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ORIGINAL PAPER

The role of remnants of Amazon savanna for the conservation of Neotropical mammal communities in eucalyptus plantations

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Abstract In this study, we investigated the effects of the partial conversion of native Amazon savanna into a eucalyptus plantation on the richness, composition, and abundance of medium and large mammals. Considering these plantations as an integral component of a patchwork savanna landscape, we verified how the negative effects of these plantations can be buffered by the conservation of remnants of native habitat within their area. We analyzed the contribution of each type of Amazonian savanna to the maintenance of the mammalian fauna and the potential of eucalyptus plantations to substitute these native habitats. A total of 23 mammal species were recorded in line-transect surveys conducted within the conserved savanna. By contrast, only eight species were recorded in the eucalyptus plantation and none of them were exclusive to this vegetation. However, the landscape patchwork formed by plantations and savanna was more diverse and contained 19 species of mammals, highlighting the potential importance of remnant savanna vegetation. The maintenance of remnants of savanna habitat may thus be essential for ensuring the conservation of mammals in the anthropogenic landscape of this region. It will also be important to include as many different subtypes of native savanna vegetation as possible and to consider the connectivity between habitats.

Keywords Abundance · Amazon savanna · Brazil · Medium and large mammals · Richness

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Introduction

Land use has changed forest cover throughout the tropics (Ellis et al. 2012). Deforestation has created a patchwork of landscapes, with forest remnants scattered among urban areas, pastures, fields, and plantation forests (Wright and Muller-Landau 2006; Barlow et al. 2007b). In the last 10 years, around 1.5 million ha of forest has been destroyed annually in the Brazilian Amazon region, and plantation forestry has contributed fundamentally to this process (Barlow et al. 2007a; Rodrigues et al. 2009; Davidson et al. 2012). Even with the drastic reduction of the conversion rates of native forest into plantations over the past few years (due to changes in Brazilian federal legislation), the Amazon region now accounts for almost 25 % of total plantation forestry of Brazil (IBGE 2011). In the Amazon region, and it is still possible to convert at least 20 % of the total area of natural vegetation cover to any type of land use that requires the clearing of this plant cover. Despite the reduced rate of conversion occurring in the present day, the plantations established in the 1970s and 1980s were mostly developed in tracts of pristine rainforest. In the Amazon savannas, the conversion of up to 35 % of the natural habitat is permitted by law. In this ecosystem, trees are planted mainly in grassland areas, with riparian forests being left largely intact.

Compared to other intensive agricultural land uses, eucalyptus plantations may provide complementary conservation services due to the fact that they present a low-contrast matrix for natural woody vegetation, with buffering edge effects and increased connectivity (Barlow et al. 2007b; Brockerhoff et al. 2008). On the other hand, the conversion of native forest into a eucalyptus plantation results in a drastic change in land cover (Barlow et al. 2008), which reduces the availability of resources for the mammalian fauna (including food and substrates), as well as altering primary productivity and the functionality of the ecosystem (Barlow et al. 2007b; Downing and Leibold 2002). Another effect is the loss of biodiversity (Lindenmayer and Fischer 2006; Barlow et al. 2008; Gardner et al. 2009). Most studies have recorded negative effects of large forestry plantations on the abundance and richness of both invertebrates and vertebrates, although the exact results will depend on the taxa analyzed (Harvey et al. 2006a, b; Barlow et al. 2007a, 2008; Gardner et al. 2007, 2008; Lo Man Hung et al. 2008; Umetsu et al. 2008; Louzada et al. 2010). Over the long term, the effects on biodiversity are likely to also affect the stability and functioning of the ecosystem (Cardinale et al. 2002; Naeem 2002; Pifsterer and Schmid 2002; Laliberté et al. 2013).

Given these considerations, what is the best scenario to reduce the impacts of eucalypt plantations on biodiversity? In this study we used experimental field studies to investigate the effects of the partial conversion of Amazon savanna into a eucalyptus plantation on the richness, composition, and abundance of medium and large mammals. We also analyzed if the negative effects of the plantations on mammalian diversity could be reduced based on data collected on a regional scale.

The Amazonian savannas encompass a diversity of habitats, including several types of vegetation with major structural contrasts, such as gallery forests and open grassland (Cole 1960; Eiten 1972). This habitat heterogeneity has a strong influence on patterns of species composition and abundance (Alho et al. 1986; Price et al. 2010), given that different habitats make distinct contributions to the maintenance of biodiversity (Mares et al. 1986; Redford and Fonseca 1986; Johnson et al. 1999; Barlow et al. 2007b). Considering the eucalyptus plantation as part of a patchwork landscape in the Amazon savanna, we also analyzed the contribution of each habitat (forest, grassland, and eucalyptus plantation) to the maintenance of mammalian diversity, and to determine if eucalyptus plantations can serve as surrogate habitats for the Amazon savanna mammal species.

Methods

Study area

This study was conducted in two landscapes of native Amazon savanna 70 km apart, located in the state of Amapá, Brazil, in the northeastern Amazon basin (Fig. 1). The first site is located in the district of Tartarugalzinho (1°30′21″N, 50°54′43″W) and encompasses around 94,000 ha of conserved Amazon savanna composed of ca. 41,000 ha of forest and ca. 53,000 ha of grassland (Fig. 1a). The second site is located between the districts of Porto Grande and Ferreira Gomes (0°42′46″N, 51°24′46″W) and encompasses a large mosaic of 2,20,000 ha, composed of ca. 87,000 ha of gallery forest, ca. 29,000 ha of savanna grassland and ca. 1,04,000 ha of eucalyptus plantation. The plantation (*Eucalyptus urophilla* and *Eucalyptus tereticornis*) was established in the 1970s on land originally covered by savanna grassland. The areas of savanna habitat were maintained intact in the riparian zones of small rivers and in deep valleys, forming corridors of native vegetation within the eucalyptus plantation (Fig. 1b, c).

The Amazon savanna is an ecosystem of high heterogeneity of habitats, which includes several types of vegetation (Cole 1960; Eiten 1972). In the present study, however, we considered all habitats to be either grassland or forest. We covered five different landscape categories (treatments) in the present study: (1) continuous savanna forest (F-SAV); (2) continuous savanna grassland (G-SAV); (3) eucalyptus plantation within a mosaic landscape (EUC); (4) remnant savanna forest within a mosaic landscape (F-EUC); and (5) remnant savanna grassland within a mosaic landscape (G-EUC).

Sample methods

The criteria used to select the sample areas of eucalyptus plantation (EUC) was the accessibility and age of the plantation. Tracts of trees of between 3 and 5 years of age, with heights of 10–14 m, were selected. Rotation time is 6 or 7 years when the plantation is clear cut. The plantations have a standard layout, with trees planted in a 3 × 2-m grid. Forest management involves silvicultural treatments to prevent the growth of native trees in the understory until the end of the second year. However, some pioneer plants can be often be observed growing within the plantations, including species such as *Vismia guianensis*, *Miconia* sp., *Cecropia* sp., *Byrsonima* sp., *Anonna sericea*, *Casearia sylvestris*, *Himatanthus articulata*, and *Bellucia* sp. There is usually a dense litter layer of eucalyptus leaves.

We collected data in four field expeditions of 20 days duration during both the wet and dry seasons, in 2009 and 2010. We used a line-transect sampling method (Buckland et al. 2004; Thoisy et al. 2008) to investigate the communities of medium and large mammals. This method consists of walking slowly (1–1.5 km/h) and in silence along a linear transect while identifying and counting all mammals or vestiges, such as feces (Rezendes 1999), encountered during the walk. Sixteen transects (or sample units) of 1.25 km were distributed within each treatment as follows: two transects each in the F-EUC and G-EUC, and four transects each in the EUC, G-SAV, and F-SAV. The minimum distance between each transect was 6 km, in order to minimize spatial autocorrelations. The transects in the eucalyptus plantations were positioned at least 300 m from the edge, but the F-EUC and G-EUC transects occasionally approached to within 80–150 m of the edge, where the savanna vegetation was distributed in narrow corridors within the eucalyptus plantation (Fig. 1c).

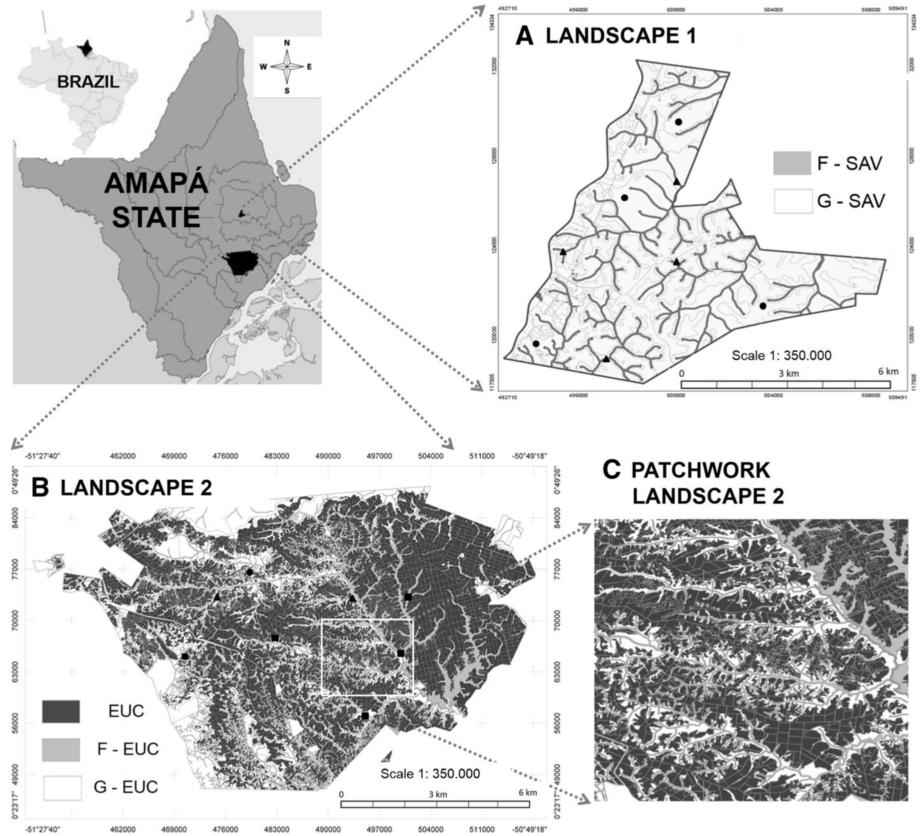

Fig. 1 Location of the study areas in Amapá State, Amazonian, Brazil, with the details of study sites. **a** Landscape 1: native and continuous Amazon savanna including savanna forest and savanna grasslands; **b**, **c** Landscape 2: patchwork landscape including, eucalyptus plantations with remaining savanna grassland and savanna forest. *Black circles* G-SAV and G-EUC, *black cones* F-SAV and F-EUC, *black squares* EUC

We conducted a daily survey from 5:30 to 9:30 a.m. and from 3:00 to 7:00 p.m. on each transect alternately. The same transect was never surveyed twice within 24 h (Buckland et al. 2004). All vestiges were removed once they had been recorded in order to avoid recounting in subsequent surveys.

The total accumulated distance walked in all transects was 900 km, but the sample effort differed between treatments due to the variation in transect length. This total included 90 km each along the F-EUC and G-EUC transects, 225 km along the F-SAV and G-SAV transects, and 270 km in the EUC.

Analyses

We compared the composition of mammal communities in the different treatments descriptively. The line-transect sampling method allowed us to compare the species abundance and richness of medium and large mammals among treatments. We calculated the relative abundance of species (Pi) using the number of individuals recorded per 10 km on each transect (Thoisy et al. 2008).

To compare the estimated species richness between treatments and landscapes, we converted the data into rarefaction curves in EstimateS 7.5.0 (Colwell 2005) using the Jackknife I estimator (Gotelli and Colwell 2001). To compare the difference between observed and estimated species richness, we used a standard statistical inference based on confidence interval estimates for the jackknife procedure, with significant differences being defined by a lack of overlap between the confidence limits of the estimates for different habitats.

To test the effect of the conversion of savanna to eucalyptus plantation on the species abundance and richness of medium and large mammals, we used a one-way analysis of variance, or ANOVA (Zar 2008). The data were checked for normality and homogeneity of variance, which permitted the use of this parametric test. An a posteriori Tukey test was applied when the result of the ANOVA was significant in order to identify which pairs of landscapes presented significantly different means.

To summarize the data on the structure and composition of the assemblages, we used a non-metric multidimensional scaling analysis, or NMDS (Delaney et al. 2000), which ordered the 16 samples based on the similarity of their composition in terms of the abundance of species. To test the differences in species composition between landscapes, we applied an analysis of factorial similarity (ANOSIM).

Results

We obtained a total of 464 records of 26 species of medium and large mammals (Table 1). Only eight species were recorded in the eucalyptus plantations (EUC), however, and none of them were exclusive to this habitat. A further 11 species were recorded in the savanna remnants within the eucalypt plantation (F-EUC and G-EUC), giving a total of 19 mammal species in the patchwork plantation landscape (Table 1). By contrast, 23 species were recorded in the conserved savanna habitats.

The deer of the genus *Mazama* and the armadillo *Euphractus sexcinctus* were notably more abundant in the eucalyptus plantation (Table 1). By contrast, all strictly arboreal species such as *Potus flavus* and the primates were recorded only in the savanna forest at both sites. With the exception of *Odocoileus virginianus*, all other ungulates and herbivorous species, such as *Mazama americana*, *Mazama nemorivaga*, and *Tapirus terrestris*, were recorded in all treatments. During the transect surveys, it was possible to occasionally observe tapir and deer feeding on the leaves of the trees of pioneer species, such as *Cecropia* sp., found within the eucalyptus plantation (but not those of the Eucalypts themselves).

Omnivorous species, such as *Cerdocyon thous* and *E. sexcinctus*, which are typical of open habitat, were more abundant in grasslands and eucalypt groves (Table 1). With the exception of *Myrmecophaga tridactyla*, all species observed exclusively in continuous savanna, such as *Eira barbara*, *Procyon cancrivorus*, *P. flavus*, *Cabassous unicinctus*, and *Tayassu pecari*, were recorded infrequently, which suggests that they may be naturally rare in the region.

None of the rarefaction curves stabilized, indicating the potential presence of additional species in all treatments, although the difference was least pronounced in the EUC and F-EUC, for which 86 % of the estimated number of species were recorded (Fig. 2). By contrast, observed species richness in G-SAV, G-EUC, and F-SAV was 69, 80, and 76 %

Table 1 Composition and relative abundance of species (Pi) of each cover land type sampled in Brazilian Amazon savanna

Taxon			Food and locomotion habits[a]	Pi per treatment				
Order	Genus/species	Common name		EUC	F-EUC	G-EUC	F-SAV	G-SAV
Primate	*Alouatta belzebul*	Howler monkey	Fo, Fr, Ar				0.010	
	Alouatta macconnelli	Howler monkey	Fo, Fr, Ar		0.077			
	Sapajus apella	Brown capuchin monkey	Fr, On, Ar		0.169		0.240	
	Saguinus midas	Golden hand monkey	Fr, In, Ar		0.045			
Carnivora	*Cerdocyon thous*	Crab-eating fox	In, On, Tr	0.156	0.015	0.183	0.080	0.421
	Eira barbara	Taira	Fr, On, Tr				0.020	0.013
	Galictis vittata	Grison	Ca, Tr			0.011		
	Nasua nasua	South America coati	Fr, On, Tr		0.015		0.010	
	Procyon cancrivorus	Crab-eating raccoon	Fr, On, Es					0.007
	Potus flavus	Kinkajou	Fr, On, Ar				0.020	
	Leopardus pardallis	Ocelot	Ca, Tr			0.032	0.020	0.020
	Puma concolor	Puma	Ca, Tr			0.022	0.010	0.026
	Panthera onca	Jaguar	Ca, Tr	0.013		0.032		0.013
Cingulata	*Cabassous unicinctus*	Naked-tailed armadillo	My, Sf					0.013
	Dasypus novemcinctus	Nine-banded armadillo	In, On, Sf			0.022	0.010	
	Euphractus sexcinctus	Yellow armadillo	In, On, Sf	0.104	0.045	0.086	0.030	0.079
	Priodontes maximus	Giant armadillo	My, Sf					0.007
Pilosa	*Myrmecophaga tridactyla*	Giant anteater	My, Tr				0.020	0.033
	Tamandua tetradactyla	Southern tamandua	My, Es		0.015			
Artiodactyla	*Mazama americana*	Red brocket deer	Fr, Hb, Tr	0.286	0.030	0.151	0.060	0.092
	Mazama nemorivaga	Gray brocket deer	Fr, Hb, Tr	0.169	0.030	0.108	0.040	0.053
	Mazama sp.	Deer	Fr, Hb, Tr	0.130	0.061	0.054	0.010	0.046
	Odocoileus virginianus	White-tailed deer	Hb, Tr			0.022		0.007
	Tayassu pecari	Collared peccary	Fr, Hb, Tr				0.010	

Table 1 continued

Taxon			Food and locomotion habits[a]	Pi per treatment				
Order	Genus/species	Common name		EUC	F-EUC	G-EUC	F-SAV	G-SAV
Perissodactyla	*Tapirus terrestris*	Brazilian lowland tapir	Hb, Fr, Tr	0.143	0.167	0.097	0.110	0.105
Rodentia	*Dasyprocta leporina*	Agouti	Fr, Gr, Tr	0.013	0.288	0.183	0.290	0.059
	Cuniculus paca	Paca	Fr, Hb, Gr, Tr		0.045		0.010	0.007

[a] Source: Paglia et al. (2012)

Food habits legend (see Paglia et al. 2012): *Ca* carnivore, *Fr* frugivore, *Fo* folivore, *On* omnivore, *Hb* herbivore grazer, *Gr* granivore, *In* insectivore, and *My* myrmecophage

Locomotion habits legend (see Paglia et al. 2012): *Tr* terrestrial, *Ar* arboreal, *Sf* semifossorial and *Es* scansorial (climber)

Treatment blocks legend: *EUC* eucalypt plantation, *F-EUC* remain forests of savanna inside the mosaic, *G-EUC* remain grasslands of savanna inside the mosaic, *F-SAV* native and continuous forests of savanna, *G-SAV* native and continuous grasslands of savanna

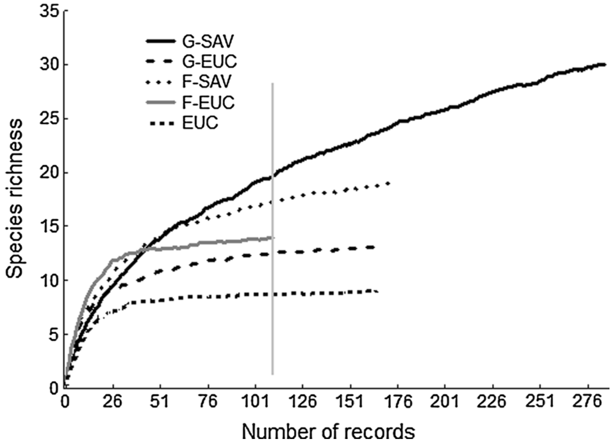

Fig. 2 Estimates of species richness for medium and large mammals in Amazon savanna in Amapá, Brazil, based on rarefaction curves. *G-SAV* conserved savanna grassland, *G-EUC* remnant savanna grassland, *F-SAV* conserved savanna forest, *F-EUC* remnant savanna forest, *EUC* eucalyptus plantation. The *grey vertical lines* represent the minimum sampling effort for each treatment

of the number of species estimated for these habitats, respectively. Despite having the greatest sampling effort (total transect length), estimated species richness was still lower in the EUC than for any other habitat category (Fig. 2). Approximately twice as many species were recorded in the conserved savanna (G-SAV and F-SAV) in comparison to the eucalyptus plantation (EUC).

Based on the confidence intervals of the species richness estimates for the grassland samples, G-SAV contained 11 more species than G-EUC, a significant difference (Fig. 3a). However, the difference in species richness between F-SAV and F-EUC was not significant (Fig. 3b). Even the grassland remnants within the eucalyptus plantation (G-EUC) had a mean of four more species than the eucalyptus plantation (Fig. 3a), and the forest remnants (F-EUC) had six more species, on average (Fig. 3b).

Together, the savanna habitats (G-SAV + F-SAV + G-EUC + F-EUC) had 15 more mammal species than the plantations (EUC). Similarly, the conserved savanna (G-SAV + F-SAV) had 12 species more than the eucalyptus plantation (EUC), and the savanna remnants (G-EUC + F-EUC), ten more species (Fig. 4).

Based on the confidence intervals, there was no significant difference in estimated richness between conserved savanna (G-SAV + F-SAV) and the remnants (G-EUC + F-EUC) within the plantations (Fig. 4). The ANOVA ($F_{(2,13)} = 3.956$ $p = 0.045$) found significant differences between conserved savanna and the eucalypt plantation (Tukey test: $p = 0.030$) and between savanna remnants and the plantation ($p = 0.046$). However, as for the confidence interval, there was no significant difference in mammalian species richness between the conserved and remnant savanna samples (Tukey test: $p = 0.942$).

No statistical difference in abundance ($F_{(1,9)} = 0.847$, $p = 0.381$) was detected among the conserved savanna habitats (Fig. 5a). Similar results ($F_{(2,8)} = 0.570$, $p = 0.587$) were obtained when we compared conserved savannas with the remnant savannas and the eucalypt plantation (Fig. 5b).

The ordination NMDS analysis clustered all eucalyptus plantation samples together, separately from the other categories. There was also a clear separation between the samples

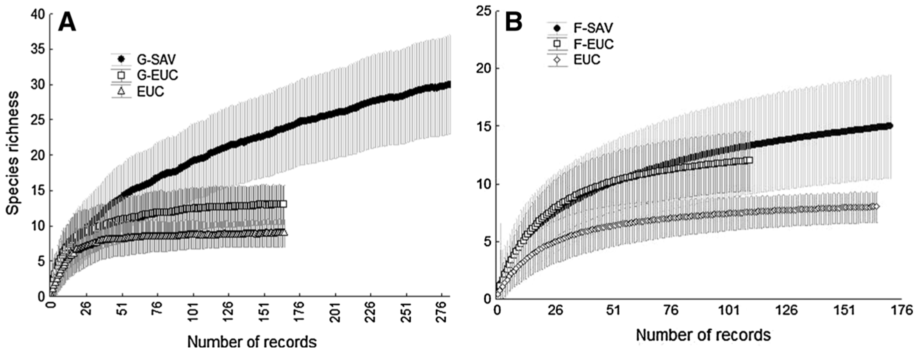

Fig. 3 Estimates of species richness for medium and large mammals in Amazon savanna in Amapá, Brazil, based on rarefaction curves with confidence intervals. **a** *G-SAV* conserved savanna grassland, *G-EUC* remnant savanna grassland, *EUC* eucalyptus plantation, **b** *F-SAV* conserved savanna forest, *F-EUC* remnant savanna forest

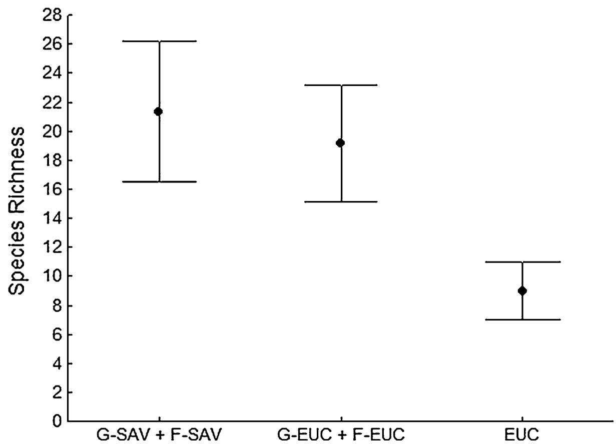

Fig. 4 Estimates of species richness for medium and large mammals in Amazon savanna in Amapá, Brazil, based on rarefaction curves. *G-SAV + F-SAV* conserved savanna (grassland and forest), *G-EUC + F-EUC* savanna remnants (grassland and forest), *EUC* eucalyptus plantation. The *bars* represent the 95 % confidence interval

from forest (F-SAV + F-EUC) and grassland savanna (G-EUC + G-SAV), reflecting the distinct mammal assemblages of these habitats (Fig. 6). These findings were supported by the ANOSIM, which confirmed that the differences among groups were significant ($R = 0.229$, $p = 0.023$).

Discussion

The patchwork landscape of eucalyptus plantations and natural savanna vegetation proved effective for the maintenance of almost 80 % of the medium and large mammal species found in the region's savannas. However, it is clear that the savanna remnants are

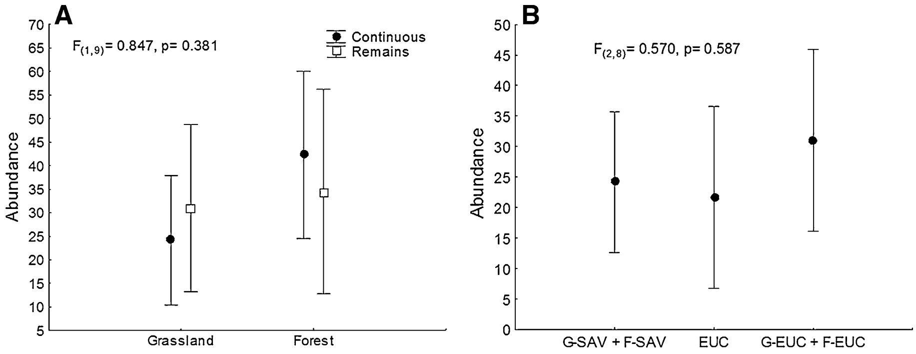

Fig. 5 **a** Abundance of medium and large mammals in different savanna habitats in Amapá, Brazil. **b** Abundance of medium and large mammals in different treatments. *G-SAV* + *F-SAV* conserved savanna (grassland and forest), *G-EUC* + *F-EUC* savanna remnants (grassland and forest), *EUC* eucalyptus plantation. The *bars* represent the 95 % confidence interval

necessary for the maintenance of mammalian diversity in this landscape. While the maintenance of almost 50 % of the original vegetation in the patchwork landscape was important here, the role of the plantations as wildlife corridors, guaranteeing the permeability of the matrix, was probably a key factor favoring the maintenance of high mammalian diversity in this landscape (Hansen et al. 1991; Hartmann et al. 2010).

Most studies of mammals in the Cerrado savannas of central Brazil have highlighted the gallery forest as the habitat richest in species, acting as natural corridors for the dispersal of mammals within the grasslands (Mares et al. 1986; Redford and Fonseca 1986; Johnson et al. 1999). In the present study, however, the savanna grassland was the richest habitat. This indicates that, in the Amazon, the savanna grasslands are as important as its forests for the conservation of mammals, and probably also that both types of habitat are strongly influenced by the surrounding Amazon rainforest. In the savannas of central Brazil, the mammalian communities of the gallery forests appear to reflect the influence of both the Amazon and Atlantic rainforests, the adjacent biomes (Mares et al. 1986; Redford and Fonseca 1986; Johnson et al. 1999).

In addition, the drastic reduction of species richness between continuous savanna grassland and the remnants of this habitat was more pronounced than that found between the forest habitats. In fact, the habitat richest in species habitat has also been the most affected by the loss of biodiversity, given that most of the local savanna grasslands have been replaced by eucalyptus plantations.

While our study has shown that the plantation mosaic can maintain a high diversity of mammals, mammal species richness declined drastically in the eucalyptus plantations (Barlow et al. 2007b; Brockerhoff et al. 2008). The presence of eight species in the plantation nevertheless indicates that some mammals are at the very least using this habitat to move between savanna remnants. With the exception of two records of herbivorous mammals feeding on understory (non-eucalyptus) plants, we found no evidence that mammals use the plantation for any other purpose than to access remnants of natural habitat within the matrix. Our conclusion is that, for medium and large mammals, the eucalyptus plantation is a permeable matrix but does not replace the original savanna in any meaningful way, in particular with regard to feeding resources.

These effects may be less deleterious in other more degraded or naturally species-poor landscapes, such as temperate forests, where eucalyptus plantations may even improve

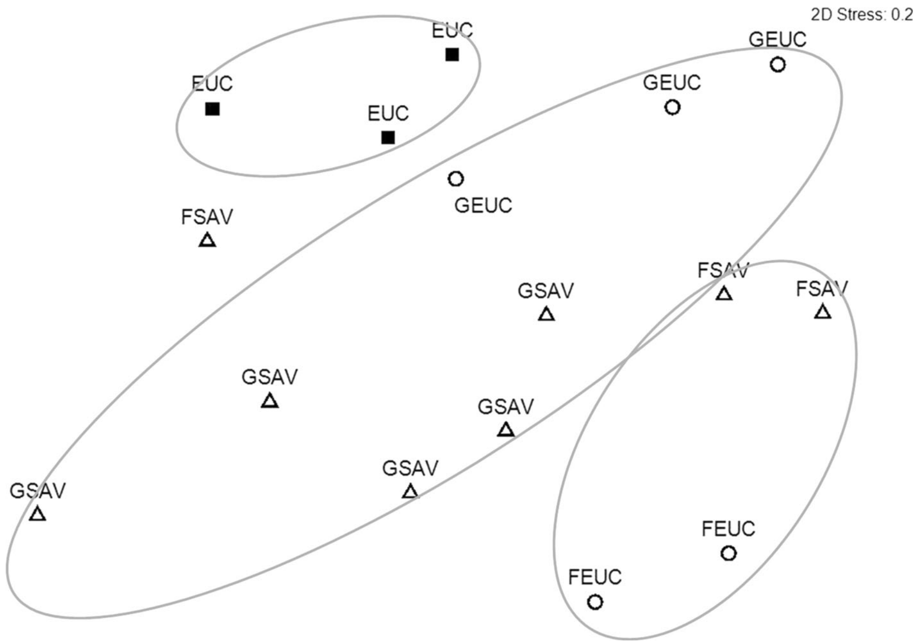

Fig. 6 Ordination scores derived from the non-metric multidimensional scaling (NMDS) of the species composition matrix of medium and large mammals in different savanna habitats in Amapá, Brazil. *G-SAV* + *F-SAV* conserved savanna (grassland and forest), *G-EUC* + *F-EUC* savanna remnants (grassland and forest), *EUC* eucalyptus plantation

wildlife conservation (Brockerhoff et al. 2008; Hartmann et al. 2010; Mazzolli 2010). It has been shown that a permeable matrix connecting habitats allows animal movements throughout the landscape and thus maintains processes essential to the persistence of carnivore populations (Lyra-Jorge et al. 2010). Our results indicate that the eucalyptus plantation has a function in connecting the patches of savanna vegetation, and this may contribute to the diversity of the carnivore assemblage in this patchwork landscape.

The simplification of the habitat caused by replacing the savanna with eucalyptus plantations may affect different mammal species in different ways (Barlow et al. 2007a, 2008; Louzada et al. 2010). In particular, the frugivores and arboreal mammals, such as *P. flavus* and primates, were the most affected, probably due to the lack of food resources, simplification of the forest strata for locomotion, and high exposure to predators (Vilela 2007; Nasi et al. 2008), but even the terrestrial frugivores seem to have been affected considerably, especially by the lack of feeding resources.

While the total abundance of medium and large mammals has not been affected, most of the records in the eucalyptus plantation were of large herbivorous ungulates. This group may often increase in abundance in areas of eucalyptus plantation or other types of anthropogenic forest (Lindenmayer et al. 2003; Parry et al. 2007; Meijaard and Sheil 2008; Andrade-Núñez and Aide 2010). Species such as *M. americana* and *M. nemorivaga* are ecologically flexible and are able to eat different plant parts, such as shoots, stems, flowers, fruits, and leaves (Dirzo and Miranda 1990; Gayot et al. 2004). These are probably the only species that are able to inhabit the eucalyptus plantations permanently (Bulinski and McArthur 2003; Andrade-Núñez and Aide 2010; Brockerhoff et al. 2013).

We conclude that for the conservation of mammals in Amazonian savanna, it is essential to maintain patches of savanna habitat within the eucalyptus plantations, including the maximum possible diversity of vegetation types and connectivity among fragments. As in other tropical ecosystems, the heterogeneity of natural habitats contributes considerably to biodiversity levels (Umetsu et al. 2008; Barlow et al. 2008; Price et al. 2010). Following this approach, it may be possible to minimize the loss of biodiversity caused by the establishment of eucalyptus plantations in the savannas of the Amazon basin.

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