We recorded medium- and large-sized mammal species in 13 landscapes with predominant matrices of coffee and pasture in Minas Gerais, Brazil. Then, we built distance-based linear models to identify the scale of effect of each landscape variable for both response variables considering eight scales (from 250 m to 2000 m). Finally, we verified the influence of the landscape on the richness and composition of mammals, considering the landscape variables in their respective scales of effect. We found 67% of the probable species occurring in the region. The scales of effect varied among landscape variables, probably due to the fact that different variables affect different aspects of organisms' ecological requirements. The proportion of pasture in the landscape explained the variation in species richness, while the proportion of forest explained the variation in species composition. In addition, the proportion of pasture in the landscape had a positive influence on species richness, indicating that this matrix may favor the presence of generalist species of habitat and/or this result is due to the higher concentration of species in the fragments immersed in this matrix. These results suggest that considering different responses to biodiversity is important to understand different aspects of the landscape's influence on biodiversity. In addition, the composition of the landscape is fundamental for the perpetuation of species and, therefore, both forest cover and types of matrices in the landscape must be considered to improve species conservation strategies. Finally, generalizing a spatial scale can lead to misinterpretations about the influence of the landscape on biodiversity.

Keywords: matrix; habitat loss; habitat fragmentation; scale of effect; landscape ecology

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1. Introduction

A large part of terrestrial ecosystems is impacted due to the conversion of natural habitats into anthropic habitats [1], which changes the composition (e.g., types and proportions of land uses) and configuration (e.g., spatial arrangement of landscape elements) of the landscape, causing the loss of native habitats and the fragmentation of the remnants [2]. Thus, habitat loss and fragmentation are the main causes of defaunation, including vertebrates of larger body size such as medium- and large-sized mammals [3–6].

Habitat amount is commonly evaluated to explain the species richness in forest fragments [7–9]. However, the matrix around the forest remnants also influences the occurrence of species and ecological dynamics [10–13]. The matrix's effects on species are mainly related to species movement and dispersion, availability of resources, and changes in abiotic characteristics [14]. In this way, anthropogenic matrices can have ambivalent effects on the impacts of habitat loss and habitat fragmentation on biodiversity.

Habitat fragmentation, per se, changes the original landscape configuration, increasing the number of forest fragments of different sizes and shapes and those under greater edge effects [15,16]. The effects of fragmentation on biodiversity have been discussed [12,16–19] and most are considered negative [18,20,21], although some are positive or neutral [16,17]. However, numerous studies have assessed the impact of habitat fragmentation without distinguishing it from habitat loss and without considering an appropriate scale [17]. Therefore, fragmentation should be evaluated using metrics associated with landscape configuration, as it involves the division of habitats, regardless of habitat loss [15,17].

Determining the optimal scale for collecting landscape composition and configuration variables poses a significant challenge in landscape-level studies [22–24]. This is a complex issue because species responses to landscape variables are influenced by ecological processes—such as metapopulation dynamics, dispersal, and inter- and intra-specific interactions—which operate at different scales [16,24–26]. One approach to tackle this challenge is to identify the scale at which each landscape variable has the most significant effect on the evaluated response variable, a concept known as the scale of effect. Adopting a multiscale approach involves assessing each variable at its respective effect scale [22,24].

The Atlantic Forest and the Cerrado are Brazilian domains with high species endemism and are highly threatened mainly due to habitat conversion for agriculture, livestock, and urbanization. Therefore, they are considered to be biodiversity hotspots [27–30]. The current forest cover of the Atlantic Forest is restricted to only 12% of its original extent, with approximately 84% of the remaining forest consisting of fragments smaller than 50 ha [31]. In the Cerrado, about 50% of the native vegetation has been converted into agriculture and pasture [30]. Consequently, the biological populations present in the forest remnants are under the influence of the landscape characteristics that persist in these fragmented landscapes.

A crucial aspect of understanding local patterns of mammal distribution is considering the influence of the surrounding environment [32]. Features such as the amount of native vegetation, landscape connectivity, and heterogeneity often correlate with species assemblages, and landscapes with greater land use heterogeneity can increase biodiversity by providing a wider spectrum of resources for species requiring different habitats [33,34], while the loss of native vegetation around habitat remnants leads to declines in native mammals species [35]. Given the ongoing loss of native ecosystems, understanding mammal distribution and land use responses in agroforestry landscapes is crucial for preventing further population declines, especially considering that mammals frequently incorporate certain agricultural matrices into their territories [36].

Thus, our main goal was to compare how landscape configuration and composition affect medium- and large-sized mammal communities in agricultural ecosystems. We also evaluated the scale of the effect of each landscape variable for both mammal richness and composition, and we compared the influence of matrix types on mammal communities. We hypothesized that landscape composition variables affect more mammal communities than landscape configuration ones. Also, we expected that the scales of effect vary among variables and the more different the matrix to the native habitat, the greater the influence of the matrix on the mammal communities. We hope that these issues will contribute to improving landscape management in agricultural settings to maintain biodiversity.

2. Materials and Methods

2.1. Study Area

We sampled medium- and large-sized mammals in 13 agricultural landscapes (1267 ha each) in Minas Gerais state, southeast of Brazil (Figure 1). This region is in a transitional zone between the Atlantic Forest and Cerrado domains, both hotspots for biodiversity conservation [27]. The study region has a subtropical climate, with the dry and colder season ranging from April to September and the wet and warmer season ranging from October to March, and a mean annual temperature and precipitation of 20.4 °C and 1460 mm, respectively [37,38].

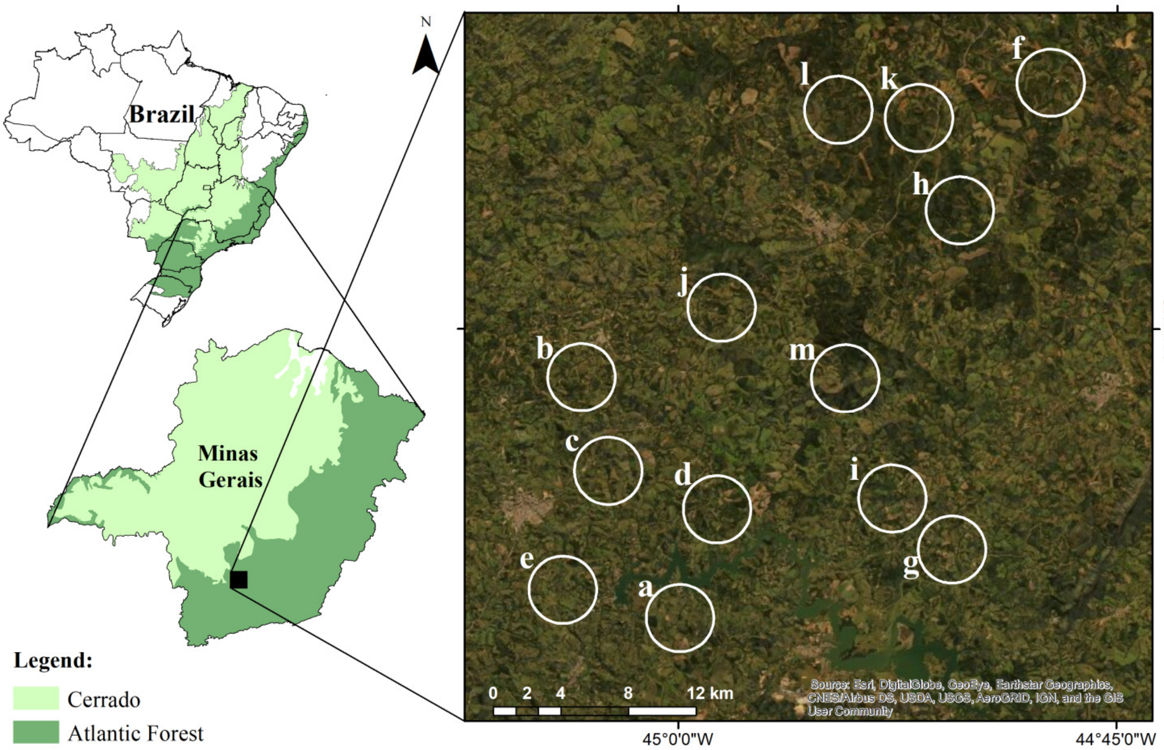

Figure 1. Study area in Minas Gerais, Brazil. The white circles in the image represent the largest buffers (2 km radius) around the focal fragment where the trap camera was installed.

We selected the landscape size (a radius of two kilometers, resulting in an area of 1267 ha for each landscape) based on similar studies that detected the influence of the landscape in medium- and large-sized mammals in landscapes smaller than or equal to two kilometers in radius [39,40]. We studied landscapes composed of small and dispersed fragments of semi-deciduous forest [31] immersed in an agricultural matrix dominated by coffee crops and pasture (Figure 1). The agricultural landscapes were chosen according to a gradient of forest cover, with the central point of each landscape located in a forest fragment. Given the high level of fragmentation in the study region, the sampled forest cover gradient varies from 10 to 47% in landscapes of 1267 ha. However, we believe this gradient is sufficient to evaluate the processes that shape the studied communities, as [8] identified a minimum threshold of 45% forest cover in landscapes of the same size to detect specialist forest species.

2.2. Data Sampling

We recorded mammal species using one camera trap (Bushnell HD, Bushnell Outdoor Products, Elk Grove, CA, USA) per landscape from December 2017 to August 2018. The cameras were installed in the central forest fragment (focal point) of each landscape, spaced at least four kilometers apart to avoid overlapping landscapes and to maintain data independence. The cameras were programmed to record three consecutive photos at three-second intervals when activated and to operate 24 h a day for four months in each landscape, totaling 1483 h of sampling effort across all landscapes. We considered photos of the same species taken at one-hour intervals as independent records [41].

We followed the patch–landscape approach to classify the landscape variables, collecting response variables in a focal fragment and landscape variables at the landscape level around the sampling point [42]. Data were collected at eight spatial scales from buffers around the focal point, with radius sizes ranging from 250 to 2000 m in 250 m intervals (Figure 2). In each spatial scale, we collected five landscape variables, as follows: forest cover, coffee cover, pasture cover, number of fragments (NPs), and mean distance among forest fragments (NNDis) (Table 1). We collected landscape data using high-resolution images with a reference scale of 1:5000 (ArcGIS 10.5 basemap imagery, Digital Globe satellites 2014–2017) and the V-Late extension (2013) in the software ArcGIS 10.5.

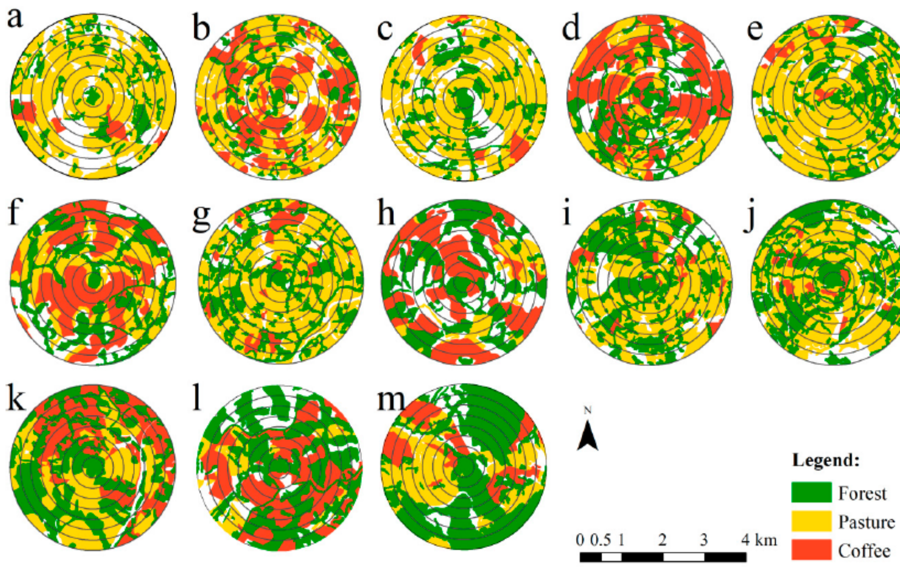

Figure 2. Landscapes sampled around the sampling point in increasing order ("**a**" to "**m**") of forest cover (see detailed description in Supplementary Table S1). The eight buffers around the focal point, where each camera was installed, represent the scales evaluated for each landscape variable.

Table 1. Landscape variables selected to evaluate the influence of landscape structure on medium- and large-sized mammals in agroecosystems in Minas Gerais, Brazil.

Variable	Meaning	Ecological Interpretation	Reference
Composition landscape variables			
Forest cover	Proportion of area covered by forest	Proxy for habitat amount in the landscape	[16]
Coffee cover	Proportion of area covered by coffee	More permeable matrix for forest species	[43]
Pasture cover	Proportion of area covered by pasture	Less or not permeable matrix for forest species	[44]
Configuration landscape variables			
NP	Number of forest fragments in landscape	More fragments indicates more fragmentation	[17]
NNDist	Mean distance among forest fragments (m)	The more isolated the fragments, the more fragmentation	[45]

2.3. Data Analysis

We considered just the terrestrial and native mammal species for the analysis, excluding eventual records from arboreal and exotic species [46,47]. First, we tested for spatial correlation between species composition and the geographical distance matrix using the Mantel Test. For this, we correlated the matrix of the presence and absence of species, using the Jaccard similarity, with the matrix of geographic coordinate points, using the Euclidean distance from the Mantel function of the Vegan package with 999 permutations in the software R (R version 3.4 and RStudio 1.0.136). There was no evidence of spatial correlation between the sampling points (r = −0.13 $p < 0.05$). Also, we evaluated the sampling effort per landscape from the 137 accumulation curves performed using the specaccum function of the Vegan package in R (R version 3.4.138 and RStudio 1.0.136). The curves were constructed based on the species richness per day of 139 samples. In general, the curves did not reach the asymptote (Supplementary Figure S1). Then, we compared the observed richness with that estimated using the first-order Jackknife estimator (Jackknife 1) [40] (Supplementary Table S1). We found a mean sampling sufficiency of 70%, which we considered enough to characterize mammals' communities in the landscapes.

For the selection of the scale of effect and the influence of landscape variables in both response variables (species richness and composition), we used distance-based linear models (DistLMs) performed in Primer 6 Permanova+ software [48,49]. We selected the scales of effect from the construction of univariate distance-based linear models using the determination coefficient (R^2 = proportion of variation explained using the model) as selection criteria. We selected according to the highest explanation value, independently from the significance of the model; as the species richness and composition are composed of species with different ecological requirements, the effect of a specific scale may not be evident [24]. So, we built eight univariate distance-based linear models, one for each scale for each landscape variable and response variable, totaling eighty models. We carried out this process for each response variable, species richness, and composition, considering the Euclidean distance and Sørensen's dissimilarity index, respectively. Finally, we verified the meaning of the influence of each explanatory variable on their respective scales of effect on species richness based on scatter plots generated in R software (R version 3.4 and RStudio 1.0.136).

After selecting the scales of effect, we tested for collinearity of the explanatory variables of each response variable using Pearson's correlation test from the rcorr function in the Vegan package of R. We found that the forest cover and pasture cover were correlated for species richness and composition (Pearson's r = −0.78; Pearson's r = −0.73, respectively). Then, we maintained the significant variable or the one with the greatest explanatory power (R^2) in the DistLM if none of them were significant. Therefore, for the general species richness model, we maintained the pasture cover, and for the general species composition model, we maintained the forest cover.

Thus, we built a general model for each response variable, including the non-correlated explanatory variables in their respective scales of effect to assess the influence of landscape structure on mammal communities. We built the general models using the stepwise strategy and selected from the adjusted R^2 with 999 permutations and a significance level of $p < 0.05$.

3. Results

We obtained 454 independent records of 24 species of medium- and large-sized mammals from 9 families, including 18 native terrestrial species, 2 native arboreal species (*Callithrix penicillata* and *Sapajus nigritus*), and 4 exotic species (*Bos taurus*, *Canis familiaris*, *Equus caballus* and *Sus scrofa*) (Supplementary Table S2). On average, we recorded six species per landscape, ranging from four to eleven species. *Dasypys novencinctus*, *Nasua nasua*, and *Leopardus pardalis* were the most recorded species, occurring in nine of the thirteen landscapes (about 70%), while *Puma concolor* and *Chrysocyon brachyurus* occurred in only one landscape.

The scales of effect varied among landscape and response variables. Pasture cover in the landscape was the only variable with an effect on the smallest tested scale (250 m) for the two response variables; however, the proportion of variation explained using the model was relatively low (Table 2). For species richness, the scales of effect for forest cover and the number of fragments were at 500 m, while for the coffee cover and NNDist at 1500 and 1250 m, respectively. For species composition, the scale of effect for forest cover was at

750 m, for coffee cover and number of fragments it was at 500 m, and for NNDist it was at 1250 m (Figure 3 and Supplementary Table S3).

Table 2. Sequential test of the distance-based linear model for species richness. Only uncorrelated variables were considered.

Variable (Scale)	Adj R^2	Pseudo-F	P	R^2	Cumul.	res.df
+Pasture cover (250 m)	0.3344	7.0298	0.024	0.389	0.389	11

Legend: Adj R^2 = proportion of the explained variation adjusted by the number of variables included in the model; R^2 = proportion of the variance explained by each variable; Cumul. = cumulative proportion of the variance explained by multiple variables; res.df = degrees of freedom of the residues.

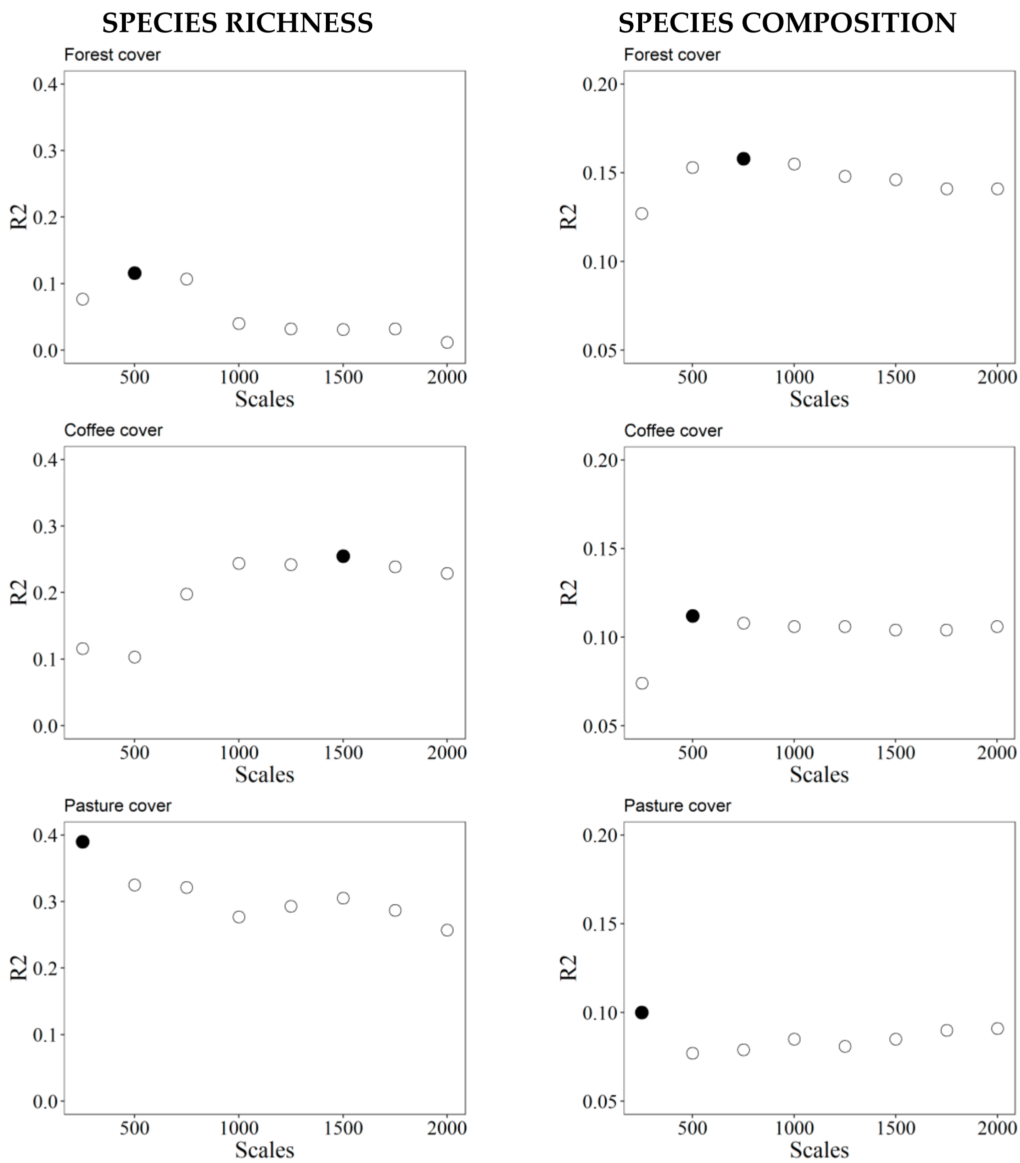

Figure 3. *Cont*.

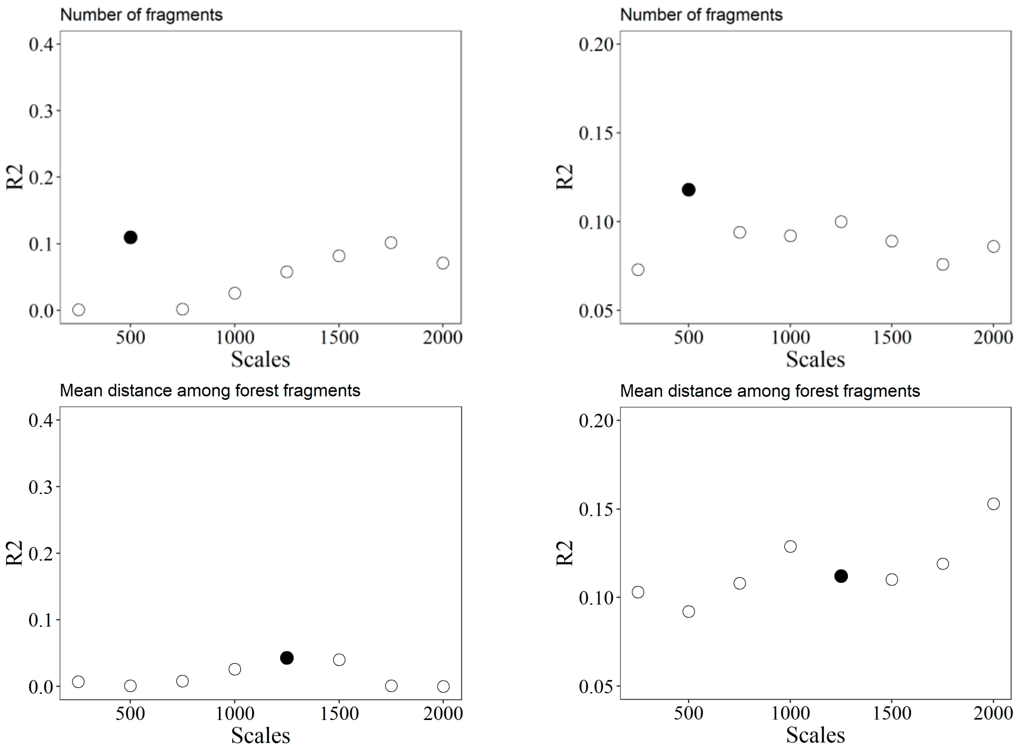

Figure 3. The scales of effect of each landscape variable for each response variable. R^2 = determination coefficient. Filled points = selected scales of effect.

In addition, considering the landscape variables in their respective scales of effect, we found that the forest and coffee covers negatively influenced the species richness. The pasture cover, number of fragments, and mean distance among the forest fragments positively influenced the mammal richness (Figure 4).

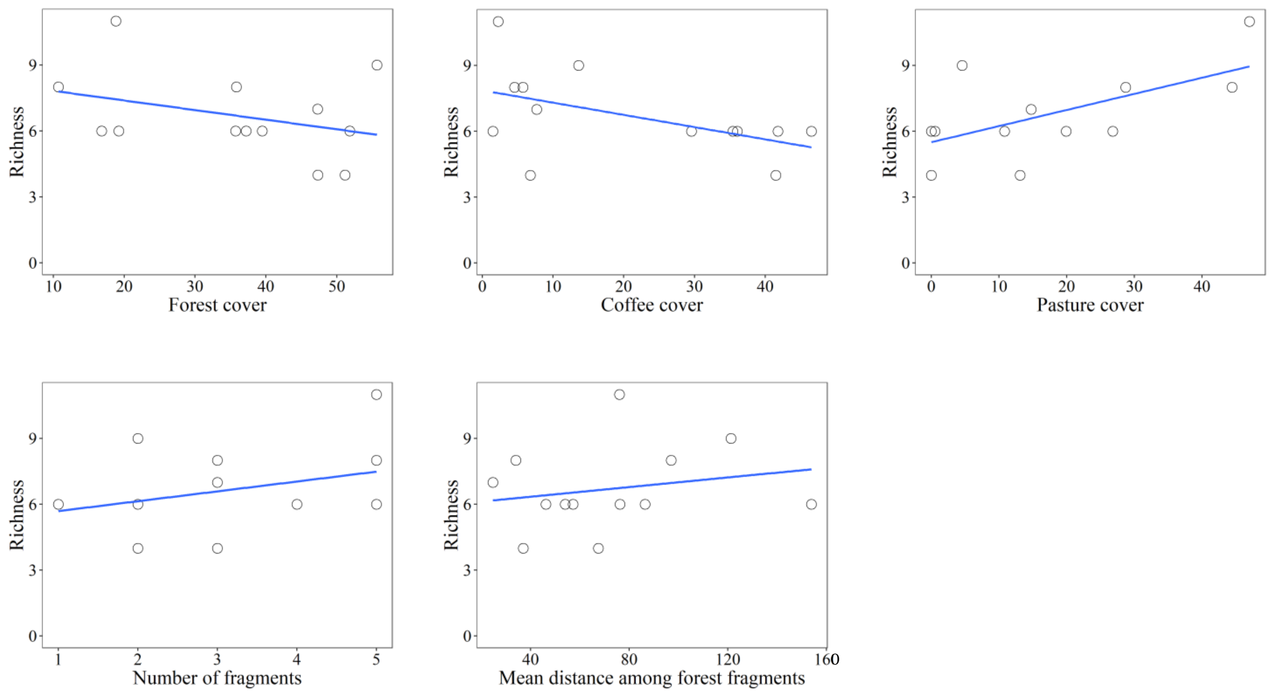

Figure 4. Scatter plots for species richness and landscape variables analyzed in their respective scale of effect.

Mammals Response to Landscape Variables

The variation in species richness was explained only by the pasture cover (adjusted R^2 = 33%, p = 0.024; Table 2). In other words, the pasture cover in the landscape influences the number of medium- and large-sized mammal species, while the variation in species composition was explained by forest cover (R^2 = 16%, p = 0.022), coffee cover (R^2 = 11%, p = 0.142), and the mean distance among the forest fragments (R^2 = 11%, p = 0.175; Table 3). The three variables together explained 17% of the variation in species composition. However, the coffee cover and the mean distance among the forest fragments were not significant ($p > 0.05$), suggesting that the inclusion of these variables did not add a substantial explanation to the model. So, the forest cover in the landscape interferes in which medium- and large-sized mammal species will be in the forest fragments.

Table 3. Sequential test of the distance-based linear model for species composition. Only uncorrelated variables were considered.

Variable (Scale)	Adj R^2	Pseudo-F	P	Prop.	Cumul.	res.df
+Forest cover (750 m)	0.0816	2.0668	0.022	0.1582	0.15817	11
+Coffee cover (500 m)	0.1226	1.5141	0.142	0.1107	0.26887	10
+NNDist (2000 m)	0.1658	1.5171	0.175	0.10547	0.37434	9

Legend: Adj R^2 = proportion of the explained variation adjusted by the number of variables included in the model; Cumul. = cumulative proportion of the variance explained by multiple variables; res.df = degrees of freedom of the residues; NNDist = mean distance among forest fragments.

4. Discussion

The scales of effect varied among the landscape and response variables, indicating that these variables affect large- and medium-sized mammal species in different aspects, highlighting the importance of evaluating different measures to understand the effect of landscape structure on biodiversity. We found that the landscape composition (forest, pasture, and coffee covers) influences the richness and composition of medium- and large-sized mammals more so than the landscape configuration (number of forest fragments and mean distance among forest fragments), and the pasture in the landscape has a positive influence on species richness, while the forest cover influences species composition.

The landscape composition and configuration influence ecological processes and can have different effects depending on the community structure and the spatial scale [25,26]. Different variables affect different dimensions of the ecological requirements of organisms leading to scale-dependent responses. For example, ecological processes such as metapopulation dynamics can shape ecological responses on larger spatial scales than processes such as competition, predation, resource availability, and anthropogenic impacts such as hunting [50,51]. In addition, different species can have different responses from the same variable at the same scale. That is, the quantity of a given agricultural matrix can be a barrier for the movement of species from the interior of the forest [10,52,53]. However, for generalist species, some agriculture matrices can function as an alternative foraging site, or even displacement corridor [54,55]. Thus, the scale of effect resulting from the response of species communities is the combination of the variation in the influence that each independent variable has on each species.

In our study, the pasture cover was the only variable that explained the variation in species richness, with a high explanation support (33%) for a positive relationship between the pasture cover and species richness. Although this result is contrary to the expected positive relation between richness and native habitat cover in agricultural landscapes [7,44,56], agroecosystems can favor the presence of generalist species from open areas and/or those typical of the Cerrado. Studies have shown that landscapes altered by anthropic processes tend to favor the occurrence of species with a low dependence on intact ecosystems or forest interior [57,58]. More than 50% of the species registered in our study have a wide geographical distribution, a varied diet, and a high movement capacity [59]; that is, species that can use different types of habitats and that can be favored in modified landscapes [60].

In other words, landscapes dominated by pastures are predominantly used by generalist species. In addition, some studies have also found no relationship between the richness of medium- and large-sized mammals and the amount of native habitat [8,21,61,62], while others have recorded a high species richness in landscapes with a strong urban [63,64] or agricultural influence [8,44,56]. In this way, species with a wide ecological niche can be favored by these modified landscapes and can, probably, maintain their populations in agricultural landscapes [65].

On the other hand, the positive relationship between species richness and the pasture cover in the landscape may be due to the use of the almost exclusive remaining fragments by the species, since the proportion of pasture is inversely proportional to that of the forest. In addition, we found, for example, that the landscape with the highest number of species (landscape P (e), Supplementary Table S4) has a high pasture cover and a low frequency of individuals of the sampled species. Consequently, the sampled fragment can be used by species present in the landscape as a foraging site, a reproduction site, or as stepping stones, mainly due to the reduced forest cover in the landscape [66,67]. In general, species with a large home range, as is the case of most medium- and large-sized mammals sampled, which persist in modified landscapes, depend on the remaining fragments present in the landscape [68], highlighting the importance of keeping small fragments in agricultural landscapes [17].

Our results also show that despite the fact that forest cover does not explain the variation in species richness, it influences species composition, explaining part of the variation between the sampled communities. Some authors [69,70] developed and improved the metapopulation theory based on the analogy to island biogeography theory [71], where the fragment size and isolation in a terrestrial landscape correspond to the size and isolation of oceanic islands. Since then, studies on habitat fragmentation include variables to represent this analogy and explain the relationship between species and area in continental environments [72,73]. However, the matrices around the fragments affect the biodiversity differently than that in the ocean, since fragmented landscapes are not binary like oceanic islands [52,74]. Nevertheless, Fahrig [16] argued that both effects of fragment size and isolation are shaped by the effect of the sampling area. That is, in a landscape of a certain size, the amount of forest habitat around the sampled forest fragment would be a better predictor for species richness [16] and other ecological responses [9,75] than fragment size and isolation [16]. In addition, Fahrig [16] adds that the matrix effect is secondary to the amount of habitat and that the landscape configuration should have little or no effect on the species. Although we have not corroborated this hypothesis for species richness, we found that the amount of native habitat (i.e., forest cover) was the variable with the greatest effect on the mammal composition, followed, and with minor importance, by the coffee cover and, finally, by mean distance among forest fragments. It is known that coffee plantation and pasture cannot provide suitable habitats for all mammal species. However, some species may use these areas as stepping stones between forest patches, such as studies in coffee areas in Costa Rica [76], Ethiopia [77], Mexico [78], and Guatemala [79]. Likewise, landscapes intensely altered by pasture tend to favor the occurrence of some generalist species that can cross these more open areas, such as pasture areas in Uruguay [39] and in the interior of São Paulo, Brazil [44].

As the landscape composition has a greater effect on medium- and large-sized mammals than landscape configuration, more heterogeneous and structurally more complex agricultural landscapes can greatly favor connectivity between the fragments and increase the diversity of species [75]. In addition, the role and management of the matrix to contribute to the conservation of biodiversity is one of the main strategies for the permanence of species in modified landscapes [14]. However, matrix management involves economic and social aspects in addition to ecological ones [80] and, therefore, an interdisciplinary approach is necessary for conservation measures in agroecosystems to be effectively applied.

Finally, exploring different responses to biodiversity can be important to understand different aspects of landscape influence on species. As well, the scale in which variables of landscape composition and configuration are measured can interfere with the species–landscape relationship. Therefore, we emphasize the importance of future studies on the relationship between landscape structure and biodiversity to consider different biodiversity responses and a multiscale approach with a wide range of scales. Also, with the advancement of geoprocessing tools and the development of free software, such studies are currently more viable. Considering landscape composition and configuration variables on an appropriate spatial scale allows us to expand our knowledge about the relationship between landscape and biodiversity and, thus, to improve management and conservation measures in agricultural ecosystems, notable to preserving the remaining forest fragments of the landscape.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/su16125066/s1, Figure S1: Species accumulation curves for each sampled landscape; Figure S2: Rarefaction and extrapolation curve. Solid line: interpolated values, dashed line: extrapolated values, gray area: confidence interval; Table S1: Values of the observed and estimated richness by the Jackknife estimator 1; Table S2: List of medium and large mammal species recorded by camera trap and their popular name; Table S3: Values of the marginal test of distance-based linear models for the species richness and composition of each scale selected for each variable. Significant values in bold. R^2 = proportion of the variation explained by each model; Table S4: Frequency of photographic records for each species in each sampled landscape. Number of occurrences = number of landscapes that each species was recorded; Total richness = total number of species, considering the arboreal and exotic species.

Author Contributions: R.F.P. and M.P. contributed to the conception and study design; R.F.P. and M.P. conducted the fieldwork and data analysis; R.F.P., C.R., and M.P. contributed to the interpretation, writing, and revision of the manuscript. All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as potential conflicts of interest.

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