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Drivers of mammal richness, diversity and occurrence in heterogeneous landscapes composed by plantation forests and natural environments



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ARTICLE INFO

Keywords: Landscape composition Landscape structure Camera trap Conservation Anthropogenic landscapes Brazilian Amazon

ABSTRACT

Agroecosystems dominate many landscapes throughout the world and it is crucial to understand the patterns of wildlife communities thriving in these areas, and the drivers shaping these patterns. Thus, we evaluated the effects of vegetation structure and landscape composition on the richness, diversity and occurrence patterns of medium and large mammal in a heterogeneous Amazonian landscape, composed by planted forest and native habitats. Based on line transects and camera trap surveys in three different environments (eucalyptus plantations, savannas and forests), we detected 17 mammal species, including two species threatened nationally and worldwide. Mammal richness and diversity were similar among the environments. Mammals were more recorded in eucalyptus plantations, at homogeneous areas (i.e. few edges), in sites with fewer roads, and with larger proportions of natural environments. The detection of Primates, Carnivora, Rodentia and Pilosa was positively correlated with the distance to savannas, while Cingulata, Artiodactyla, and Perissodactyla show the same pattern towards forest patches. Primates, Carnivora, and Rodentia were also associated with taller vegetation. Didelphimorphia was registered mostly in heterogeneous areas (i.e. higher total edge amount) while five orders were mainly recorded in homogeneous areas. Eucalyptus plantations immersed in a landscape containing significant patches of savanna and forest can maintain part of the local biodiversity, although plantations alone may not be enough to support populations of most mammal species. Indeed, eucalyptus plantations, savannas, and forest patches have a complementary role in mammal richness and occurrence patterns. Since distinct drivers influence occurrence patterns of different taxonomic groups, the existence of areas with different characteristics in the same landscape will favor higher total biodiversity.

1. Introduction

The establishment of protected areas is one of the main conservation strategies adopted to stop and reverse biodiversity loss, in which a more or less pristine area is spared for nature protection purposes; however, depending of its status (e.g. natural park, natural reserve) it can harbor some human activities (e.g. tourism, collection of natural products by local settlers - Dudley, 2008). Protected areas cover about 15% of the world's land surface and this proportion is increasing slowly (UNEPWCMC and IUCN, 2016). However, there are some deterrents for the expansion of protected areas, such as area availability, creation and maintenance costs and lack of public support to the creation of new areas (Bruner et al., 2004; McDonald and Boucher, 2011). Also, it is

likely that protected areas alone will not be enough to guarantee the conservation of most of the Earth's biodiversity (Myers et al., 2000). Thus, it is necessary to consider alternatives that enhance biodiversity conservation within anthropogenic landscapes. Some agroecosystems, depending on its management regime (e.g., intensive, extensive) and type of production, can be a part of a wider framework for biodiversity conservation. That being so, plantation forests are a good example of agroecosystems that are capable of maintaining part of the original local biodiversity (Chapman and Chapman, 1996; Loumeto and Huttel 1997; Barlow et al., 2007a, 2007b, 2007c; Gardner et al., 2009; Coelho et al., 2014; Luck et al., 2014; Peltzer and MacLeod, 2014) and should represent one alternative towards a land sharing solution. However, forest plantations are most likely to reduce biodiversity to some extent,

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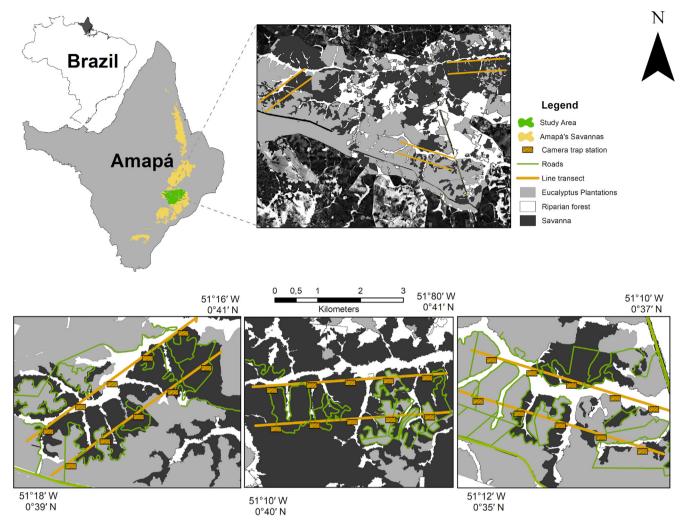


Fig. 1. Location of the study area within the state of Amapá, northeastern extreme of the Brazilian Amazon. Mammals were surveyed in three RAPELD (Rapid Assessments for Long-term Ecological Research) modules composed of two parallel transects (orange lines) interspaced by 1 km, and by camera traps (orange rectangles) installed at every 1 km along these transects. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and whether there will occur a net loss of species and the extent of this loss will depend mostly on the context where the plantation forest is implemented (Bremer and Faley, 2010) and on the taxonomic group (Felton et al., 2010). Negative impacts of planted forest on biodiversity are related to limiting dispersal, constraining food and shelter availability (Teixeira et al., 2017). Also, ecosystem services, such as pollination, pest control, storm protection and nutrient cycling are generally reduced in planted forests (Brockerhoff et al., 2013).

There are several factors that may contribute to increase biodiversity within landscapes dominated by plantation forests, such as landscape heterogeneity (Lindenmayer et al., 2003; Barbaro et al., 2007), structural complexity of the plantations (Lindenmayer et al., 2003; Nájera and Simonetti, 2009), undergrowth development (Stallings, 1990; Marsden et al., 2001; Carrilho et al., 2017), plantation age (Wilson et al., 2006; Brockerhoff et al., 2008; Timo et al., 2015), the presence of plantations with different ages within the same landscape (Lindenmayer and Hoobs, 2004; Timo et al., 2015), diversity of planted trees (Proença et al., 2010), and the maintenance of fallen trunks within plantations (Harltey, 2002). Considering this, it is clear that a correct implementation of planted forests, associated with adequate management, should enhance biodiversity in these landscapes.

Nevertheless, there are still some knowledge gaps. For example, most of the studies about the effects of plantation forests on biodiversity are from temperate areas (e.g. Wilson et al., 2006; Barbaro et al., 2007;

Brockerhoff et al., 2008; Proença et al., 2010), while in tropical regions such studies are less common, and most encompass landscapes historically dominated by forests (e.g. Stallings, 1990; Barlow et al., 2007a, 2007b, 2007c; McShea et al., 2009). Indeed, there are differences in the conservation value of plantation forests depending on the landscape matrix in which they were implemented. In general, there is a decrease in the richness and diversity of plants and animals in planted forests in landscapes dominated by tropical forests (Barlow et al., 2007a, 2007b, 2007c). However, in some savanna-dominated landscapes, there may be even an increase of biodiversity in planted forests due to its colonization by forest species (Loumeto and Huttel, 1997; Peltzer and MacLeod, 2014).

Despite the fact that savannas are biologically rich ecosystems, they have been often neglected by scientists, policy makers and land managers, that frequently consider them as the result of deforestation (Overbeck et al. 2015; Veldman et al., 2015a), being the target of afforestation and agricultural conversion to improve carbon sequestration and produce commodities (Veldman et al. 2015b). Therefore, there is an urgent need for a better understanding of the effects of planted forests on savannas ecosystems, especially targeting regions dominated by forests (e.g. Amazonian savannas).

Therefore, our study goals are to survey the assemblage of medium and large mammals in a heterogeneous landscape in the Brazilian Amazon, composed of savanna and forest patches associated to native areas converted into eucalyptus plantations, and to evaluate the effects of vegetation structure and landscape composition on mammal richness, abundance and occurrence patterns.

To achieve our objectives, we tested the following hypothesis:

- **H1.** Eucalyptus plantations retain a significant proportion of the local mammal species, although species richness will be smaller than natural environments (savannas and forests) since the former environments often provide lower resource availability (e.g. Majer and Recher, 1999);
- **H2.** Mammal richness and abundance increase with the age of eucalyptus plantations, considering that older plantations have more developed undergrowth (Timo et al., 2015);
- H3. The proximity to natural environments (i.e. savanna and forest patches) will increase the richness and abundance of mammals within eucalyptus plantations, because it may enhance resource availability and diversity (e.g. Rosenzweig and Abramsky, 1993; Zanuncio et al., 1998), and landscape heterogeneity;
- **H4.** High road density will decrease mammals richness and abundance because it may represent higher disturbance (e.g. Timo et al., 2015);
- **H5.** Denser tree canopy and taller vegetation will increase the richness and abundance of mammals because it may represent an increase in the niche space (e.g. Sushma and Singh, 2006; Louys et al., 2011);
- **H6.** Denser undergrowth will favor the occurrence of mammals because it may provide increased resource availability (e.g. Carrilho et al., 2017);
- **H7.** Different mammal species will be favored differently by distinct vegetation and landscape attributes due to niche differences (Louys et al., 2011).

2. Materials and methods

2.1. Study site

This study was carried out in the central region of the Amapá state (0°38′N; 51°12′W), northeastern extreme of the Brazilian Amazon (Fig. 1). The natural vegetation of this region is dominated by Amazonian savannas, interspaced with riparian forests. Amapá's savannas occupies over 10,021.4 km² and are a unique and rich environment, which includes endemic and rare species (e.g. Axonopus amapaensis and Borreria amapaensis; Hilário et al., 2017; Mustin et al., 2017). Furthermore, according to Hilário et al. (2017) and William D. Carvalho (unpublished data), these savannas are home for seven threatened mammal species: Myrmecophaga tridactyla, Priodontes maximus, Tapirus terrestris, Tayassu pecari, Alouatta belzebul and Leopardus tigrinus, which are classified as Vulnerable, and Pteronura brasiliensis, considered Endangered (IUCN, 2019).

Most of the study region was converted into eucalyptus plantations about 40 years ago, but plantations were placed within patches of native savanna and rainforest, whose maintenance is legally determined by the Brazilian law (Law 12.651/2012 - Fig. 1). This heterogeneous landscape occupy ca. 160558 ha (GEA et al., 2016), in which natural environments are interspersed within a matrix of plantations. The landscape matrix is composed of patches of eucalyptus plantations with different ages, heights and understory density. Understory management is infrequent in the area, leading to a relatively well-developed understory in older plantations. In Brazil, eucalyptus plantations are generally harvested in ~ 7 years (Santos, 2014).

The climate in the region is classified as Koppen's Am, with a mean annual temperature of $26.5\,^{\circ}\mathrm{C}$ and an average annual rainfall around $2,300\,\mathrm{mm}$. Rainfall is concentrated in a rainy season, from December to July. Nevertheless, even the driest months usually present rainfall above $60\,\mathrm{mm}$ (Oliveira et al., 2010; Tavares, 2014).

2.2. Sampling design

Our sampling design followed the RAPELD (Rapid Assessments for Long-term Ecological Research) protocol (Magnusson et al., 2005). We established three modules, each composed of two 5-km parallel line transects 1 km apart from each other (Fig. 1). Based on satellite imagery, we distributed the modules aiming to represent each of the sampling environments (savannas, eucalyptus plantations and forests). Nevertheless, it was impossible to distribute the transects evenly across the three environments.

In each transect, at every 1 km, we installed one camera trap station, starting 500 m from the beginning of the transect. Camera traps were placed 100 m off the transect to avoid theft. Cameras were attached to a tree/shrub trunk about 50 cm above the ground, in places that may maximize mammal detection (e.g. trails). Herbaceous vegetation was cut in front of the cameras to enhance mammal records and identification, and to reduce misfired shots.

We installed 30 camera trap stations (10 in each module). Following habitat availability and transect position, sixteen stations were located in savanna patches, eight in eucalyptus plantations and seven in forest patches. We used ten Bushnell Trophy Cam HD, that were moved between stations every 15 days to avoid seasonal biases, assuring that all sites were sampled every season. Cameras were configured to record 10-second videos, with a 10-second lag between consecutive videos. Cameras were turned on for 24 h a day, leading to a total sampling effort of 895 camera-days. Twenty-eight stations had a sampling effort of 31 camera-days, while two stations had a reduced sampling effort (12 and 15 camera-days), due to the harvest of eucalyptus plantations. If the same species were registered by the same camera, we only considered them as two independent detections if the interval between them was > 1 h, following Rovero and Marshal (2009) and Tobler et al. (2008).

Transects were traversed at a speed of approximately $1.25\,\mathrm{km}\,\mathrm{h}^{-1}$ searching for direct and indirect (e.g. tracks, scats) evidence of mammalian presence, starting at 7:00 in the morning and at 14:00 in the afternoon. The transects were swept clear of debris to avoid making noise and enhance detection of mammals. We never walked the same transect twice on the same day or on two consecutive days and changed always the direction in which the transect was walked to assure independence of the records. We walked 100 km in five transects and 102 km in one transect, totaling a sampling effort of 602 km. Indirect evidences were rare (three detections) and were not included in the analysis. Taxonomic nomenclature followed Wilson and Reeder (2005).

2.3. Vegetation structure

For the collection of data on vegetation structure, we divided the transects into $100\,\mathrm{m}$ sections and measured three vegetation variables in the middle point of each of these sections: vegetation height, canopy cover, and understory density. Overall, the six transects totaled 300 sections, with 51.7% of the transects covering savanna environments, 25.3% forest patches and 23.0% eucalyptus plantations.

Vegetation height for savanna and forest sampling points was accessed through radar imagery with a resolution of 2.5 m taken in 2015 and made available by Amapá State Secretary of Environment. Considering that the height of eucalyptus plantations changes relatively fast, we measured their height *in loco* with a rangefinder (Nikon Laser 600). Canopy cover was accessed with a 180° fisheye lens attached to the smartphone camera (Tichý, 2016). We took three photographs in each sampling point with the camera at 1.5 m above the ground and with the lens forming a 90° angle with the soil surface. The three photographs were taken at a distance of 5 m from each other, forming an equilateral triangle. Canopy cover of each point was considered as the average of the proportion of pixels represented by vegetation in the three photographs. To access the understory density, we positioned a 2.0 m tall, 1.45 m wide white canvas at 4.5 m from the sampling point

and took a photograph with the smartphone camera positioned 1 m above ground. We replicated this methodology twice at each point, perpendicularly to the transect for both sides. The understory density was accessed by the proportion of the white canvas that was covered in the photograph (Marsden et al., 2002). The photographs of the canopy and understory were analyzed with the Gap Light Analysis Mobile App -GLAMA (Tichý, 2016) and with the software Sidelook 1.1 (Nobis 2005), respectively. We also accessed vegetation height and canopy cover at the camera trap stations. However, we did not access understory density at these stations because we cut the herbaceous vegetation around some cameras to improve detection and avoid misfired shots. All sampling occurred between January and September 2018. A comparison of the vegetation structure between the three environments is presented in the supplementary material.

2.4. Landscape variables

Considering that mammal occurrence should not depend only on local characteristics but also on the surroundings of the point in which they were detected, for each camera trap station and for each transect point, we assessed the following landscape variables: (1) The distance to the nearest forest patch and distance to the nearest savanna patch; (2) the proportion of forest and savanna within buffers of three different radii (100 m, 200 m, and 500 m); (3) landscape heterogeneity, assessed by the total amount of edges (i.e. transitions among the different environments) within the buffers (Wu et al., 2000; Metzger, 2003); and (4) the length of roads within the buffers as a proxy of human presence and disturbance. To avoid overlap between buffers of consecutive points, buffers of 500 m radius were used only for camera trap data. The analyses were performed in the software ArcGIS 10.3.1 (ESRI, 2015).

2.5. Statistical analyses

2.5.1. Richness and diversity of mammals between environments

We estimated the richness and diversity of species recorded by camera traps and transects, using interpolated and extrapolated species accumulation curves, corrected by Hill numbers, which were constructed in the iNEXT R package (Hsieh et al., 2016). The Hill numbers used in the estimation were: q = 0 (species richness), q = 1 (Shannon diversity) and q = 2 (Simpson diversity). For each sampling method, we compared the Hill numbers up to a sample size of twice the size of the smallest sample (i.e. 20 individuals in the forest for camera traps, and 28 individuals in the savanna for transects), as recommended by Chao et al. (2014). The comparison of the richness and diversity curves between environments (hypothesis H1) were made based on the overlap of the estimated 95% confidence interval (Chao and Chiu, 2016). The Simpson diversity was considered as the effective number of dominant species (Hsieh et al., 2016). Eucalyptus was not included in the comparison of the curves for the transects, as it presented only one record throughout the study. Since mammal detection is different in cameras trap and transects, we estimated mammal richness and diversity separately for each method. We used a Venn diagram to display the species detection in each environment.

2.5.2. Assessment of drivers of mammal richness, abundance and occurrence

We applied ANOVA and Tukey post-hoc tests to assess whether the environments differed in the abundance of mammals (i.e. the number of records per sampling point). We used bivariate Pearson correlation to test if mammal richness and abundance recorded by the camera trap stations located within eucalyptus plantations are affected by plantation age (hypothesis H2).

To identify the drivers of mammal richness and abundance (dependent variables) (hypotheses H3, H4, and H5), we applied Poisson Generalized Linear Models (GLM) for camera trap data with the following independent variables: environment of the camera trap station

(savanna, forest patch or eucalyptus plantation), proportion of savanna within the buffer, proportion of forest within the buffer, distance to the nearest savanna patch, distance to the nearest forest patch, amount of edges within the buffer, length of roads within the buffer, vegetation height, and canopy cover. Nevertheless, some of these variables are correlated (tested through bivariate Pearson's correlation) and were not included in the models together. We used only one buffer size to assess all the landscape variables in a given model. Considering these restrictions for not including some variables together in the models, we tested different combinations of independent variables using the function "dredge" of the package MuMIn (Barton, 2016) and chose the best models using the lower AICc (Akaike Information Criterion corrected for small samples - Burnham and Anderson, 2002). We did not consider interactions between dependent variables in the models. Since sampling effort varied among camera trap stations, sampling effort was used as weight in the models. We checked whether the models met statistical requirements, such as absence of multicollinearity (checked through Variance Inflation Factor (VIF) with the package car - Fox and Weisberg, 2011), the absence of spatial autocorrelation in the residuals (checked through Moran's I with the package ncf - Bjornstad, 2018), and homogeneity and normality of the residuals (checked through residuals vs fitted and QQ-plots) following Fortin and Dale (2005) and Zurr et al. (2009). We provide the detailed procedure of model selection in the supplementary material. All analyses were carried in the software R 3.5.3 (R Core Team, 2019).

For transect data, two or more mammal detections occurred in only two of the 300 sections, and in none of them, a species were detected twice or more. Thus, we decided to analyze the transect data as presence/absence of mammal records in each point (dependent variable), instead of using the number of mammal records and the number of species per point. We selected a random sample of absences to achieve a more balanced number of presences and absences (32 presences and 50 absences) in the logistic model (Salas-Eljatib et al., 2018). Also, mammal detection was biased towards one of the transects (20 out of 32 detections). Therefore, we used binomial Generalized Mixed Models (GLMM) with transect identification as a random factor, through the function "glmer" of the package lme4 (Bates et al., 2015). We tested the same independent variables used with camera trap data (hypotheses H3, H4 and H5), and included understory density (hypothesis H6). We ran all possible models excluding correlated variables (after checking for multicollinearity by VIF) and chose the model with the highest AUC (Area Under the Curve) as the best model. We also checked for absence of spatial autocorrelation in the residuals.

To assess the drivers of mammal detection (hypothesis H7), we used Redundancy Analysis (RDA) with the package vegan (Oksanen et al., 2016) in R. Given that some species had only a few detections, we grouped species into orders. For camera trap data, the dependent variables were the number of registers of each mammal order in each station, while for transect data, we used the presence/absence of each order in each transect segment. We used the same set of independent variables used in GLM/GLMM analyses for camera trap and transect data. Since the largest buffer tested had the best results in the GLM analysis used to predict mammal richness and abundance, we assumed that the landscape is influencing mammals in broader scales, and used the data from the 500 m buffer for camera traps and from the 200 m buffers for transects. We used forward stepwise with the function "ordistep" of the vegan package to select the best set of environmental variables following Borcard et al. (2011). We used the VIF to check for multicollinearity in the chosen set of independent variables. Statistical significance was assessed through 4999 permutations.

3. Results

3.1. Patterns of mammal richness and abundance

We had 58 records of mammals in camera traps and 36 in line

Table 1

Mammal species recorded in camera traps and line transects within the state of Amapá, northeastern extreme of the Brazilian Amazon, including the environments in which they were detected. E - Eucalyptus plantations; S - Savanna patches; F - Forest patches.

Species	Order	Number of cameras with records	Number of records in cameras	Number of records in line transects	E	S	F
Didelphis marsupialis	Didelphimorphia	5	11	_	Х		X
Myrmecophaga tridactyla	Pilosa	2	2	-		X	
Tamandua tetradactyla	Pilosa	2	3	-	X		
Dasypus sp.	Cingulata	3	3	-		X	X
Euphractus sexcintus	Cingulata	3	3	1	X	X	
Alouatta macconnelli	Primates	-	_	4			X
Cebus olivaceus	Primates	-	_	2			X
Saguinus midas	Primates	1	1	7	X	X	X
Saimiri sciureus	Primates	-	_	1			X
Sapajus apella	Primates	-	_	10			X
Leopardus pardalis	Carnivora	2	2	-			
Cerdocyon thous	Carnivora	2	2	-	X		
Eira barbara	Carnivora	1	1	3		X	X
Tapirus terrestris	Perissodactyla	6	13	2	X	X	X
Mazama americana	Artiodactyla	1	1	4	X	X	X
Odocoileus virginianus	Artiodactyla	2	3	1		X	
Dasyprocta leporina	Rodentia	7	13	1	X	X	X

transects, corresponding to 17 species (13 in camera trap and 11 in line transects - Table 1) pertaining to eight orders. Six species were recorded exclusively by camera traps (Table 1), while four species (all primates) were recorded exclusively in line transects. Two of the recorded species are threatened, *Myrmecophaga tridactyla* and *Tapirus terrestris*, by the IUCN red list (IUCN, 2019) and the Brazilian red list (ICMBio, 2016).

The analysis of species richness and diversity did not show any difference between the tested environments, for camera traps or line transects (Fig. 2). The estimated richness was 16.0 ± 2.6 species for cameras trap sampling, and 14.8 ± 5.2 for transects. Forest was the environment with the greatest number of exclusive species (5), and four species were common to all three environments (Table 1, Fig. 3). Eight species were recorded in eucalyptus plantations, two of which were exclusive to this environment (*Tamandua tetradactyla* and *Cerdocyon thous*).

Considering the data from camera traps, records were evenly distributed among stations (abundance) in each environment (F $_{2;27}=0.523;~p=0.598$ - Fig. A.1), although slightly higher in eucalyptus plantations. However, the number of records in transects, adjusted for the distance walked in each environment, was significantly higher in forests (29.0 detections/10 Km) than in the savannas (18.0 detections/10 Km) and eucalyptus plantations (2.3 detections/10 Km - F $_{2;297}=20.94;~p<0.001$). Plantation age did not affect species richness (r = -0.4733621; df = 6; p = 0.2361) or abundance (r = 0.03615363; df = 6; p = 0.9323) at camera trap stations.

3.2. Drivers of mammal richness and abundance

The models that best predict mammal richness and abundance recorded in camera traps, indicate that mammals were more likely to be recorded in eucalyptus plantations (negative relationship with forest and savanna), at homogeneous areas (fewer transitions between different environments, i.e. edges), in sites with fewer roads, and with large proportion of forest within 500 m buffers (Table 2). Regarding the line transect data, no model was able to predict mammal presence/ absence reliably.

3.3. Drivers of mammal detection per taxonomic group

Mammal taxonomic groups (orders) composition was determined by environmental heterogeneity (amount of edge in 500 m buffers), distance to the nearest savanna patch, distance to the nearest forest patch, and vegetation height. According to the stepwise selection, the latter two variables were included only in the analysis of line transect data. Environmental variables explained 15.2% and 17.4% (adjusted R²) of

the variance of mammal records by cameras traps and line transects, respectively. Primates, Carnivora, Rodentia and Pilosa were recorded mostly away from the savannas, while Cingulata, Artiodactyla, and Perissodactyla were recorded mostly away from the forest. Primates, Carnivora, and Rodentia were also observed mainly in sites with taller vegetation. Didelphimorphia was most recorded in heterogeneous areas (many transitions between different environments) while Cingulata, Pilosa, Artiodactyla, Perissodactyla, and Rodentia were found mainly in homogeneous areas (Fig. 4).

4. Discussion

4.1. Patterns of mammal richness and abundance

Landscapes that are somewhat changed by human activities usually evidence a decrease in biodiversity (da Silva et al., 2019). Our results corroborate this pattern, since we detected only 43,6% of the mammal species whose distribution range overlaps with our study area (Silva et al., 2013). Nevertheless, this heterogeneous landscape still provides resources that support the presence of two threatened species. Coelho et al. (2014) found a similar species richness (N = 19) in a similar nearby landscape, with a similar sampling effort; however, five of these species were not detected in our study (Galictis vittata, Nasua nasua, Puma concolor, Mazama nemorivaga, and Cuniculus paca). Considering only eucalyptus plantations, we found a similar number of species (N = 8) to that reported by Coelho et al. (2014) (N = 7), with five species being common to both studies. Therefore, there are at least 10 medium and large mammal species using eucalyptus plantations of central Amapá, and this number is probably higher, considering that both mammal inventories may have not recorded some species. Some species may be using eucalyptus plantations as corridors between natural vegetation patches, while other may even feed on the eucalyptus undergrowth (Coelho et al., 2014). Indeed, although eucalyptus plantations are an anthropogenic environment, it can host significant richness and abundance of medium and large mammals, comparable to that of natural environments. A similar pattern was already detected in the Neotropics (Barlow et al., 2007a; Dotta and Verdade, 2011; Martin et al., 2012), but also in other regions where eucalyptus plantations are important agroecosystems (e.g. Portugal - Teixeira et al., 2017).

Mammal species richness was similar between the environments in our study, but some species were exclusive of some environments. This means that the three environments are complementary habitats, making the whole landscape more diverse. This pattern is in accordance with habitat heterogeneity hypothesis, i.e., an increase in the number of habitats leads to an augment in species diversity in a landscape

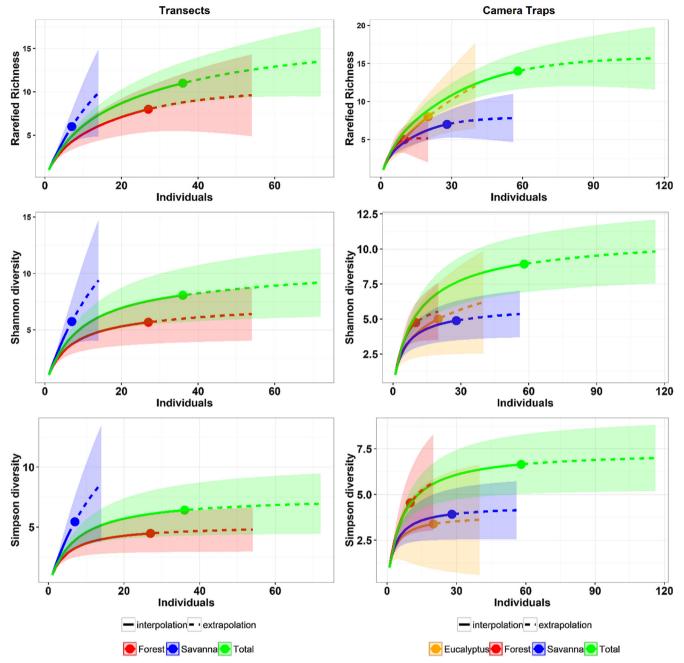


Fig. 2. Curves of rarefied species richness and diversity (Shannon and Simpson indexes), with 95% confidence intervals (shaded area), from mammals in eucalyptus plantations, and savanna and forest patches in the state of Amapá, northeastern extreme of the Brazilian Amazon. (2-column fitting image).

(MacArthur and MacArthur, 1961). The same pattern has already been observed for bats in Amapá's Savannas (Carvalho et al., 2018).

Contrary to other studies (e.g. Timo et al., 2015), we did not detect an effect of plantation age in mammal richness and abundance within eucalyptus plantations. This may be associated to the absence of an effect of understory density on mammal occurrence. However, the small number of camera trap stations within eucalyptus plantations (N=7) and the other factors that affected mammal occurrence within this environment (e.g. proportion of and distance to patches of natural environments, density of roads, and landscape heterogeneity), may have also influenced this result.

There was some inconsistency in the patterns of richness and abundance estimated by camera trapping and by line transects, with the former method recording similar values for the three environments, while the latter showed that forests present higher richness and abundance than savannas and eucalyptus plantations. This variation might be explained by the detection of five arboreal species (primates) in the forest during the surveys in line transects. Neotropical primates are poorly detected by camera traps (Tobler et al., 2008), and are dependent on habitats with connected tree canopies (Chapman and Peres, 2001; Louys et al., 2011). Both factors will result on primates being detected only in transects and within forests. Therefore, forest complexity (i.e. presence of different vertical strata, including a well-connected canopy), results in higher mammal richness in the studied landscape by creating conditions for primates to find the resources and to move. Primates may occasionally use plantation forests (Galán-Acedo et al., 2019); indeed, we registered Saguinus midas once in the eucalyptus plantation undergrowth. However, most of the use of plantation forests by Neotropical primates is in shaded plantations of cocoa and coffee (Galán-Acedo et al., 2019), where primates may still

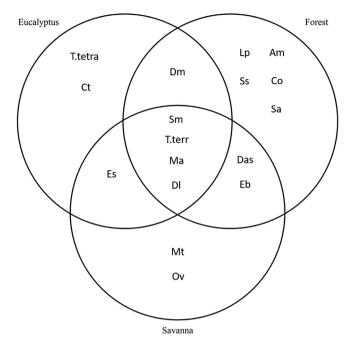


Fig. 3. Venn diagram showing the detection of the different mammal species in eucalyptus plantations, and savanna and forest patches in the state of Amapá, northeastern extreme of the Brazilian Amazon. Am: Alouatta macconnelli; Co: Cebus olivaceus; Ct: Cerdocyon thous; Das: Dasypus sp.; Dl: Dasyprocta leporina; Dm: Didelphis marsupialis; Eb: Eira barbara; Es: Euphractus sexcintus; Lp: Leopardus pardalis; Ma: Mazama americana; Mt: Myrmecophaga tridactyla; Sa: Sapajus apella; Sm: Saguinus midas; Ss: Saimiri sciureus; Ov: Odocoileus virginianus; T.terr: Tapirus terrestris; T.tetra: Tamandua tetradactyla. (Single column fitting image).

find connected canopies. The absence of connectivity between eucalyptus tree canopies (i.e. absence of thick horizontal branches that allow movement of medium and large mammals between trees) may pose a problem for Neotropical primates to use this environment. To the best of our knowledge, *Sapajus nigritus* and *Alouatta pigra* were the only Neotropical primates observed in eucalyptus plantation prior to our study (Bonilla-Sánchez et al., 2012; Liebsch and Mikich, 2015).

4.2. Drivers of mammal richness and abundance

Both natural environments (forests and savannas) had negative effects on the richness and abundance of mammals, indicating that eucalyptus plantations may favor mammal detection. This unintuitive result, which contradict some already published studies (e.g. Martin et al., 2012) may have been influenced by the frequent detection of *Didelphis marsupialis* and *T. tetradactyla* within eucalyptus plantations. These scansorial species may have gone under-detected in forest patches because of their use of higher forest strata (Hayssen, 2011; Vieira et al., 2012). Since eucalyptus plantations do not have a connected canopy, these species may be forced to use the floor, increasing their

detection in this environment. Indeed, if we remove these two species from the analyses, both richness and abundance of mammals become slightly smaller in eucalyptus plantations than in the natural environments. The models also showed that mammal richness and abundance are correlated with the amount of forest in the surrounding areas. Thus, eucalyptus plantations alone may not be enough to maintain populations of most mammal species, and they may depend on other resources found in natural environments. The fact that 500 m buffers were more efficient in explaining mammal richness and abundance patterns, also indicates that mammals depend not only on local conditions, but also in the surrounding characteristics. Indeed, several studies also concluded that the maintenance of mammals within planted forests depend on natural environment patches within the landscape (Hartley, 2002; Lindenmayer and Hoobs, 2004; McShea et al., 2009).

Mammal richness and abundance were negatively affected by the length of roads in the 500 m buffers. This variable is a surrogate of the disturbance level, and the detected pattern may be caused by human activities, such as hunting and car traffic, which are more common in or nearby roads (Trombulak and Frissell, 2000; Spellerberg, 1998; Pinto et al., 2018). Moreover, while roads themselves are naked land and do not bear food resources for most of the mammals, their presence also modify the surrounding environment (Trombulak and Frissell, 2000; Spellerberg, 1998); thus, high road densities may reduce resource availability for some mammal species.

Environmental heterogeneity is often associated with higher species richness in planted forests (Lindenmayer et al., 2003; Barbaro et al., 2007; Nájera and Simonetti, 2009; Azhar et al., 2014; Castaño-Villa et al. 2019). Nevertheless, in this study, heterogeneity was negatively related with both mammal richness and abundance. It is not clear what may have caused this negative relationship, but we detected a high number of taxonomic groups that are disfavored by environmental heterogeneity, which might be influencing the detected pattern.

We did not find any significant driver to mammal richness and abundance patterns found in line transects. This may be explained by the low detection of mammals (only 36 registers), and the concentration of records in one of the line transects, which had a greater proportion of forest. Such data distribution and the modelling results may be an indication that other factors that we did not assess are influencing mammals within this landscape. Lastly, the fact that different species and taxonomic groups differ in their drivers of detection may deter the identification of overall drivers of richness and abundance.

4.3. Drivers of mammal detection per taxonomic group

The analysis per taxonomic group showed some spatial specialization among species. For example, Primates, Carnivora, Rodentia and Pilosa presence was positively correlated with the distance to savannas, while Cingulata, Artiodactyla, and Perissodactyla were detected mostly away from forests. A dense understory may negatively affect the detection of larger species from Artiodactyla and Perissodactyla orders, especially when using camera traps (Burton et al., 2015), but also may increase the predation risk especially from predators that hunt by ambush, such as the jaguar and puma (Crawshaw and Quigley, 2002).

Table 2
Estimates of parameters of the best Generalized Linear Models, selected by lower AICc, to best predict mammal richness and abundance recorded by camera traps in eucalyptus plantations, savanna patches and forest patches in the state of Amapá, northeastern extreme of the Brazilian Amazon.

Independent variables	Richness			Abundance	Abundance		
	Estimate	Std. Error	p	Estimate	Std. Error	p	
Environment (Forest)	-0.938	0.121	< 0.001	-1.351	0.105	< 0.001	
Environment (Savanna)	-1.058	0.080	< 0.001	-1.061	0.065	< 0.001	
Amount of edges in a 500 m buffer	-0.354	0.032	< 0.001	-0.336	0.027	< 0.001	
Length of roads in a 500 buffer	-0.351	0.044	< 0.001	-0.513	0.036	< 0.001	
Proportion of forest within a 500 m buffer	0.112	0.040	0.005	0.158	0.033	< 0.001	

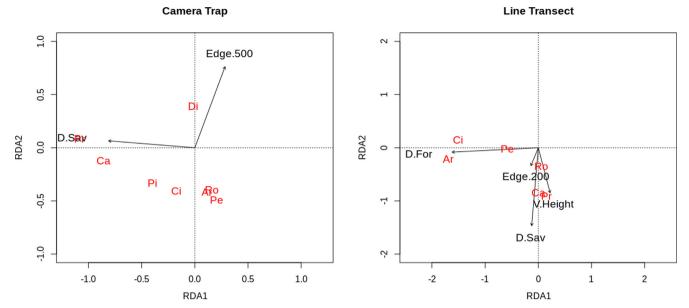


Fig. 4. Biplot with the first two axes of the Redundancy Analysis (RDA) relating the mammal records in camera traps and line transects to the environmental variables (arrows) in eucalyptus plantations, savanna patches and forest patches in the state of Amapá, northeastern extreme of the Brazilian Amazon. Mammal records were clustered in orders (red). D.Sav: Distance to the nearest savanna patch; D.For: Distance to the nearest forest patch; Edge.500: Amount of edges in 500 m buffers; V.Height: Vegetation height. Ar: Artiodactyla; Ca: Carnivora; Ci: Cingulata; Di: Didelphimorphia; Pe: Perissodactyla; Pi: Pilosa; Pr: Primates; Ro: Rodentia. (2 Column fitting image). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Conversely, Primates and scansorial species such as *Eira barbara*, may avoid savannas due to the absence of connected canopies, also supported by their occurrence in areas with taller vegetation.

Habitat heterogeneity also showed a contrasting influence pattern between mammal taxa. Didelphimorphia was most recorded in heterogeneous areas, while Pilosa, Rodentia, Cingulata, Artiodactyla and Perissodactyla were recorded mainly in homogeneous areas. This may be due to home range variation between species. *D. marsupialis* use smaller areas (Cárceres and Monteiro-Filho, 2001) and may benefit from different resources that are found in different environments, thus, being favored by high local heterogeneity. Conversely, other mammals, specially Pilosa, Artiodactyla and Perissodactyla, have larger home ranges (Tiepolo and Tomas, 2011; Duarte et al., 2012; Medici et al., 2012; Miranda et al., 2015; Ohana et al., 2015), when compared to the 500 m buffer, and considering their association to specific environments, they will be favored by homogeneous areas within the 500 m buffers.

5. Conclusions

We have shown that eucalyptus plantations immersed in a landscape that also contains significant patches of natural habitat can support some mammalian species, including threatened ones. The use of eucalyptus plantations by medium and large mammals depend on specific ecological requirements of each species and, thus, the existence of areas with different characteristics in the same landscape may attend these requirements and support high biodiversity. In addition, landscape heterogeneity and the presence of patches of native vegetation may favor mammal use of this altered landscape. Therefore, although eucalyptus plantations can host some Neotropical species, its aptitude to maintain such species will surely depend on the implementation system used that allows the co-existence of native patches within plantations to provide a variety of resources throughout the year. Such management may help conciliate economic production with biodiversity conservation. Vegetation structure (height) was important only for some mammal species (arboreal and scansorial). Amapá savannas are now threatened by soybean plantation expansion (Hilário et al. 2017; Mustin et al. 2017) and considering that eucalyptus plantations are more complex environments that permit the development of native undergrowth vegetation, these plantations may be pointed as a more favorable alternative for biodiversity maintenance.

Declaration of Competing Interest

This study was partially supported by AMCEL - Amapá Florestal e Celulose S.A, the enterprise that owns the eucalyptus plantations in which the study was carried.

Acknowledgments

We are grateful to CAPES for the scholarship to Tony Piña, and to AMCEL - Amapá Florestal e Celulose S.A. for supporting fieldwork. This study was carried with support of the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) - Process 88881.314420/2019-01 and Finance code 001. William Douglas de Carvalho is supported by a post-doctoral scholarship by Programa Nacional de Pós Doutorado of the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (PNPD-CAPES). LMR thanks the financial support provided by the University of Aveiro (Department of Biology), CESAM (UID/AMB/50017), cE3c (UID/BIA/00329/2013), and FCT/MEC through national funds, and FEDER within the PT2020 Partnership Agreement and Compete 2020. We also thank two anonymous reviewers for the valuable suggestions made on a first draft of this manuscript.

Funding

This work was supported by AMCEL (Amapá Florestal e Celulose S.A.), UNIFAP (Federal University of Amapá) and PPGBio (Postgraduate Program in Tropical Biodiversity)

Role of the funding source

AMCEL provided housing and food during fieldwork, while UNIFAP and PPGBio provided funds for transportation and field helpers. The sponsors did not have any involvement in neither the study design, nor in the collection, analysis and interpretation of data.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2019.117467.

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