



Tree plantations replacing natural grasslands in high biodiversity areas: How do they affect the mammal assemblage?



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ABSTRACT

Monoculture plantations of fast-growing trees are increasing worldwide and, in many cases, these replace highly diverse natural environments. The Mesopotamian Savannas and the Iberá marshes ecoregions of northeastern Argentina are a mosaic of habitat types in which extensive areas of natural grasslands have been replaced by the planting of non-native pines (*Pinus* spp.). Their impact on the natural communities is unknown. We evaluated the effect of these plantations, the landscape configuration and the forestry management practices on the assemblages of medium to large-size terrestrial mammals of this region at landscape and stand levels. Camera-trap stations were deployed in three environments: 89 in natural grasslands, 54 in native forest patches, and 91 in tree plantations. At a landscape level, we evaluated the effect of the type of environment and of the extent of different land covers on mammal richness per station using GLM, and on species composition using one-way PERMANOVA and redundancy analysis. At a stand level, we assessed the effect of understory vegetation, and of the age and density of tree plantation stands, on the similarity in mammal species composition between tree plantations and native environments, using non-metric multidimensional scaling analyses and GLM. Species richness and species composition differed between native forests and other environments, but not between grasslands and plantations. The variations in composition between the environments differed among the two ecoregions: the species composition in the plantations was different from the grassland assemblage only in the Iberá marshes, which suggests that the impact of tree plantations depends on the local pool of species. Mammal assemblages were also affected by the proportion of forests and wetlands and the environmental heterogeneity in the landscape. The similarity between the mammal assemblages of pine plantations and those of native forests increased with the age of the stand and at intermediate tree densities. In this grassland-dominated but heterogeneous landscape, it seems that most medium and large grassland mammals do not perceive tree plantations as a barrier, regardless of their management. Actions at a stand level, such as planting at intermediate tree densities and promoting longer rotation times, are desirable to encourage the forest mammal assemblage to use the plantations. Forests and wetlands are acting as keystone habitats for many species that are clearly associated with the presence of these environments in the landscape. Keeping large areas of natural grasslands and wetlands sprinkled with forests is essential for the conservation of the mammal assemblages of this region.

1. Introduction

The expansion and intensification of industries has accelerated the conversion of natural environments to agriculture and to human infrastructure, and is one of the most important causes of biodiversity loss (Haddad et al., 2015; Newbold et al., 2015). Monoculture plantations of fast-growing trees are increasing worldwide (40% between 1990 and

2015 according to FAO; Keenan et al., 2015), a fact that can have strong local and regional effects on biodiversity (Koh and Gardner, 2010). Despite the general management recommendations to minimize the negative impacts of tree plantations (e.g. Lindenmayer and Hobbs, 2004), tree farming practices vary between regions and their impact may also depend on landscape configuration and the pool of native species involved (Brockerhoff et al., 2013, 2008).

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Table 1
Hypotheses tested regarding the effects of pine plantations and landscape characteristics on the richness and/or composition of mammal assemblages in the Southern Cone Mesopotamian Savanna and Iberá marshes of Argentina. The variables included in the models to represent each hypothesis at landscape and stand levels are described.

Hypothesis	H2. Effect of the extent of different land covers		
	H2a. Proportion of different environments in the landscape	H2c. Habitat heterogeneity	
Predictions	<p>H1. Effect of structural similarity of pine plantations with the native environments</p> <p>Landscape level. The assemblage of mammals in tree plantations will be more similar to that of forests than to that of grasslands.</p> <p>Stand level. The similarity of tree plantation mammal assemblages to those of native environments will be related to the similarity of the understory vegetation of the plantations to that of the native environments.</p> <p>Stand level. Tree plantation mammal assemblages will be more similar between younger pine stands with low tree densities and grasslands, and more similar between older stands with intermediate tree densities and forests.</p> <p>Type of environment (grassland, forest, tree plantation)</p>	<p>H2b. Forests and wetlands as keystone habitats</p> <p>Mammal richness will increase (up to a certain point) with the proportion of native forest and/or wetland in a grassland dominated landscape.</p> <p>At landscape level, the proportion of different environments in the landscape (each with its characteristic fauna) will be associated with differences in mammal assemblage composition.</p> <p>At stand level, the plantation mammal assemblage will show greater similarity to that of a particular native environment (e.g., forest) as the proportion of that environment increases in the landscape.</p>	<p>Heterogeneity of the environments in the landscape will be associated with greater mammal richness and differences in assemblage composition.</p>
Variables evaluated at landscape level	<p>% of each main environment (“% of grassland”, “% of forest”, “% of plantation”, and “% of wetland”) around the stations¹</p>	<p>% of forest and % of wetland around the station¹</p>	<p>Heterogeneity of environments around the stations^{1,2} (“heterogeneity”)</p>
Variables evaluated at stand level	<p>Structural complexity of the understory vegetation (“understory”)</p> <p>Stand age (“age”)</p> <p>Stand density (“density”)</p>	<p>% of grassland and % of forest around the tree plantation station¹</p>	<p>Structural complexity of vegetation in each environment (“vegetation”)</p> <p>Livestock density (“livestock”)</p> <p>Level of anthropogenic impacts, such as hunting (“cost of access”)</p> <p>Livestock density (“livestock”)</p> <p>Level of anthropogenic impacts, such as hunting (“cost of access”)</p>

1. We evaluated these variables at four different radii centered on the camera-trap locations (200, 500, 1000 and 2000 m) to detect community responses at different scales (e.g. Nagy-Reis et al., 2017; Zurita et al., 2017).

2. Heterogeneity was estimated with the Shannon-Wiener index (Shannon and Weaver, 1949) using the number of pixels of environment in the Fragstat software (ver. 4.2).

To better understand the effect of tree plantations on biodiversity, it is necessary to know what kind of environment preceded their establishment (Bremer and Farley, 2010; Pawson et al., 2008), since similarity to the original habitat type may influence how many and which species are retained in the new communities (Dormann et al., 2007; Lindenmayer et al., 2019). Several authors suggest that it may be more detrimental to biodiversity when plantations replace non-forest ecosystems (i.e. grasslands or wetlands) than when they replace native forests (Brocknerhoff et al., 2008). Even in landscapes with diverse ecosystems, such as savannas or steppes combined with native forests, tree planting had a greater negative environmental effect on non-forest than on forest animal assemblages (Coelho et al., 2014; Lantschner et al., 2008), but the real impact on mammals of replacing non-forest natural environments with tree plantations is still little studied (Felton et al., 2010).

There are several features of productive landscapes that can mitigate the negative impacts of tree plantations on biodiversity. For example, the configuration of the landscape elements can significantly affect the conservation of regional biodiversity (Bakker et al., 2002; Dormann et al., 2007). The presence of remnants of native grassland or forest (e.g. riparian forests) in productive areas can contribute to the persistence of specialist species in each environment, thus maintaining the native assemblages in the landscape (Coelho et al., 2014; Lees and Peres, 2008; Paolino et al., 2018). Even within a landscape dominated by grasslands, forests and wetlands can function as “keystone habitats”, as they provide resources and/or refuges for many species in the landscape, leading to an increase in biodiversity regionally (Hitchman et al., 2018; Tews et al., 2004). In addition, the presence of different natural environments and land uses contributes to landscape heterogeneity (Brocknerhoff et al., 2013; Lindenmayer et al., 2008), which can favor species richness and diversity (Bennett et al., 2006; Tews et al., 2004). These mosaics of environments offer a variety of habitats for different animal species, some of which are restricted to the original natural elements, and others which are able to use anthropogenic elements, such as crops and tree plantations (Daily et al., 2003; Renjifo, 2001).

Some tree-plantation stand management practices can promote landscape-scale biodiversity conservation (Brocknerhoff et al., 2013, 2008; Fonseca et al., 2009). For example, promoting the growth of understory vegetation in tree plantations can provide food and shelter for some mammals and thus maintain higher levels of biodiversity (Fonseca et al., 2009; Simonetti et al., 2013). In addition, the age and density of plantation stands will influence the structural and vertical heterogeneity of their understory vegetation. Thinned plantations with longer rotation cycles produce an understory vegetation that resembles that of the native forest (Brocknerhoff et al., 2008, 2003; Lindenmayer and Hobbs, 2004; Seiwa et al., 2012; Trentini et al., 2017), while the understory of young stands with very low tree densities tends to be dominated by pastures typical of grassland environments (Wilson and Puettmann, 2007). Therefore, the age and density of the plantation stand can determine whether its animal community is predominantly of typical forest species (Bergner et al., 2015; Pietrek and Branch, 2011; Santoandré et al., 2019; Timo et al., 2014; Zurita and Bellocq, 2012) or of grassland species (Michelson, 2005; Pereira et al., 2006; Rishworth et al., 1995; Santoandré et al., 2019).

The Southern Cone Mesopotamian Savannas (hereon, SCM Savannas) and the Iberá marshes are Neotropical ecoregions that encompass extensive natural grassland and savanna communities (Bilenca and Miñarro, 2004; Viglizzo et al., 2005; WWF, 2019). They consist of a mosaic of habitats in which grasslands intermingle with wetlands and isolated woodlands and gallery forests. Cattle ranching has traditionally been the most important industry, but monoculture tree farming is expanding (Miñarro and Bilenca, 2008). Fast-growing monospecific plantations of the non-native genera *Pinus* (mostly *Pinus taeda* and *Pinus elliottii*) and *Eucalyptus* (mainly *Eucalyptus grandis*) are gradually replacing pastures, currently totaling approximately 325,000 ha. The effect of tree planting and cattle ranching in this region, either alone or combined in silvopastoral systems, has been studied in lizard (Cano and

Leynaud, 2010) and ant communities (Santoandré et al., 2019), but the response of mammal assemblages is still unknown.

The aim of this study was to assess the effects of replacing the native environments of the SCM Savannas and the Iberá marshes eco-regions with pine plantations on the richness and composition of the mammal assemblages of grasslands and forests. We describe the mammal assemblages that occur in these environments and in tree plantations, and we test two main hypotheses (Table 1): H1) Structural similarity of tree plantations with the native environments (either grasslands or forests) determines the tendency of grassland- or forest-dependent mammals to use these areas. H2) The relative extension of different land covers in the landscape affects the richness and composition of mammal assemblages. We evaluated three specific hypotheses within the latter main hypothesis: H2a) The composition of the mammal assemblages is affected by the proportion of each of the different environments in the landscape; H2b) Native forests and wetlands function as keystone habitats that provide critical resources for native mammals, resulting in an increase of mammal richness up to a certain proportion of these in the landscape; H2c) Mammal richness and the composition of the assemblage changes with the heterogeneity of habitats in the landscape. We evaluated these hypotheses at both landscape and tree plantation stand level (Table 1).

2. Material and methods

2.1. Study area

We conducted this study in northeastern Corrientes province and southern Misiones province, Argentina (an area of approximately 25,000 km² centered at 56°35'W 28°15'S; Fig. 1), comprising a large portion of the SCM Savannas and the Iberá marshes. The study area consists of a mosaic of habitat types, including temporarily flooded grasslands, marshes, woodlands, gallery forests and wetlands (WWF, 2019). Several threatened or near-threatened mammals inhabit the area, such as the maned wolf, *Chrysocyon brachyurus*, and the marsh deer, *Blastocercus dichotomus* (Pereira et al., 2019; Soler et al., 2019). In the central and southern portion of the study area (sub-areas B and D in Fig. 1), the landscape is dominated by subtropical savannas, and in the west by marshes and wetlands (sub-area A, Fig. 1). Both portions contain numerous small (0.5–10 ha), circular, isolated natural semi-deciduous forests. Cattle ranching and tree farming are the main industries (Viglizzo et al., 2005; Fig. 1). In the northeast, larger forest fragments resembling those typical of the Upper Paraná Atlantic Forest ecoregion are interspersed in a matrix of tree plantations, pastures and crops of yerba mate, tea and maize (sub-area C, Fig. 1). Grasslands (with and without cattle) and wetlands represent > 70% of the whole study area (53% grasslands and 47% wetlands), while native forests occupy 3.5% and tree plantations 8.5% of the area (Fig. 1). Tree plantation stands, owned by forestry companies or local ranchers, range in size from approximately 3 to 160 ha. Both ranchers and timber companies own grasslands and forests usually dedicated to cattle production, where livestock is produced in silvopastoral systems under low-density tree plantations. The study area also includes some strictly protected areas (e.g. the Iberá National Park) where extractive and other industries (except tourism) are not allowed.

2.2. Sampling design

To study the assemblage of terrestrial mammals, we conducted a camera-trap survey between May 2016 and March 2017. We deployed 234 camera-trap stations, each consisting of a single Reconyx® model HC500 unit located at distances of > 50 m from a road or human trail and attached to the base of a tree or to a stake at about 30–40 cm above ground level. Stations were not baited, and cameras were set to take 10 successive pictures per trigger with a 30 s delay between detections. The cameras were active for an average of 44.9 days (range: 21–67 days), amounting to a total effort of 10,494 camera-days. A > 1-hour period had to pass for two successive pictures of the same species to be considered independent records.

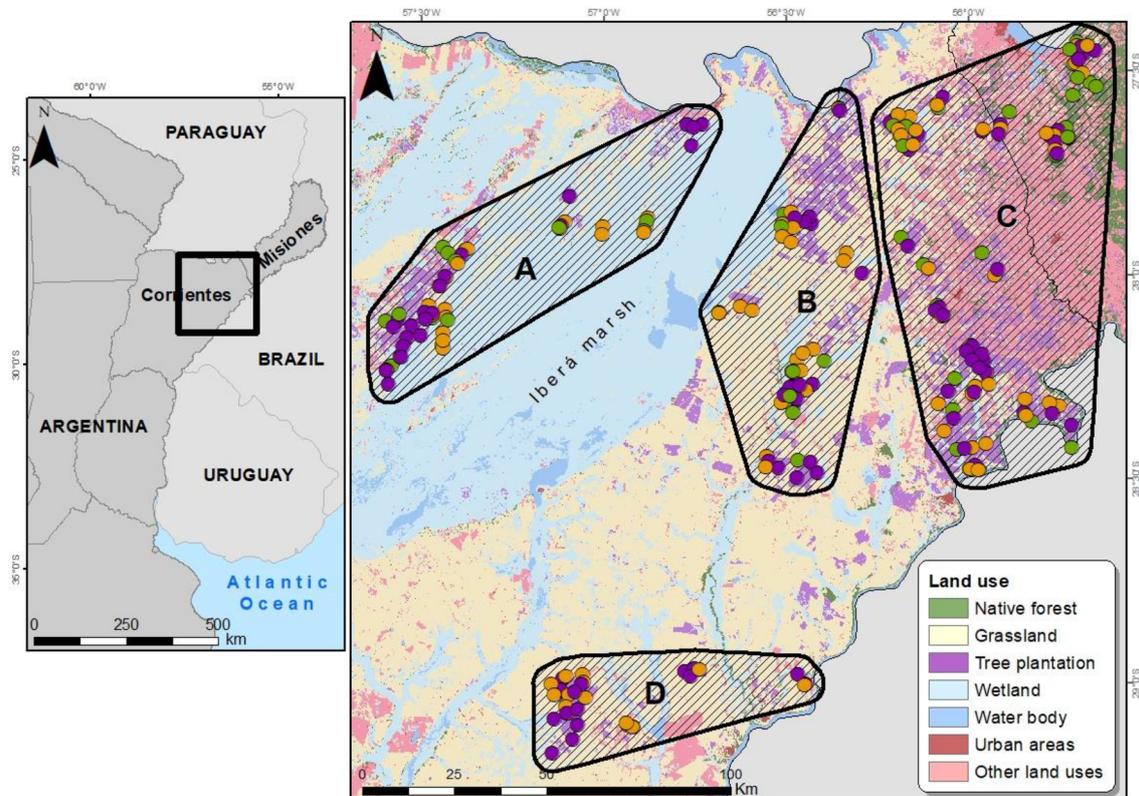


Fig. 1. Location of the study site and camera-trap stations in the Southern Cone Mesopotamian Savanna and Iberá marshes of Argentina. Yellow points correspond to grassland stations (89), green points to native forest stations (54), and purple points to stations located in pine plantations (91). The study area was divided in four sub-areas (A-D). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

We deployed the stations in three environments: native grassland (89 camera-trap stations), native forest (54 stations), and tree plantations (91 stations; Fig. 1). The closest stations located in the same environment were no nearer than 2 km. The plantations where the stations were located were 1- to 30-year-old pine stands with densities ranging from 200 to 1666 trees/ha. Within each environment, approximately half of the stations were located in cattle paddocks (Table S1). Given the extension of the study site and sub-regional differences in soil types and vegetation that follow a NE-SW gradient (INTA, 2013; Oyarzabal et al., 2018), we divided the area into 4 sub-areas (letters A-D; Fig. 1). Stations were located following a balanced design among environments within each sub-area and throughout the sampling period.

2.3. Estimation of independent variables

To test our two main hypotheses, we constructed independent variables to evaluate their effect on the richness and composition of mammal assemblages throughout the landscape and in tree plantation stands (Table 1).

We estimated the percentage of each environment, the heterogeneity of the environments, and the cost of access from a Geographic Information System using a land-use layer (pixels of 30x30 m) created for 2013–2014 by Zuleta et al. (2015) in ArcGIS 10.3.1 (ESRI Inc.). We measured vegetation complexity at each station with surveys of tree density, structure and cover of the typical grassland, and understory life forms.

Vegetation complexity was represented by the first two axes of Principal Components Analysis (PCA) based on the vegetation survey (Table S2). The first axis (“vegetation 1”) discriminates stations dominated by an arboreal structure (native forests and pine plantations, positive values) from those dominated by grasslands (negative values, Table S2). The second axis (“vegetation 2”) corresponds to a gradient ranging from locations with less understory and vegetation cover in the

lower strata (negative values) to locations with denser and more structurally complex vegetation (positive values, Table S2).

To study the effect of understory vegetation complexity in tree plantations, we generated two different variables with another PCA based on the features measured in the stations of this environment (Table S3). This second PCA axis 1 differentiated stations with higher abundances of cespitose perennial grasses, typical of native grasslands (e.g. *Andropogon lateralis*), and with higher vegetation density in the lower strata (positive values) from stations with scarce understory (negative values, “understory 1”). Axis 2 differentiated stations with higher abundance of shrubs, ferns, and short herbaceous (positive values) from stations with scarce understory (negative values, “understory 2”, Table S3).

Livestock density was estimated as the number of independent records of domestic animals per sampling effort (in days) at each camera-trap station (see details in Appendix A).

The variable cost of access was created following De Angelo et al. (2011) and Iezzi et al. (2018) but adapting the values to the study area. It represents the human accessibility cost, measured as the hours needed to access the camera-trap station from the nearest town or city (see details in Appendix A).

2.4. Statistical analysis

2.4.1. Landscape level analysis

To test the hypotheses at landscape level, we analyzed the effects of the variables on the richness, alpha diversity (Appendix B), and composition of the assemblage of terrestrial mammals (Table 1) using the complete set of sampled stations.

2.4.1.1. Structural similarity: Species composition and indicator species.

For the analysis of species composition and indicator species

of the three environments, we used the relative frequency of records, estimated as the number of independent records of each mammal species divided by sampling effort (camera-trap days). To evaluate the similarity of the assemblages among the environments, we generated all possible pairwise comparisons among stations using three similarity indices from the general multiple-assemblage overlap measure C_{qN} (Chao et al., 2008; Jost et al., 2011): the multi-assemblage Sørensen index, which measures similarities in species identities; the generalized Horn index for similarities in common species (Horn, 1966); and the generalized multi-assemblage Morisita-Horn index for similarities in dominant species. To determine differences in species composition among environments, we compared C_{qN} values using one-way PERMANOVA (Anderson, 2001) with 9999 permutations and using the sub-area as a strata (Oksanen et al., 2007). To identify indicator species of each environment, we used the Indicator value analysis (IndVal) proposed by Dufrene and Legendre (1997).

Similarity matrixes were generated in R 3.2.2 with the “vegetarian” package (Charney and Record, 2012). PERMANOVA and the variation partitioning were performed with the R “Vegan” package (Oksanen et al., 2007). IndVal analysis was performed with the R “labdsv” package (Roberts, 2016).

2.4.1.2. Effect of land cover on species composition. To determine if species composition was affected by land-use patterns, we included the percentage of each environment (grassland, forest, tree plantation and wetland) and the variable “heterogeneity” as independent variables in a one-way PERMANOVA (Section 2.4.1.1). To select the best radii for these variables, we compared each univariate model using the estimated AIC and selected the variant included in the model with the lowest value (Table S4). We also included the structural complexity of vegetation (“vegetation 1 and 2”), livestock density, and cost of access in these models, to control the potential effects of these variables on species composition.

To evaluate the effect of each independent variable on species occurrence, we performed a redundancy analysis (RDA), using the relative frequency of records of the species with a Hellinger transformation (Legendre and Gallagher, 2001; Legendre and Legendre, 2012). The RDA was performed with the R “Vegan” package (Oksanen et al., 2007).

2.4.1.3. Effect of land cover on mammal richness. To test our hypotheses regarding species richness, we used generalized linear models (GLM), including the number of species observed per station as a response variable, and the environment and the variables “% of wetland”, “% of forest”, and “heterogeneity”, as fixed effects. We also included the vegetation cover in the lower strata (“vegetation 2”), livestock density, cost of access, and the “sub-area” as fixed effects in the models, to control possible effects of these variables on species richness or any differences between the different sub-regions of the study area. Models were assumed to have a Poisson distribution with a log link ($\Theta = 0.84$). Since survey effort varied among stations, we included the number of days that each camera remained active as an offset term. Best models explaining species richness were selected using a multiple-hypotheses model-selection approach (Anderson et al., 2000; Franklin et al., 2001; Johnson and Omland, 2004), generating models with all possible combinations of non-correlated variables. Models were ranked by their Akaike Information Criterion for Small Samples (AICc) ascending value (Burnham and Anderson, 2002). We selected the variables that were included in the models that had a $\Delta AICc \leq 2$ in relation to the best model, and evaluated the effect and importance of each variable by assessing whether the 95% confidence interval (CI) of their parameter estimates included zero. As there was more than one model with $\Delta AICc \leq 2$, we averaged these to estimate the beta values of each variable with its 95% CI. We used one-tailed tests in all cases, except for the contrast between the “grassland” and “forest” environments as this comparison does not correspond to a directional hypothesis. To select the best radii for variables “% of forest”, “% of wetland” and “heterogeneity”, we compared the AICc

values of the univariate models and selected the variant with the lowest value for further model selection procedures (Table S5).

For the statistical analyses we used the “car” (Fox, 2007), “MuMin” (Bartoń, 2016), “multcomp” (Hothorn et al., 2016) and “DHARMa” (Hartig, 2017) packages in the software R ver. 3.2.3. Figures were produced with the “ggplot2” and “visreg” packages (Breheny and Burchett, 2016; Wickham, 2014). For more details on statistical analysis, see Appendix A.

2.4.2. Stand level analysis

2.4.2.1. Similarities between plantations and native environments. To study the effect of tree-plantation management on native mammals, we estimated the similarity in dominant species composition between the tree plantation assemblage and those in the native environments. For this, we used the relative frequency of records of each species at each station and performed two non-metric multidimensional scaling analyses (NMDS, Kruskal, 1964; Minchin, 1987) using the Morisita-Horn index, one for the contrast between native forest and tree plantation and the other for the contrast between grassland and tree plantation. Following Peyras et al. (2013), we estimated the centroids of the sites of each native environment in each sub-area (see Fig. S1 and S2) using the scores of the NMDS bi-plots and used these as reference communities. Then, we calculated the Euclidean distance between each tree plantation station and the centroid of the reference community within each sub-area. The distance to the centroids represents the dissimilarity in the composition of the tree plantation mammal assemblage in relation to the assemblages of the native environment. We excluded sites with ≤ 1 record (17 stations) from these analyses.

Using the distances to the centroids as response variables, we performed two sets of GLM, with understory vegetation, stand age and density, percentage of native environments and livestock density as fixed effects, assuming a Gaussian distribution. For models using the distance to the grassland centroids as a response variable, we used “% of grassland” and “understory 1” as independent variables. For models using the distance to the native forest centroids as a response variable, we used the “% of forest” and “understory 2” as independent variables. Since we expected the similarity between pine plantations and native forests to be maximal at intermediate tree densities (mean native forest tree density was 628.36 trees/ha), in the latter models we included a quadratic term for “density”.

We generated models with all possible combinations of non-correlated variables. The selection of best radii and of model follows the procedures described in 2.4.1.c (Table S6). We used one-tailed tests in all cases. Since there were some low-density pine stands that were intentionally planted as silvopastoral systems ($N = 9$) to favor the growth of pastures and livestock grazing in the same area (Esquivel, 2012), we contrasted the model that included the combination of the variables “livestock” and “density” with one that included a dichotomous variable “silvopastoral” and selected the variable/s included in the model with the lowest AICc value (Table S7). For statistical analysis, we used the software and packages described in Section 2.4.1. NMDSs were performed with the R “Vegan” package.

3. Results

We obtained 4460 independent records of 31 native mammal species and 96 records of 3 exotic feral mammal species (feral pig, European hare, and chital, Table S8). Only 23.3% ($n = 1065$) of the records were obtained in stations located in tree plantations, even though these represent 38.9% of the stations and 39.2% of the effort (camera-traps days) The number of species recorded per station ranged from 0 to 10 (mean = 3.42, SD = 1.75). Stations located in forests had the highest mean richness per station, followed by those located in grasslands. The lowest mean richness per station was observed in the tree plantations (Table 2). There were no differences between grasslands and plantations in species richness (Fig. 2).

Table 2

Total number of species (Total spp.) and mean number of species per station (Spp. p/station; SD within brackets) of mammals observed in three environments (native forests, grasslands and tree plantations) in the Southern Cone Mesopotamian Savanna and Iberá marshes of Argentina. Sampling completeness (SC) and mean effort per station (in days) are also indicated.

Environment	# Stations	Total spp.	Spp. p/station	SC	Mean effort per station (SD)
Native forest	54	28	4.66 (1.67)	0.98	45.01 (7.07)
Grassland	89	24	3.28 (1.71)	0.99	44.53 (9.58)
Tree plantation	91	23	2.82 (1.44)	0.99	45.26 (7.59)

3.1. Results of landscape level analyses

3.1.1. Is the mammal assemblage of tree plantations more similar to that of forests?

Mammal assemblages of forests differed from those of other environments when using pairwise similarities in species identity (Sørensen index), common species (Horn index), and dominant species (Morisita–Horn index) (Table 3). The species identity of grassland and plantation assemblages were not dissimilar from each other. However, variation in composition between the environments differed among the sub-areas: in Iberá (sub-area A) there were no differences in species identity among the 3 environments, and grassland was the only environment that differed in the common and dominant species (Table S9), while in the SCM Savanna (sub-areas B, C, and D) the differences occurred only between forests and the other environments (Table S9).

Indicator species associated with the native forest were the nine-banded armadillo (*Dasypus novemcinctus*), Azara's agouti (*Dasyprocta azarae*), the white-eared opossum (*Didelphis albiventris*), the gray brocket deer (*Mazama gouazoubira*), the coati (*Nasua nasua*), the crab-eating raccoon (*Procyon cancrivorus*), Geoffroy's cat (*Leopardus geoffroyi*), the paca (*Cuniculus paca*), the ocelot (*Leopardus pardalis*), and the sigmodontine rodents (all with $p < 0.05$, Table S8). Grassland indicator species were the pampas fox (*Lycalopex gymnocercus*), the capybara (*Hydrochaeris hydrochaeris*), and the maned wolf (all $p < 0.05$, Table S8). There were no pine plantation indicator species (Table S8).

3.1.2. Effect of the extent of the different land cover

The percentage of native forest (within a 200 m radius) and of wetland (within 1 and 2 km radii) in the surroundings had a significant effect on species composition (Table 3). There was also an effect of environment heterogeneity within a 200 m radius and vegetation structure in the lower strata ("vegetation 2") (Table 3). In particular, the gray brocket, the coati, Azara's agouti, and the white-eared opossum were most

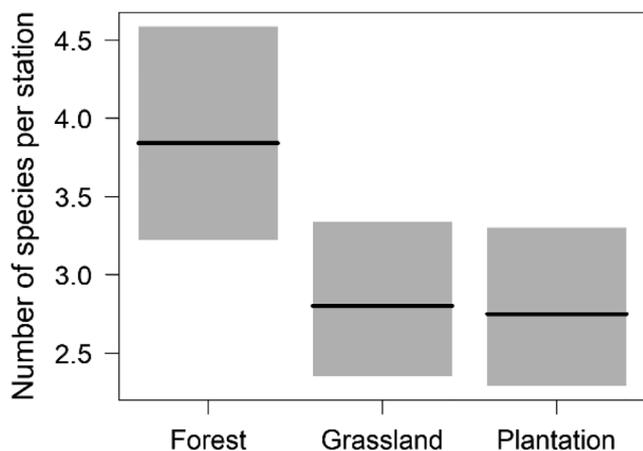


Fig. 2. Mammal richness per station in the three environments studied in the Southern Cone Mesopotamian Savanna and Iberá marshes of Argentina. The black line corresponds to the estimated average richness per station while the gray area represents its 95% confidence interval obtained from the average of the best weighted generalized linear models (with $\Delta AICc \leq 2$).

affected by the percentage of forest in a 200 m radius and arboreal structure ("vegetation 1", Fig. 3). The pampas fox was positively affected by the percentage of grassland in a 200 m radius, while the capybara and the marsh deer were associated with sites surrounded by wetlands (within a 2 km radius) and sites inaccessible to humans (Fig. 3).

Species richness was higher in stations with a higher percentage of forest (200 m radius), wetlands (2 km radius), and with a greater heterogeneity of land-use (200 m radius) in their surroundings. Sites with higher cost of access and with greater vegetation cover in the lower strata also had higher species richness (Table 4).

3.2. Results of stand level analyses

3.2.1. Effect of stand age and tree density

Several models explained the dominant species similarity between tree plantations and native forests (Table S11). Understory vegetation was not included in the best models (Table S11). The best models showed that older pine stands with intermediate densities (700–1000 trees/ha) had mammal assemblages more similar to those of forests (Fig. 4, Table S12). Pine stands with lower livestock density also had mammal assemblages more similar to those of forests (Fig. 4, Table S12). Species similarity was not affected by the proportion of forest around the tree plantation station.

Comparing the dominant species composition of mammal assemblages of plantations with those of grasslands, their similarity tended to be higher in silvopastoral systems that had higher understory vegetation density dominated by grasses (Tables S7 and S11) and were surrounded by grasslands (within a 500-m radius). However, no model was different from the null model (Table S11).

4. Discussion

The mammal assemblages of the SCM Savannas and the Iberá marshes were partially affected by the replacement of native environments by pine monocultures. Some but not all of our hypotheses were supported by the results. Contrary to our first prediction, at landscape level the structural similarity of the tree plantations with the native environments does not determine their tendency to be used by grassland or forest-dependent mammals. Pine plantations do not appear to have a substantial negative effect on the assemblage of grassland mammals, despite the structural differences between these two environments. However, there are important differences between their mammal assemblages and those of forests, both in terms of number of species and of relative abundances. This does not mean that structural similarity among environments has no effect on the similarity of their mammal assemblages, as the stand level analyses showed (see 4.2 below). In addition, as predicted by our second hypothesis, changes in species richness and composition also depend on the relative extent of some land covers in the landscape, such as the amount of remaining forest and wetland, as well as on the heterogeneity of environments.

4.1. Effect of structural similarity

4.1.1. Landscape level effects

Contrary to the predictions of the first hypothesis and to what was observed by other authors (Andrade-Núñez and Aide, 2010), the

Table 3

Pairwise mammal assemblage comparisons of C_{qN} values (PERMANOVA test using the sub-area as a strata) among 224 camera-trap stations, distributed in three environments (grasslands, native forests, and tree plantations) in the Southern Cone Mesopotamian Savanna and Iberá marshes of Argentina. To test for differences among environments and to evaluate the effect of the variables, we used the pseudo-F statistic (Anderson, 2001). The Bonferroni correction was applied to the contrasts between environments.

Variable	Df	Sørensen index (all species)		Horn index (common species)		Morisita-Horn index (dominant species)	
		F _{pseudo}	p value	F _{pseudo}	p value	F _{pseudo}	p value
Environment:	2	2.011	0.037	2.565	0.014	2.521	0.021
<i>Forest vs. Grassland</i>		17.8	0.001	20.06	0.001	18.61	0.001
<i>Forest vs. Plantation</i>		10.36	0.001	11.62	0.001	11.05	0.001
<i>Grassland vs. Plantation</i>		2.23	0.161	3.703	0.019	4.121	0.011
% of Wetland	1	8.474*	0.007	7.485**	0.002	6.231**	0.007
% of Grassland (200 m)	1	0.537	0.701	0.546	0.655	0.591	0.606
% of Plantation (2 km)	1	0.654	0.654	1.037	0.457	1.253	0.337
% of Forest (200 m)	1	3.796	0.007	4.976	0.001	3.917	0.009
Heterogeneity (200 m)	1	3.406	0.019	5.256	0.001	5.289	0.002
Cost of Access	1	7.408	0.105	4.894	0.257	3.975	0.244
Livestock	1	1.036	0.372	2.036	0.097	2.377	0.072
Vegetation 1	1	0.688	0.566	0.363	0.796	0.247	0.859
Vegetation 2	1	4.681	0.002	6.511	0.001	6.301	0.001
Residual	212						

* 1-km radius. ** 2-km radius.

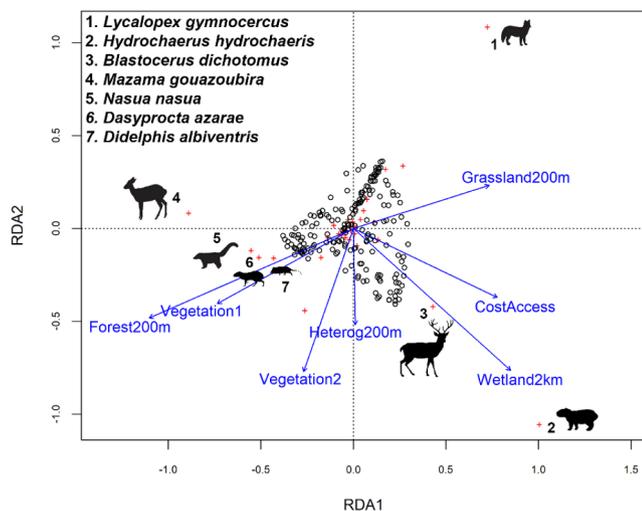


Fig. 3. Redundancy analysis (RDA) ordination of mammal species occurrence in relation to variables that had a significant effect ($p < 0.05$), in the Southern Cone Mesopotamian Savanna and Iberá marshes of Argentina. White circles correspond to the ordination of the camera-trap stations and the red crosses to the ordination of the species. Species with a goodness of fit ≥ 0.1 are indicated with illustrations. There was a significant relationship between species composition and explanatory variables ($R^2 = 0.19$; $p = 0.001$). The vectors show the correlation between the variables and the relative frequency of records of the species. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

replacement of native grasslands by afforestation did not favor the replacement of the grassland mammal assemblage by a forest mammal assemblage. Mammal assemblages of pine plantations were more similar to those of grasslands than to those of forests in terms of species richness and composition (see also Fig. S1 and S2). However, in the Iberá marshes, to the west of the study area where grassland species are associated with marshes and wetlands, the pattern of species composition matched that predicted by our hypothesis (H1): pine plantations had a mammal assemblage similar to that of the native forests, and their common and dominant species were different from those of the grasslands (see also Fig. S2). One explanation for this difference between regions could be that, in the eastern portion of the study area, forest communities are composed of many forest specialists typical of the Upper Paraná Atlantic Forest, such as the agouti, the ocelot, and the

Table 4

Variables that affect mammal richness per station (per day) in the Southern Cone Mesopotamian Savanna and Iberá marshes of Argentina. Beta values, standard errors, and 95% confidence intervals were obtained from the average of the best weighted generalized linear models (with $\Delta AICc \leq 2$). Variables and contrasts in bold had a statistically significant effect according to 95% confidence intervals and Tukey contrasts.

Variable	Parameter estimates	Standard Error	95% confidence interval	
			Lower limit	Upper limit
% of Forest 200 m	0.006	0.002	0.003	0.008
% of Wetland 2 km	0.005	0.002	0.001	0.009
Vegetation 2	0.091	0.028	0.044	0.137
Heterogeneity 200 m	0.289	0.105	0.115	0.463
Cost of Access	0.122	0.067	0.011	0.233
Tukey Contrasts				
Grassland vs. Forest	-0.316	0.091	-0.494	-0.139
Plantation vs. Forest	-0.335	0.107	-0.511	-0.159
Plantation vs. Grassland	-0.019	0.096	-0.176	0.139

paca, which do not find plantations an optimal habitat (Cruz et al., 2018; Iezzi et al., 2018). In the Iberá ecoregion, forest assemblages are dominated by generalist species such as the gray brocket and the crab-eating fox (*Cerdocyon thous*; Iezzi et al., 2018) that use tree plantations as an alternative habitat, and grassland assemblages are dominated by wetland-dependent species, such as the capybara which was very little recorded in tree plantations (Table S8). The differential effect of tree farming on two very similar mammal assemblages (those of the SCM Savannas and the Iberá marshes) suggests that the impact of this industry is highly dependent on the local pool of species.

Mammal assemblages of pine plantations in our study region are composed of species typical of both native environments. No species appeared exclusively in tree plantations and none was an indicator species of this environment. The mammal species most affected (i.e., most frequently lost) in pine plantations are those typical of the Upper Paraná Atlantic Forest (Table S8; Iezzi et al., 2018). Thus, the differences observed between tree plantation and forest mammal assemblages are mostly due to a loss of species and to changes in their relative abundance. This also explains the striking differences in recording rates and richness between forests and tree plantations.

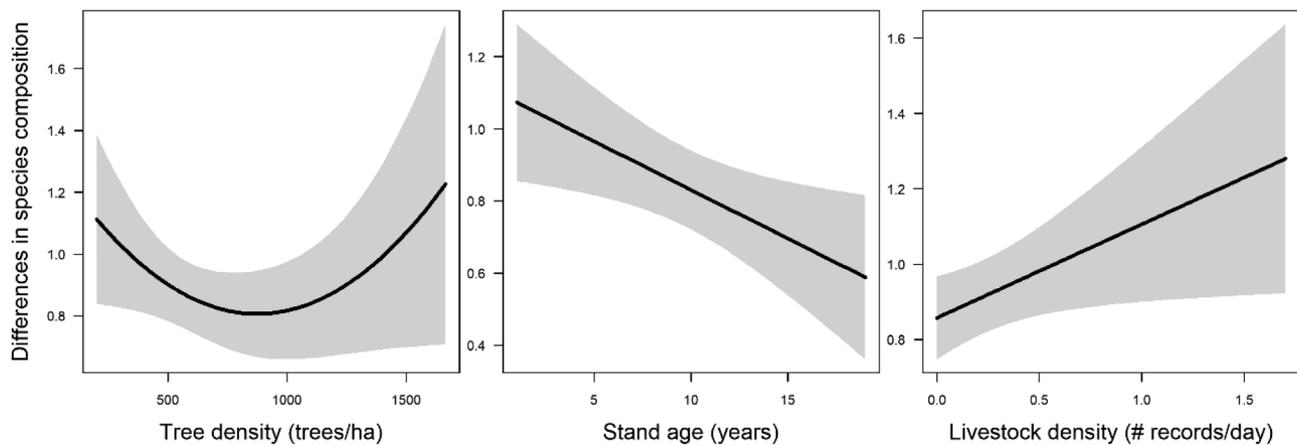


Fig. 4. Representation of the best model for the differences in composition of mammal dominant species in tree plantation with respect to the native forest of the Southern Cone Mesopotamian Savanna and Iberá marshes of Argentina. Differences in species composition were measured as the Euclidean distance from each tree plantation station to the centroid of forest stations (the reference community) in a NMDS bi-plot, so less distance (response variable of the model) implies more similarity. The black line corresponds to the parameter estimates for the average of the best models (using the median value for the rest of the variables) with the 95% confidence interval represented by the gray area.

In contrast, the mammal richness of pine plantations did not differ from that of grasslands, despite the fact that this monoculture had lower alpha mammal diversity than the native environments (see [Appendix B](#)). Also, the identity of the species recorded in the plantations and their abundances were similar to those recorded in grasslands, with many species frequently recorded in both environments ([Table S8](#)). Most of the species frequently recorded in grasslands are generalists and/or species that tolerate disturbed environments (in fact, most coexist with cattle), so it is not surprising that they frequently use other environments as well (e.g. [Andrade-Núñez and Aide, 2010](#); [Michelson, 2005](#)). This region still has a relatively low proportion of tree plantation cover compared to other regions, such as the Argentinian Atlantic Forest, and they also have a wider range of management regimes (differences in tree densities and stand ages; see [Iezzi et al., 2018](#)). Most grassland species seem not to perceive pine plantations as a barrier under current conditions. However, it is likely that the ongoing expansion of pine and eucalyptus plantations in this region associated with an increase in their age and density (as this industry takes momentum) will lead to significant changes in the richness and composition of mammal assemblages as is expected by our first hypothesis.

4.1.2. Stand level effects

As predicted by our first hypothesis, the structural similarity between native forests and tree plantations affected mammal assemblage similarity at stand level. Stand age, tree and livestock density within pine stands are variables that indirectly affect understory vegetation, and all of these had an important effect on the composition of the dominant mammal species when comparing plantations with native forests. Stands that were planted at high density (~ 1200 trees/ha) and had no thinning tend to have very high canopy cover and, therefore, a very poor understory, with the absence of most native plant species ([Seiwa et al., 2012](#); [Trentini et al., 2017](#)). The scarcity of vegetation in high-density plantations adversely affects the presence of many mammal species that are dependent on dense undergrowth ([Simonetti et al., 2013](#); [Sullivan et al., 2007](#)). Therefore, older stands with intermediate tree density (600–1200 trees/ha) provide a better habitat for forest mammal species, due to the presence of an understory typical of the native forest ([Simonetti et al., 2013](#); [Sullivan et al., 2002](#); [Timo et al., 2014](#)). On the other hand, in young and/or in intensively thinned stands with low tree densities (< 400 trees/ha), high solar radiation allows the growth of plant species typical of open environments and grasslands ([Wilson and Puettmann, 2007](#)), especially if they were planted in replacement of grasslands or cattle fields ([Brockhoff et al.,](#)

[2003](#)). This explains why mammal assemblages of plantations differ markedly from those of forests at low pine densities, at younger ages, when cattle are present and when the understory vegetation is simpler ([Fig. 4](#) and [Table S12](#)), which create the conditions for a typical grassland community.

4.2. Effect of different land cover in the landscape

As predicted by our second hypothesis, the proportion of some environments in the landscape was associated with changes in mammal richness and composition at landscape level, with wetlands and forests showing the greatest effect. These two environments are probably acting as keystone habitats providing resources and/or refuge for many mammal species, since their richness increases with the proportion of these environments in the landscape ([Hitchman et al., 2018](#); [Tews et al., 2004](#)). Also, the presence of these environments produces changes in assemblage composition, with an increase in the abundance of certain species such as the gray brocket in sites surrounded by forest, or the capybara and the marsh deer in sites surrounded by wetlands (see also, [Fracassi et al., 2015](#)). This result was expected, as both environments have naturally more mammal diversity than the grasslands and the anthropogenic environments, which highlights the importance of their preservation in the landscape ([Andrade-Núñez and Aide, 2010](#); [Felton et al., 2010](#); [López-Ricaurte et al., 2017](#); [Lyra-Jorge et al., 2008](#); [Tews et al., 2004](#)).

As expected, the heterogeneity of environments in the landscape was an important factor that affected the richness, composition, and relative abundance of species. The prevailing environments in the study area are grasslands and wetlands, with the productive environments and native forests contributing to the landscape heterogeneity. There are species that are able to exploit different types of crops, so the presence of different productive environments, added to a greater proportion of forest in the landscape, can favor an increase in species diversity ([Bennett et al., 2006](#); [Reynolds et al., 2018](#)) and promote changes in assemblage composition ([Saito and Koike, 2013](#); [Tews et al., 2004](#)). Future studies are needed to evaluate the effect of each type of crop on mammal assemblages, as they may not contribute equally to species diversity ([Reynolds et al., 2018](#)).

4.3. Main conclusions and recommendations

In naturally open environments, tree plantations usually have more harmful effects on biodiversity than livestock grazing, other types of

agricultural crops, or human activities (Brockerhoff et al., 2008; Filloy et al., 2010). According to our results, in the SCM Savannas ecoregion, assemblages of medium and large grassland mammals seem still not to be significantly affected by afforestation. However, tree plantations are less diverse than the native forests in this region, and their similarity in species composition mainly depends on the management practices at stand scale. On the other hand, the plantations in the Iberá area had a significant effect on the composition and relative abundance of grassland species assemblages, and so the preservation of grasslands and wetlands in this region is clearly of vital importance for the conservation of native mammals.

In this grassland-dominated but heterogeneous landscape, there are mammal species associated with each type of natural environment, and there are marked differences in species composition between forests and grasslands (see Appendix C). Forests and wetlands act as keystone habitats, emphasizing the importance of their preservation while maintaining large areas of natural grasslands with their characteristic mammal assemblages. In addition, the use of roads by the forestry industry and the increased human accessibility they provide is associated with other anthropogenic pressures such as hunting (Benítez-López et al., 2017; Ferreguetti et al., 2018), which causes a reduction in mammal richness and in the abundance of some species (capybara and marsh deer –Fig. 3). Thus, it is also important to incorporate direct protection actions within the productive areas, such as the control of poaching to reduce hunting pressure.

Even though most grassland species still do not perceive tree plantations as a barrier regardless of forest management, planting pines at low densities in this region seems to encourage the growth of an understory typical of native grasslands and to promote the use of plantations by a grassland mammal assemblage, as occurs in silvopastoral systems with low livestock density. The presence of tall grasses and a complex vegetation structure in the lower strata is also an important factor that is affected by the presence of livestock and some stand level management practices. In areas adjacent to extensive native forests, plantation management actions such as maintaining stands with intermediate tree densities, promoting longer rotations, and excluding cattle, are desirable to promote the development of an understory similar to the native forest.

Tree plantations still represent a relatively small area in this region but an increase above a critical threshold could lead to significant changes in the richness and composition of native mammal assemblages. For this reason, their effects on biodiversity should be monitored and, if necessary, their expansion limited where they may negatively affect the native communities.

CRedit authorship contribution statement

M.E. Iezzi: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Writing - original draft, Visualization, Project administration, Funding acquisition. **C. De Angelo:** Conceptualization, Methodology, Resources, Writing - review & editing, Visualization, Supervision, Project administration, Funding acquisition. **M.S. Di Bitetti:** Conceptualization, Methodology, Investigation, Resources, Writing - review & editing, Visualization, Supervision, Project administration, Funding acquisition.

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Declaration of Competing Interest

None.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2020.118303>.

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