



# Fragment configuration or environmental quality? Understanding what really matters for the conservation of native mammals in the Atlantic Forest of Argentina

Iezzi María Eugenia<sup>a,b,\*</sup>, Cruz Paula<sup>a,b</sup>, Varela Diego<sup>a,b</sup>, Di Bitetti Mario S.<sup>a,b,c,1</sup>, De Angelo Carlos<sup>a,b,1</sup>

<sup>a</sup> Instituto de Biología Subtropical (IBS), Universidad Nacional de Misiones (UNaM) – CONICET, Bertoni 85, Puerto Iguazú, Misiones, Argentina

<sup>b</sup> Asociación Civil Centro de Investigaciones del Bosque Atlántico (CeIBA), Bertoni 85, Puerto Iguazú, Misiones, Argentina

<sup>c</sup> Facultad de Ciencias Forestales, UNaM, Eldorado, Misiones, Argentina

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## ABSTRACT

The fragmentation of natural environments is one of the most important threats to biodiversity and involves changes in landscape configuration and habitat quality. The Atlantic Forest of South America has been highly fragmented, which creates concern for the conservation of its biodiversity. We evaluated the effects of forest loss and fragmentation on the terrestrial mammal assemblage of the Atlantic Forest of Misiones, Argentina. The area still contains large fragments and a forest cover > 50%. We evaluated the effect of the configuration of the fragments (area, isolation) and the quality of the environment surrounding them (% of forest, land uses, poaching). We sampled mammal assemblages with camera-traps. We used generalized linear models, with the number of species in smaller forest fragments (49 stations) and the difference in their composition to that of the largest forest fragment (control situation; 53 stations) as response variables. Species richness in the fragments increased with the proportion of forest in their surroundings and decreased with the distance to population sources. The dissimilarity of the assemblages of smaller fragments to those of the largest fragment increased with forest disturbance and by the contrast of the land uses (e.g., annual crops) surrounding the fragments. We modeled and mapped these effects, which can be used as spatially explicit planning tools for the conservation of the mammal assemblage in this landscape. The effect of fragmentation on the mammal assemblage is mediated by both anthropic effects that affect the quality of the environment and by the spatial configuration of fragments in the landscape.

## 1. Introduction

Habitat loss and fragmentation of natural environments are among the most important threats to biodiversity (Haddad et al., 2015; Laurance et al., 2006; Sanderson et al., 2002), although the processes behind their detrimental effects continue to be a subject of debate (2017, Fahrig, 2003; Fahrig et al., 2019; Fletcher et al., 2018; Miller-Rushing et al., 2019; Villard & Metzger, 2014). The fragmentation process involves not only the subdivision of the original vegetation into fragments or patches, but also a decrease in their size and quality, an increase in their isolation and edge effects, a reduction in the amount of the original environment, and the increase in anthropogenic pressures on the environment associated with the productive matrix (Bennett &

Saunders, 2010; Fahrig, 2003). How these factors work and what is their relative importance for affecting biodiversity may depend on the characteristics of the system studied and the scale of analysis (Bennett & Saunders, 2010).

According to the theory of island biogeography, the number of species on an island is related to its area and distance from the mainland (its isolation; Mac Arthur & Wilson, 1967). This theory was extended from islands to terrestrial patches of original environments, where isolation is now the result of habitat loss (Fahrig, 2003; Haila, 2002), and can be measured as the distance of a patch to its neighbor (s), or to a large fragment of native environment, that could act as population source for many species (Bender, Tischendorf, & Fahrig, 2003; Lindenmayer et al., 2008). Under this theory, the probability of

\* Corresponding author at: Instituto de Biología Subtropical (IBS), Universidad Nacional de Misiones (UNaM) – CONICET, Bertoni 85, Puerto Iguazú, Misiones, Argentina.

E-mail address: [maru.iezzi@gmail.com](mailto:maru.iezzi@gmail.com) (M.E. Iezzi).

<sup>1</sup> These authors contributed equally to this work.

occurrence of species increases with patch size (Bennett & Saunders, 2010; Bennett, Radford, & Haslem, 2006), and decreases in more isolated fragments (Fahrig, 2013), with several examples in the highly fragmented Atlantic Forest (e.g. Boscolo & Metzger, 2011; da Silva, Ribeiro, Hasui, & Aparecida, 2015; Martensen et al., 2012; Uezu, Metzger, & Vielliard, 2005).

A more comprehensive approach to the effects of habitat fragmentation on ecological communities should not only account for the species richness but should also include an analysis of changes in species composition (Dormann et al., 2007; Koleff, Gaston, & Lennon, 2003; Soininen, McDonald, & Hillebrand, 2007). Some species are more affected by changes in landscape configuration while others easily colonize patches and may even be favored by the transformation of the original habitat (Beca et al., 2017; Crooks, 2002; Pardini, De Souza, Braga-Neto, & Metzger, 2005). Therefore, smaller and/or more isolated patches tend to support a subset of the species present in the larger fragments, mainly due to the loss of rare and specialist species (Bennett & Saunders, 2010), although changes in diversity and composition could be unpredictable in extremely fragmented landscapes where generalized regional extinctions of species have already occurred (e.g., Mendes Pontes et al., 2016).

In terrestrial landscapes, patches of native environments may be embedded in a heterogeneous matrix where some land uses are not necessarily an inhospitable environment for animals or may even be a suitable habitat for some species (Fischer & Lindenmayer, 2007; Haila, 2002; Laurance, 2008). The effect of matrix permeability has been studied in different landscapes (da Silva et al., 2015; Heer, Helbig-Bonitz, Fernandes, Mello, & Kalko, 2015; Uezu, Beyer, & Metzger, 2008) and it may even be more important than the size and the degree of isolation of the fragments (Bender & Fahrig, 2005; Brady, McAlpine, Possingham, Miller, & Baxter, 2011; Prugh, Hodges, Sinclair, & Brashares, 2008). In fact, several studies show that the effects of fragments configuration emerge only when the matrix is very different from the original habitat (see Ferraz et al., 2003), or when the amount of native vegetation remaining is low (Hanski, 2015; Pardini, de Bueno, Gardner, Prado, & Metzger, 2010).

There are other anthropogenic pressures associated with landscape transformation that may affect the diversity and composition of animal communities (Laurance, 2008). For example, the extension of roads associated with productive systems facilitates human access, which in turn can increase extractive activities such as hunting and logging in forested environments. Poaching can have strong effects on the abundance of some species (Benítez-López et al., 2017), causing predictable changes in the composition of mammal assemblages (Peres & Palacios, 2007). On the other hand, wood extraction not only causes a decrease in the density of large trees in forest patches (Cannon, 1998; Okuda et al., 2003), but also produces changes in vegetation structure, such as an increase in bamboos or grasses that may replace typical understory species of mature forests (Campanello, Gatti, Ares, Montti, & Goldstein, 2007, 2012; Zaninovich, Montti, Alvarez, & Gatti, 2017), which may have effects on the fauna (Laurance & Laurance, 1996; Pardini et al., 2005). Therefore, habitat fragmentation is a complex process involving not only changes in the structure of the landscape but also a combination of changes and pressures acting together over the original ecosystem.

The Atlantic Forest is considered a hotspot of biodiversity (Mittermeier, Myers, Thomsen, da Fonseca, & Olivieri, 1998; Myers, Mittermeier, Mittermeier, Fonseca, & Kent, 2000) but is an ecoregion that has suffered a long process of fragmentation due to the conversion of native forest to different productive land uses (Galindo-Leal & de Gusmão Câmara, 2003). As a result, it is one of the most threatened forests in the world, with only 11–17% of its original cover remaining (Ribeiro, Metzger, Martensen, Ponzoni, & Hirota, 2009). The Argentinean portion of the Atlantic Forest has declined almost 20% in the last 40 years due to its conversion to perennial crops and commercial tree plantations (Izquierdo, De Angelo, & Aide, 2008; Zuleta et al., 2015).

However, in this country there are still large and relatively continuous forest remnants (i.e. > 300,000 ha), with forests covering more than 50% of the original landscape occupied by the Atlantic Forest (Zuleta et al., 2015).

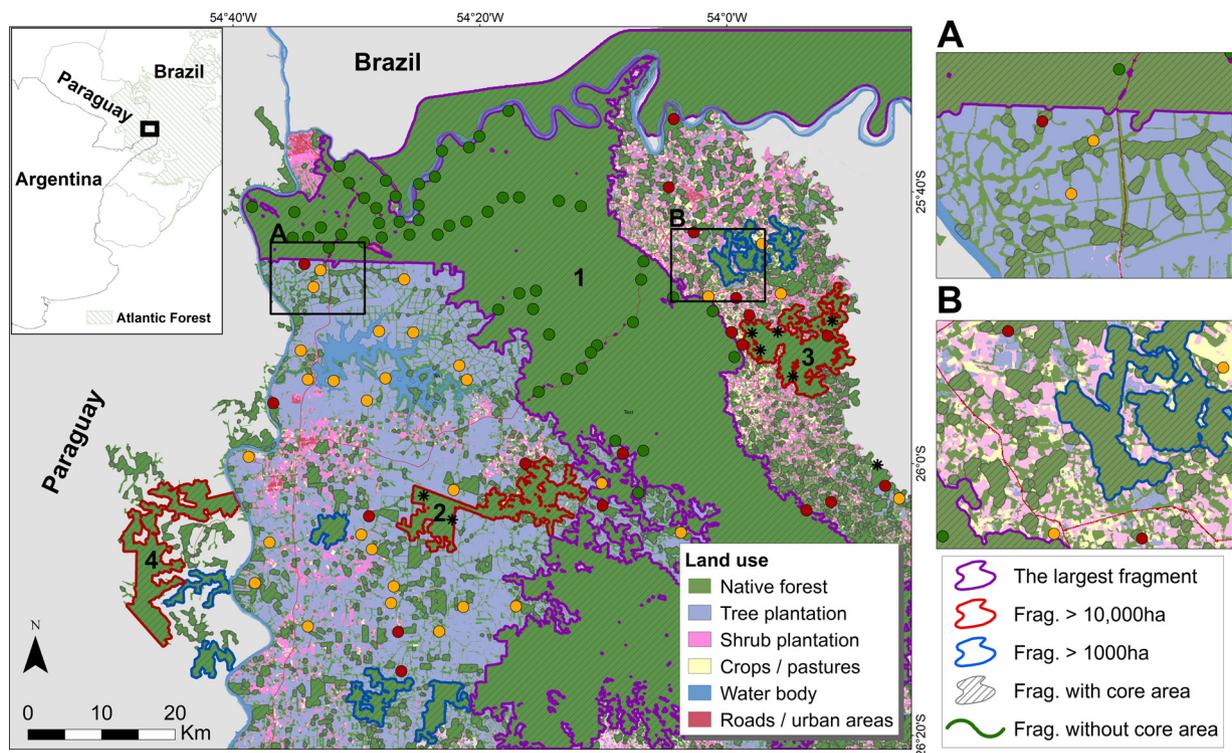
Mammals are among the groups of species that have been severely affected by the degradation and loss of the Atlantic Forest (Bogoni, Pires, Graipel, Peroni, & Peres, 2018; Galetti, Brocardo, Begotti, Hortenci, & Bernardo, 2017; Jorge, Galetti, Ribeiro, & Ferraz, 2013; Paviolo et al., 2016). The effects of habitat loss and fragmentation in mammal assemblages have been documented in different portions of the Atlantic Forest, where the amount of remaining forest is considerably low (< 30%) and the patches present a high degree of isolation (Beca et al., 2017; da Silva et al., 2015; Magioli, Ribeiro, Ferraz, & Rodrigues, 2015, 2016; Pardini et al., 2010, 2005; Uezu et al., 2005; Vieira et al., 2009), reaching the highest rates of fragmentation in its northern portion (Mendes Pontes et al., 2016). In the Atlantic Forest of Argentina instead, the productive matrix contains multiple fragments of native forest of different sizes, most of which are highly connected, including large remnants of forest dominated by protected areas. However, the unceasing process of habitat loss in this area has increased the need to understand the effects of these changes on animal populations, which is fundamental to carry out adequate territorial planning and management of productive systems to develop appropriate strategies for biodiversity conservation (Gardner et al., 2009).

The aim of this study was to evaluate the effect of forest loss and fragmentation on the terrestrial medium to large-sized mammal assemblage in the remaining fragments of the Atlantic Forest of Argentina. In particular, we evaluated the effect of the characteristics of the native forest fragments and their surroundings on the richness and composition of mammals. We tested two not mutually exclusive hypotheses: (1) The configuration of the fragments (area, isolation) has an effect on the richness and composition of mammal assemblage. (2) The quality of the environment has a strong effect on the mammal assemblage, with two components that we evaluated: (2a) the characteristics of the fragment's surroundings (amount of forest vs. other land uses) and (2b) other anthropogenic pressures (human accessibility, degree of disturbance).

## 2. Material and methods

### 2.1. Study area

We conducted this study in the northern part of Misiones province, Argentina, in the Upper Paraná Atlantic Forest ecoregion, one of the ecoregions that comprise the Atlantic Forest. The original environment is a semi-deciduous subtropical forest that still contains the complete regional native mammal assemblage (Galindo-Leal & de Gusmão Câmara, 2003). The study area, of approximately 500,500 ha (Fig. 1), contains 68% of native forest, including part of the largest fragment of this ecoregion (~370,000 ha, counting portions of Brazil's bordering forests) mainly composed of protected areas, and multiple forest remnants of different sizes and with varying degrees of anthropogenic disturbance (Campanello, Gatti et al., 2007; Paviolo et al., 2009). In addition to native forest, predominant land uses include commercial tree plantations (mainly pine, *Pinus taeda*), shrub plantations (mainly yerba mate, *Ilex paraguayensis*), annual crops (tobacco, corn, and cassava), and pastures for cattle-grazing. Forest plantations are mainly located to the west of the province, covering almost 20% of the study area (Fig. 1) and belonging to large companies (Cariola, Izquierdo, & Hilgert, 2018). Conversely, shrub plantations (8%) and annual crops or pastures (summing 2%) are located mainly to the east of the study area (Fig. 1), in small-scale properties (10–200 ha) belonging to local farmers (Furlan, Cariola, García, & Hilgert, 2015).



**Fig. 1.** Location of the study site and camera-trap stations in the Atlantic Forest of Misiones province, Argentina. The map highlights the remnants of forest that were classified as fragments with core area and all those that were larger than 1000 ha. The numbered fragments correspond to those larger than 10,000 ha and partially composed of protected areas: fragment n°1 corresponds to the largest forest fragment (the control situation); fragment n°2 corresponds to Sierra Morena; fragment n°3 corresponds to the Uruguáí - Foerster Corridor; and fragment n°4 corresponds to Ñacunday National Park and private areas of Paraguay. The green dots correspond to the stations located in the largest forest fragment (53), the red dots to those located within the smaller fragments with core area (19), and the yellow dots to those located within the smaller fragments without core area (30). Asterisks correspond to the 8 stations randomly excluded from the original data set to avoid pseudo-replication from same smaller forest fragments (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

## 2.2. Sampling design

To study the assemblage of terrestrial mammals, we conducted a camera-trap (Reconyx HC500) survey between May 2013 and December 2014. For this study, we used the information from 102 camera-trap stations that belonged to a larger survey described in Iezzi, Cruz, Varela, De Angelo, & Di Bitetti (2018). We distributed the stations using a stratified-random design: we randomly distributed the stations using a grid of  $2 \times 2$ -km cells (with a minimum distance of 2 km between stations) located at distances of  $> 50$  m from nearest road or human trail, with no more than one station in each cell, but, for logistical reasons, we did not consider cells situated further than 500 m from a road or trail for locating cameras. Each station consisted of a single camera-trap unit located off-road and attached to the base of a tree at a height of about 30–40 cm above ground level. Stations were not baited and cameras were set to take three successive pictures per trigger with no delay between detections. The cameras were active for an average of 50 days (min. 12, max. 123 days), reaching 5115 camera days. A  $> 1$ -h period had to pass for two successive pictures of the same species to be considered independent records.

From the survey described in Iezzi et al. (2018), we used the 53 stations located in the largest forest fragment (control situation) and 49 stations located in smaller forest fragments (Fig. 1). We defined the control fragment stations as those located in the largest native forest fragment with the proviso that they had to be surrounded by more than 75% of forest cover in a 2-km radius to qualify as such. Stations in smaller forest fragments were those placed in native forest remnants outside the largest forest fragment. Since a few stations were located in the same forest fragment (three large fragments, 11 stations), we decided to randomly select only one station per fragment so that all

stations acted independently (8 stations excluded). To verify that this removal would not affect the results, the whole statistical analysis was repeated with three different data sets, two of them removing 8 different stations and one with the complete set of stations ( $N = 110$ ), and the best statistical models included the same variables in all cases (Table A1). We randomly selected one of the two data sets with the 8 stations removed for the final results.

## 2.3. Estimation of independent variables

To test the proposed hypotheses, we estimated variables associated with the configuration of the fragments and variables related to the quality of the environment.

### 2.3.1. Configuration variables

**Area.** As the forest remnants had different sizes and shapes, to estimate the area of each one we first classified them according to the existence or not of a core area. The core area was defined as the area of the fragment that is less affected by the edge effects caused by the contact with non-forest areas (Saura, Vogt, Velázquez, Hernando, & Tejera, 2011). We defined an edge width of 200 m based on a review of different studies in areas or contexts similar to the study site (e.g. Beier, 1993; Lenz, Jack, & Spironello, 2014; Rabinowitz & Zeller, 2010; Stevens & Husband, 1998). Using this width, we identified 1376 fragments with core area, ranging from 12.5 to 10,391 ha (median = 28.14 ha, Fig. 1), excluding the largest forest fragment. Nineteen of the stations were located in these fragments with a core area, comprising a range of fragments between 14 to 10,391 ha (median = 200.83 ha, Fig. 1), plus 30 stations located in remnants composed 100% by edge (less than 400 m wide, Fig. 1). As it was impossible to

measure the size of these small fragments with no core area because most of them had lineal shapes and were connected to each other, we decided to evaluate the effect of the area by testing two possible variants: “Core area”, a dichotomous variable distinguishing fragments with core area vs. fragments without it; and, “Area”, an ordinal variable with five categories ordered by their size (“no core area”,  $N = 30$ ; 14–100 ha,  $N = 8$ ; 100–1000 ha,  $N = 9$ ; 1000–10,000 ha, no stations;  $> 10,000$  ha,  $N = 2$ ).

**Isolation.** We used two alternative measures of isolation: the distance to the nearest fragment with core area (“Near distance”); and, the distance to main population sources. We estimated distances using a lower-cost functional connectivity model that takes into account the heterogeneity of the matrix in the landscape (Adriaensen et al., 2003; Epps, Wehausen, Bleich, Torres, & Brashares, 2007). We created a friction grid in a Geographic Information System (GIS) with different movement costs assigned to each land use for a generic medium and large native mammal following Iezzi et al. (2018) and we used the Cost-Distance function to measure the cumulative cost through the least-cost paths from each station to the border of the nearest fragment or source. We considered all fragments  $> 1000$  ha as possible main population sources, including those located in neighbor countries, and classified them into three groups for testing their importance (Fig. 1): a) the largest forest fragment (“Distance to Largest fragment”); b) fragments  $> 10,000$  ha (three fragments partially composed of protected areas; “Distance  $\geq 10,000$ ”); and, c) fragments of between 1000 and 3200 ha (10 fragments without formal protection; “Distance  $\geq 1,000$ ”). When the station was located within a fragment considered as a possible source, we assigned a value of 0 to the distance to that source.

As the stations were located at different distances from the edge of the fragment, we measured the closest distance to the border with the non-forest area (“Distance edge”) to control its possible effect on the mammal assemblage.

### 2.3.2. Environmental quality variables

a) **Station immediate surroundings.** To evaluate the effect of the landscape immediately surrounding the fragments we estimated an environment permeability index (EPI) following da Silva et al. (2015). This index estimates the proportion of each land use in a buffer around each station, weighted by a Permeability Value (PV) that represents the cost for movement or permanence of a generic medium and a large native mammal, using the following formula:

$$EPI_b = \frac{\sum (PV_s * A_s)}{A_b}$$

Where  $EPI_b$  = Environment Permeability Index for station b;  $PV_s$  = Permeability Value of land use type s;  $A_s$  = Area occupied by land use type s;  $A_b$  = Total buffer area around station b; b = Sampling station; s = Land use (native forest; tree plantation; shrub plantation; crops or pastures; main roads or urban areas, see Fig. 1). The permeability value assigned to each land use was equal to the movement cost assigned to the friction grid previously used. If the index value equals 1 it means that the station is surrounded 100% by native forest, and as its value increases the greater is the proportion of the structurally more contrasting and less permeable land uses. We used the logarithm of the EPI to have a linear relation with the response variables. Since this index takes into account the proportion of forest in the buffer, in order to evaluate whether the land use type has an effect or simply the proportion of forest in the environment is the most important factor for species richness and composition, we contrasted the models containing EPI as a variable with those containing the percentage of forest (“% of Forest”). As there is large variability in the mean home ranges of the mammal species composing the assemblage, it is expected that the scale at which each one perceives the environment also varies (e.g. De Angelo, Paviolo, Wiegand, Kanagaraj, & Di Bitetti, 2013; Lyra-Jorge, Ribeiro, Ciochetti, Tambosi, & Pivello, 2010; Umetsu, Metzger, &

Pardini, 2008). For this reason, we estimated different variants of these fragment surroundings variables using radii of 500, 1000 and 2000 m. We decided not to include smaller radii as they would represent the forest of the same fragment.

a) **Other anthropogenic pressures.** To evaluate the effect of other possible anthropogenic pressures, at each station we estimated two variables indirectly associated with current or past human impacts: the vegetation degradation (“vegetation”); and, the time for a human to reach the station from the closest town or city, a variable that indirectly measures the level of human extractive activities such as hunting (“cost of access”).

**Vegetation.** We measured vegetation complexity at each station with surveys of typical understory species and tree structure. For this purpose, we estimated the relative abundance (on a scale from 0 to 3) of some of the dominant understory species or genera considered characteristic of different types of forests in Misiones (well preserved primary forests, forests with high levels of intervention and secondary forests, Table A.2) at 10-m distance from the camera-trap, towards the four cardinal points ( $N = 4$  points). In addition, at each point we estimated tree density (for trees with DBH  $> 10$  cm) and basal area per ha, using the quarter method (Krebs, 1989). Finally, we counted the number of *Euterpe edulis* adult palms present in an area equivalent to  $\frac{1}{4}$  ha centered at the camera-trap station as this is a keystone species usually absent in highly degraded forests (Gatti, Campanello, & Goldstein, 2011). These features were summarized using Principal Components Analysis (PCA) based on correlations. We used the values of the stations on the first principal component axis (% of variance explained = 33.6), which corresponds to a gradient from locations with understory vegetation dominated by mature forest species and with a high tree density and basal area (positive values), to locations with higher abundance of grasses and bamboos, characteristics of forests with a high degree of disturbance (negative values; Campanello, Garibaldi, Gatti, & Goldstein, 2007; Zaninovich et al., 2017; Table A.2).

**Cost of Access.** This variable was created following De Angelo, Paviolo, and Di Bitetti (2011) and modified by Iezzi et al. (2018); it represents the human accessibility cost measured as the hours needed to access the camera-trap station from the nearest town or city. In this model, the speed of human movement inside protected areas was halved, so the variable incorporates the deterrence of poaching inside them (Iezzi et al., 2018).

In order to define the extent of the largest forest fragment, to delimit the fragments with core area, and to estimate the configuration variables, the environment permeability index and the cost of access, we used a land-use raster layer (pixels of 30 x 30 m) created for 2013–2014 by Zuleta et al. (2015). We used ArcGIS 10.3.1 (ESRI Inc.) to select the location of the stations and for GIS analyses.

### 2.4. Statistical analysis

We analyzed the effects of the above mentioned variables on the richness and species composition of native mammals using Generalized Linear Models. Records of the small ( $< 200$  g) sigmodontine rodents were categorized as “sigmodontines” because of the difficulty of identifying them at species level. We also excluded from the analysis 110 records that were impossible to identify at species level and records of three exotic species (domestic dog, 17 records; domestic pig, four records; and cattle, four records).

#### 2.4.1. Estimation and distribution of response variables

In order to evaluate the effect of the variables on mammal richness, we used a Poisson distribution with the number of observed species per station as the response variable in the models. As the sampling effort varied among stations, we included the number of days that each camera remained active as an offset term.

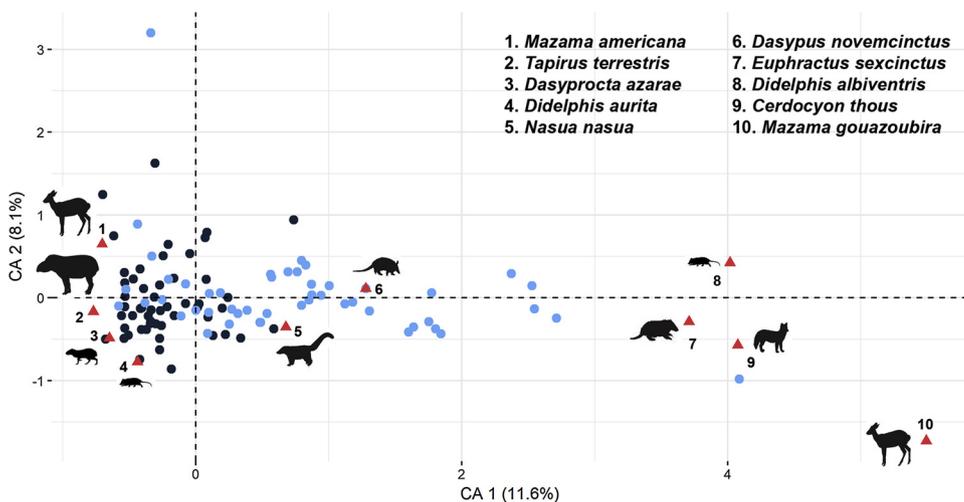


Fig. 2. Ordination of camera trap stations on the first two axes (CA 1 and CA 2) of a Correspondence Analysis based on the frequency of records of medium- to large-sized mammal (corrected by effort) in the Atlantic Forest of Argentina. The light blue dots correspond to the stations located in the smaller forest remnants (49) and the dark blue ones to the stations located in the largest forest fragment (53). To avoid excessive information to the first axis are depicted (red triangles). The first principal axis scores of the smaller fragment stations were used as a response variable representing the differences in species composition in relation to the largest fragment assemblage (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

To study the effect of the independent variables on the composition of the mammal assemblage, we used the relative frequency of records, estimated as the number of independent records of each native mammal species divided by sampling effort (camera-trap days). With the records of the stations located in the smaller forest fragments and in the largest forest fragment, we performed a Correspondence Analysis (CA) that preserves the  $X^2$  distance among sites (Legendre & Legendre, 1998). This analysis, which is robust to the inclusion of rare species with lots of zeros (Borcard, Gillet, Legendre, & Legendre, 2011), ordered the sampling sites according to their mammal composition, resulting in a gradient along the first axis from locations with greater frequency of records of indicator species of well-preserved forest (mainly the largest fragment stations) to locations with generalist species that are commonly observed in disturbed areas, like tree plantations (Iezzi et al., 2018; Fig. 2). We used the first axis scores of the smaller fragment stations as a response variable that represents the difference in composition of their assemblages in relation to the largest fragment assemblage which serves as the reference. In the species composition models, we assumed a normal distribution.

#### 2.4.2. Model selection and predictive maps

Within each main hypothesis, we looked for the particular variants of variables or combination of variables that were best supported by the data. Once we had selected the variable(s) that best represent the configuration of the fragments and the quality of the environment, we looked for the combination of them that best explained the mammal richness and composition. To select the best variables within each set of hypotheses (main and particular), we generated models with all possible combinations of non-correlated variables (Spearman coef. < 0.7). Each set of models was ranked by their Akaike Information Criterion for Small Samples (AICc) ascending value (Burnham & Anderson, 2002) and we selected the variables that were included in the models that had a  $\Delta AICc \leq 2$  (and had a  $\Delta AICc < 2$  with respect to the null model). For the best ranked final models, we estimated their relative importance using the cumulative AIC weights ( $w$ ) and evaluated the effect and importance of each variable evaluating if the 95% Confidence Interval (CI) of a parameter estimate included zero. In cases where more than one model was selected, we averaged them to estimate the beta values of each variable with its 95% CI. The variables whose CIs did not include zero are those we considered to have strong evidence of an effect on the response variable (Anderson, 2008). As all variables correspond to directional hypotheses, we used one-tailed tests in all cases.

To select the best isolation variant (Distance  $\geq 1000$ , Distance  $\geq 10,000$ , Distance to Largest fragment or Near Distance) and the best area variant ("Core area" vs. "Area") we compared each univariate model using the AICc and selected the variant included in the model

with the lowest value (Table A.3). We followed the same procedure to select the best radii for the variables "% Forest" and EPIb and to contrast the model that included the best variant of EPIb with the one that included the best variant of "% of Forest" (Table A.4).

Finally, using ArcGIS 10.3.1 (Map Algebra Tool), we created predictive maps summing up the grids obtained from the best models using the beta values of the variables included in them, weighted by their AIC weights (model average). As it was impossible to extrapolate the variable vegetation to the whole landscape because its value was only available for the locations of the camera-trap stations, we used an average value for that variable for extrapolation. Moran's I index of spatial autocorrelation (Moran, 1950) was calculated on the residuals of the best final models using the Spatial Statistic Tools to test for possible spatial autocorrelation not accounted for by the models. In order to identify the individual species that are being most affected by the independent variables, we represented the relation between the relative frequency of records of the 10 mammal species with the highest contribution to the first axis of the CA and the variables with a strong effect on the response variable in the species composition models. To evaluate correlations between explanatory variables, we performed Spearman correlations using the Infostat software (Di Rienzo et al., 2015). For the rest of the statistical analyses, we used the software R ver. 3.2.3. With the "car" package we checked whether there was collinearity between the variables with the "vif" function (Variance Inflation Factor, Fox, 2007). We performed the CA to estimate changes in composition using the "vegan", the "FactoMineR" and the "factoextra" packages (Kassambara & Mundt, 2017; Lê, Josse, & Husson, 2008; Oksanen et al., 2007). For AICc model selection and for model averaging we used the "MuMin" package (Bartoń, 2016).

### 3. Results

We obtained 2799 independent records of 33 species of native mammals (Table A5). The number of species per station in the largest forest fragment varied between 1 and 15 and in the forest remnants between 1 and 10 species (Table 1).

For species richness, the distance to fragments > 10,000 ha was the variable that best represented the effect of landscape configuration (Tables 2, A.3 and A.6). The proportion of forest in a 500 m radius presented a better fit than the Environment Permeability Index (Table A.4), but the cost of access and vegetation structure also explained species richness in the quality of the environment model (Tables 2 and A.7). The combination and comparison of these models resulted in five important models for species richness, and the average model included all the variables selected for the environmental quality and landscape configuration (Tables 2 and A.8). The number of species increased with

**Table 1**

Total number of species recorded (Total spp.) and mean number of species per station (Spp. p/station; SD within brackets) of mammals recorded in the largest forest fragment and the smaller forest fragments (with and without core area) in the Atlantic Forest of Misiones province, Argentina. Mean effort per station (in days) is also indicated (SD within brackets).

	# stations	Total spp.	Spp p/ station	Average effort
<b>The largest fragment</b>	53	30	7.92 (2.50)	49.04 (17.18)
<b>Smaller fragments</b>	49	30	5.69 (2.22)	51.33 (23.21)
<b>Fragments with core area</b>	19	24	5.84 (2.19)	50.70 (20.15)
<b>Fragments without core area</b>	30	30	5.60 (2.28)	51.72 (25.27)

**Table 2**

Models that best represented the configuration of fragments and the quality of the environment surrounding the camera trap stations showing the greatest effect on mammal richness and differences in species composition in the smaller forest fragments with respect to the largest fragment of the Atlantic Forest of Misiones, Argentina. These models had a  $\Delta AICc < 2$  in relation to the best model for representing each hypothesis (Tables A.4 to A.6) and also had a  $\Delta AICc < 2$  with respect to the null model. For each model (including the null one) the AICc and  $R^2$  values are reported. The z value corresponds to the Moran index (values greater than 2 or lesser than -2 imply spatial autocorrelation, Moran, 1950) which was estimated for the best models.

Model	$R^2$	AICc	w	z value
<b>Richness</b>				
<b>Configuration</b>				
Isolation (Distance $\geq$ 10,000 ha)	0.13	213.5		
<b>Quality of the environment</b>				
% Forest (500 m) + Cost of Access + Vegetation	0.19	214.8		
<b>Configuration + Quality of the environment</b>				
Isolation (Distance $\geq$ 10,000 ha)	0.13	213.5	0.3	-0.77
Isolation (Distance $\geq$ 10,000 ha) + Vegetation	0.17	213.9	0.25	-0.79
Isolation (Distance $\geq$ 10,000 ha) + Vegetation + Cost of Access	0.20	214.8	0.16	-0.60
% Forest (500 m) + Cost of Access + Vegetation	0.19	214.8	0.16	0.61
Isolation (Distance $\geq$ 10,000 ha) + Cost of Access	0.15	215.2	0.13	-0.66
<b>Null model</b>		218.2		
<b>Composition</b>				
<b>Configuration</b>				
-				
<b>Quality of the environment</b>				
log EPI <sup>a</sup> (2 km) + Vegetation	0.33	124.5		
log EPI <sup>a</sup> (2 km) + Vegetation + Cost of Access	0.35	125.9		
<b>Configuration + Quality of the environment</b>				
log EPI <sup>a</sup> (2 km) + Vegetation	0.33	124.5	0.67	0.25
log EPI <sup>a</sup> (2 km) + Vegetation + Cost of Access	0.35	125.9	0.33	0.37
<b>Null model</b>		140.0		

$R^2$  was estimated as 1- (residual deviance / null deviance).

<sup>a</sup>EPI = Environment Permeability Index.

the proportion of forest in the environment and decreased with the distance to population sources (Table 3, Fig. 3). Vegetation structure and cost of access were also included in the best models but they did not have strong evidence of an effect on the response variable (Table 3).

There were no important configuration variables that explain mammal species composition (Table A.6) and the best models only included the environment quality variables: the vegetation structure; the Environment Permeability Index in a 2-km radius; and, the cost of access (Tables 2 and A.7), although the latter's 95% IC included zero in the average model (Table 3). Differences in species composition of the smaller fragments with respect to the largest fragment assemblage increased with a higher degree of vegetation disturbance, with an increase in the frequency of contrasting land uses (e.g. annual crops) in the environment and with an increase of human accessibility (Table 3 and Fig. 4). The red brocket deer *Mazama americana*, the lowland tapir *Tapirus terrestris*, Azara's agouti *Dasyprocta azarae* and the black-eared

**Table 3**

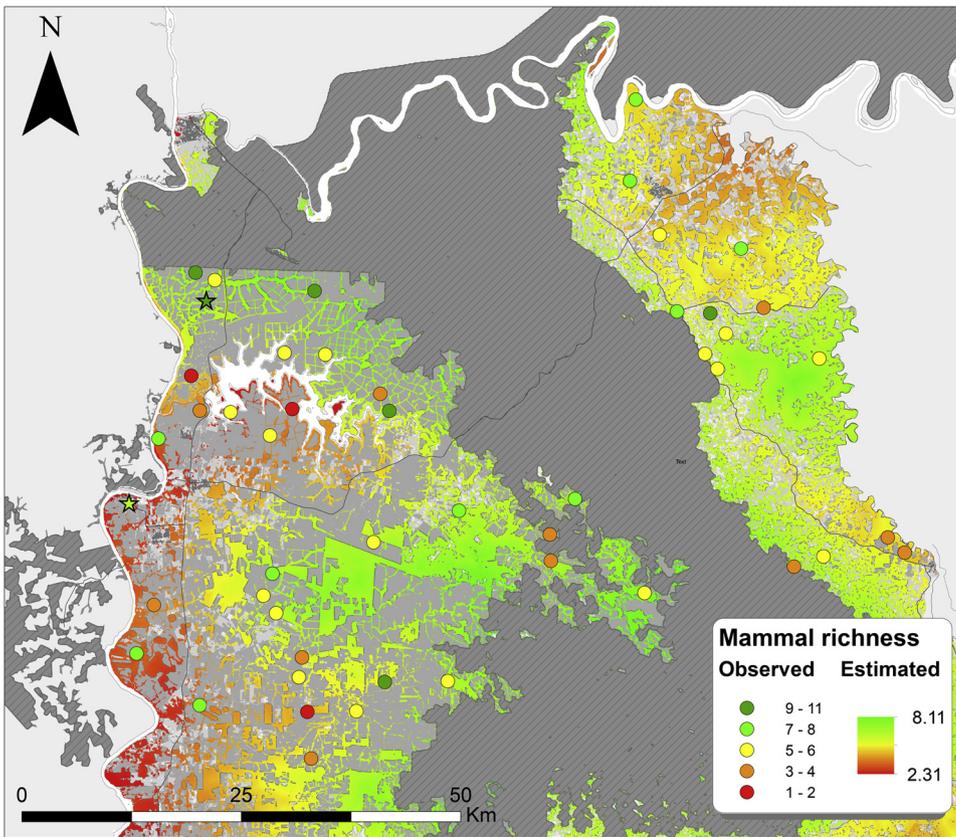
Variables that affect the mammal richness per station (per day, Poisson distribution) and the species composition in the smaller forest fragments with respect to the largest fragment of the Atlantic Forest, Misiones. Differences in composition were measured as the first axis scores of a Correspondence Analysis (Gaussian distribution) where lower values imply more similarity to the largest fragment assemblage. Beta values, standard errors, and 95% confidence intervals for one tail probabilities were obtained from the average of the best weighted ( $\Delta AICc < 2$ ) generalized linear models, using standardized and centralized variables. Variables in bold had a strong evidence of an effect on the response variable according to 95% confidence intervals.

Variable	Parameter Estimates	Standard Error	95% Confidence Interval	
			Lower limit	Upper limit
<b>Richness</b>				
Intercept	-2.228	0.062	-2.349	-2.107
<b>Distance <math>\geq</math> 10,000 ha</b>	<b>-0.157</b>	<b>0.065</b>	<b>-0.264</b>	<b>-0.050</b>
Vegetation	-0.116	0.073	-0.236	0.005
Cost of Access	0.091	0.074	-0.030	0.213
<b>% of Forest (500 m)</b>	<b>0.157</b>	<b>0.068</b>	<b>0.044</b>	<b>0.270</b>
<b>Composition</b>				
Intercept	0.796	0.116	0.568	1.023
<b>log EPI<sup>a</sup></b>	<b>0.355</b>	<b>0.132</b>	<b>0.138</b>	<b>0.572</b>
<b>Vegetation</b>	<b>-0.373</b>	<b>0.119</b>	<b>-0.569</b>	<b>-0.177</b>
Cost of Access	-0.146	0.144	-0.382	0.091

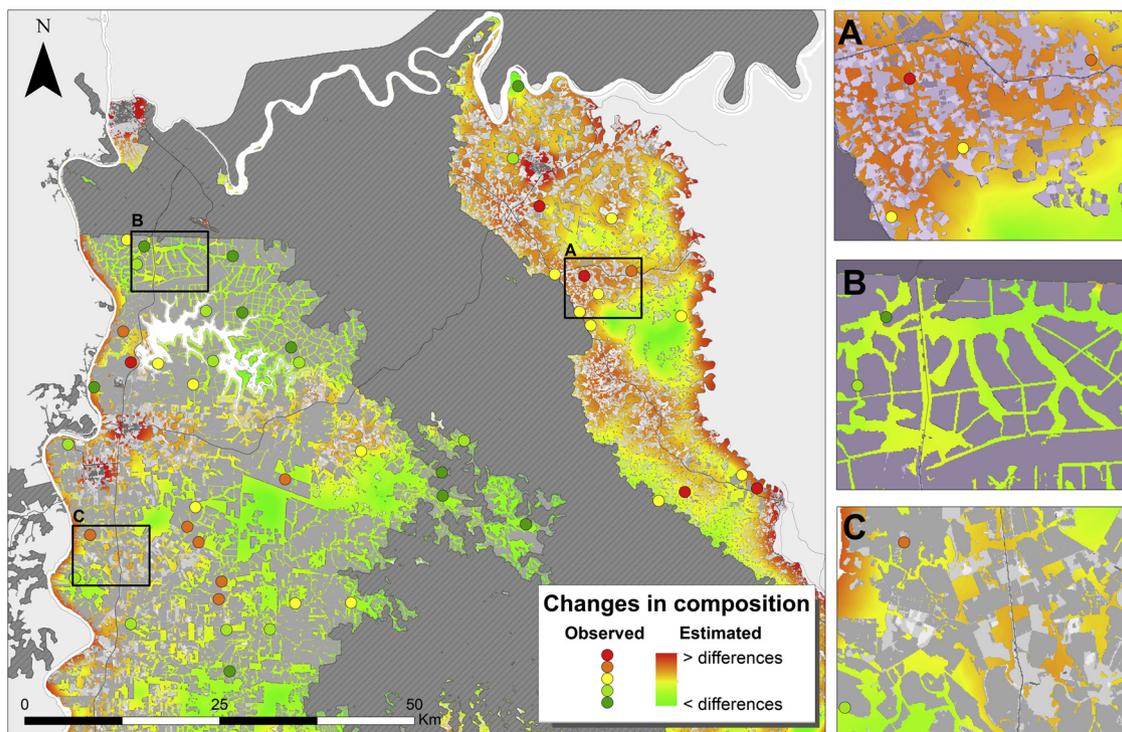
opossum *Didelphis aurita* were more frequently recorded in the largest forest fragment than in the smaller ones (Fig. 2 and 5). The red brocket deer was associated with the best condition of the three environment quality variables, Azara's agouti and the black-eared opossum were more frequently recorded in areas with understory vegetation structure similar to the largest forest fragment, and the lowland tapir and the black-eared opossum were less frequently recorded in more accessible sites (Fig. 5). The South American coati *Nasua nasua*, the nine-banded armadillo *Dasypus novemcinctus*, the white-eared opossum *Didelphis albiventris*, the crab-eating fox *Cerdocyon thous* and the gray brocket deer *Mazama gouazoubira* were more frequently recorded in the smaller forest fragments than in the largest one (Fig. 2 and 5). In particular, the white-eared opossum and the crab-eating fox were more frequent in sites surrounded by more contrasting land uses and in sites that are more accessible to humans, the latter species were also frequent in sites with a higher degree of vegetation disturbance (Fig. 5).

#### 4. Discussion

The assemblage of native mammals of the Atlantic Forest remnants in Argentina was affected by the spatial configuration of the fragments that resulted from the replacement of the native forest by different land uses, and by human encroachment and use of the environment. The amount of forest and the type of land use in the surroundings are the variables that most influenced changes in mammal richness and composition in forest patches. The number of species present in them was also affected by the distance to large fragments, which are probably acting as population sources, and species composition by the degree of vegetation disturbance in the fragment. These results are consistent with what other authors have suggested: in landscapes that still have a high proportion of native vegetation cover, as is the case of northern Misiones, it is expected that the configuration of fragments is not the most important factor associated to the richness and composition of species, but that habitat loss and the quality of the environment are the main determinants of biodiversity conservation in the landscape (Andr n, 1994; Pardini et al., 2010).



**Fig. 3.** Map with the predicted values of mammal richness in the forest remnants of northern Misiones province, Argentina, according to the the best models that included the % of forest in a radius of 500 m, the cost of human access, the distance to fragments > 10,000 ha and the vegetation structure. The map was created summing up all the grids obtained from the best models using the beta values of the variables included in them, weighted by their AIC weights (model average). The effect of vegetation structure was included using an average value in all the models due to the impossibility of extrapolate this information to the rest of the study area. The points correspond to the location of the stations in the remnants showing the observed values of richness. The stations symbolized with a star were discarded from the analysis for being atypical data in the residual plots.



**Fig. 4.** Predicted values for the differences in species composition in the samller forest remnants of northern Misiones province, Argentina, with respect to the largest forest fragment (dark gray) according to the best models that include the logarithm of the Environmental Permeability Index (EPI) in a 2 km radius, the vegetation structure and the cost of human access. The map was created summing up the two grids obtained from the best models using the beta values of the variables included in them, weighted by their AIC weights (model average). The mean value of vegetation structure was included in the models due to the impossibility of extrapolating this information to all the study area. The points correspond to the location of the stations in the remnants showing the differences in composition observed. Smaller differences correspond to lower values of the Correspondence Analysis first axis (more similarity to the largest fragment assemblage, see Fig. 2). The large-scale maps illustrate in detail the observed and predicted values in three different contexts: A) remnants surrounded by a high proportion of "more contrasting" land uses (higher values of EPI); B) remnants surrounded by tree plantations (lower values of EPI); C) remnants surrounded by an intermediate situation.

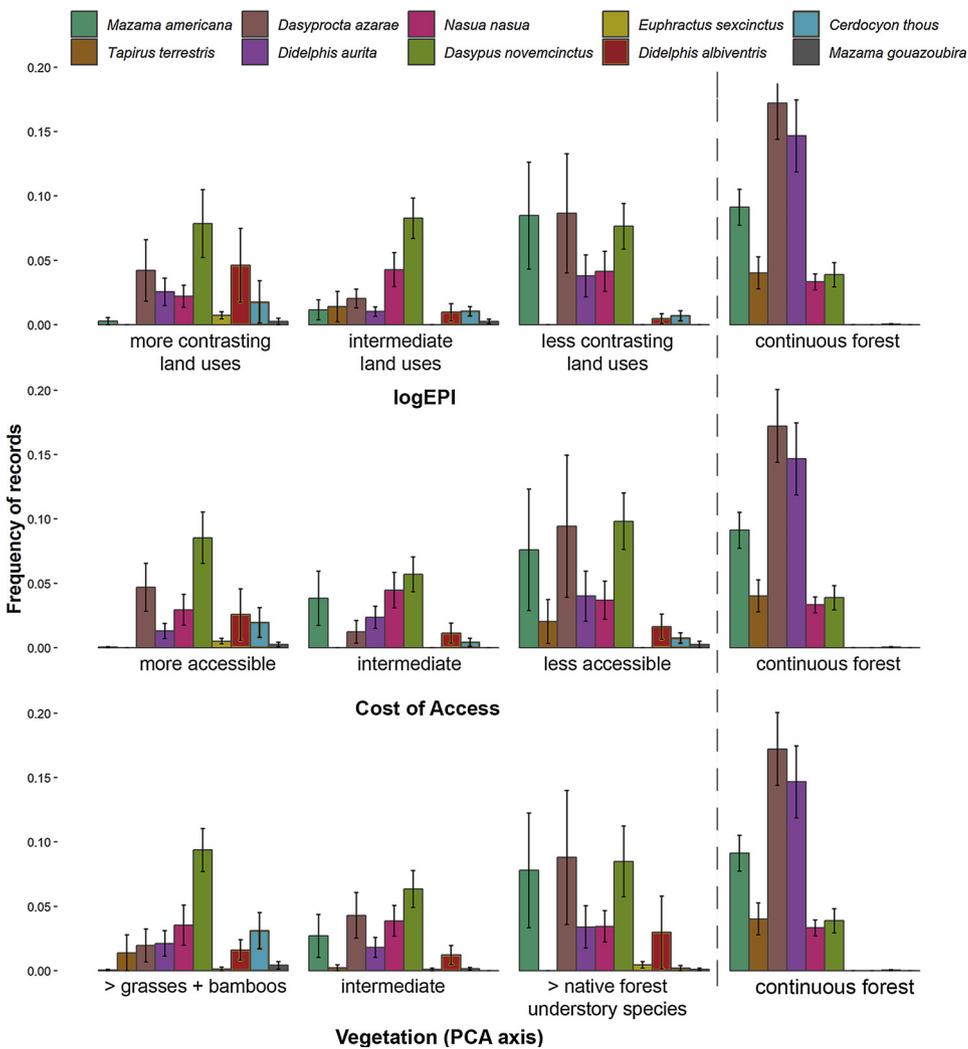


Fig. 5. Relative frequency of records (mean # of independent records / # of camera-trap days) of the 10 mammal species with the highest contribution to the first axis of the Correspondence Analysis that was used as response variable in the species composition models. The average of the relative frequency of records (standard errors depicted with the error bars) was represented for the largest forest fragment ( $n = 53$ ) and for the smaller forest fragments ( $n = 49$ ) stations of the Atlantic Forest, Misiones, Argentina, and in relation to the variables included in the best models that showed the greatest effect on differences in species composition in the smaller fragments with respect to the largest one: the logarithm of the Environmental Permeability Index (EPI) in a 2 km radius, the cost of human access and the vegetation structure. Categories of the variables were generated using Jenks natural breaks.

#### 4.1. Effect of landscape configuration: area and isolation

While the theory of island biogeography (Mac Arthur & Wilson, 1967) is widely used to try to predict changes in species richness of fragmented environments (e.g. Prugh et al., 2008; Vieira et al., 2009), in the landscape that we studied and at the scale of our work, the size of the fragments had no effect on the native mammal richness. However, as expected, the large forest fragments are probably acting as sources for most mammal species since the distance and connectivity to them was a determining factor in the species richness of the smaller ones. Iezzi et al. (2018) already demonstrated the importance of the largest forest fragment as a reservoir for native species and the effect of distance to it on species richness in this landscape. The largest forest fragment of northern Misiones is mainly composed of protected areas, but the other forest fragments that surround it mostly belong to private owners and have no or weak protection. It is therefore important to encourage the implementation of incentives to avoid clearcutting and to increase the protection level of these areas (e.g., improving anti-poaching measures, Di Bitetti, Paviolo, Ferrari, De Angelo, & Di Blanco, 2008; Paviolo et al., 2016) and to improve the connectivity between them (De Angelo et al., 2013; Martínez Pardo, Paviolo, Saura, & De Angelo, 2017).

#### 4.2. Effect of environmental quality: effect of fragment's surroundings and other anthropogenic pressures

The loss and replacement of the native forest by other productive

uses have negative effects on the richness and composition of native mammal assemblages in the Atlantic Forest (Beca et al., 2017; Cruz et al., 2018; De Angelo et al., 2011; Iezzi et al., 2018; Pardini et al., 2010). A reduction in the amount of forest is likely to lead to local extinctions of some species requiring a minimum area of forest to survive and/or that are too sensitive to modifications in the small surrounding fragments (such as Azara's agouti -*Dasyprocta azarae*-, the black-eared opossum -*Didelphis aurita*-, the ocelot -*Leopardus pardalis*-, or the lowland tapir -*Tapirus terrestris*-; Beca et al., 2017; Cruz, Iezzi et al., 2019, 2018; Iezzi et al., 2018). However, our results suggest that the type of land use that replace the forest also affects the assemblage. Although the mammal assemblages recorded in pine plantations are relatively depauperate and different from those of the largest forest fragment (Iezzi et al., 2018), these plantations, in the current landscape context, seem to be a relatively permeable matrix for most mammal species (Iezzi et al., 2018; Paviolo et al., 2018). Conversely, cattle pastures and crops, such as yerba mate, tea, tobacco, and cassava plantations, have a more pronounced effect on the composition of the species present in the forest remnants, suggesting that they represent barriers for many species (e.g. the red brocket deer) and favors the presence of other (e.g. the white-eared opossum; see also Cruz, Iezzi et al., 2019), producing mammal assemblages very different from the original one (i.e., in the largest forest fragment) in fragments surrounded by these land uses.

Since the presence of canopy trees seems to be an important factor for the presence of many mammals, agroecological productions (e.g. crops grown under cover) could be an alternative to mitigate the

negative effect that some traditional agricultural systems (e.g. annual crops and pastures) have on mammal's assemblages (Cassano, Barlow, & Pardini, 2012; Cassano, Barlow, & Pardini, 2014). The differential effect of agricultural activities on the fauna has been recorded in several previous works in the region (Cruz, De Angelo et al., 2019; Filloy, Zurita, Corbelli, & Bellocq, 2010; Giménez Gómez, Verdú, Gómez-Cifuentes, Vsz-de-Mello, & Zurita, 2018; Gómez-Cifuentes, Munevar, Gimenez, Gatti, & Zurita, 2017; Zurita & Bellocq, 2009). Despite the general suggestion that crops under cover would have a lesser impact on the fauna, studies are still needed to assess the effects of different agricultural modes of production on mammal assemblages in order to generate rural development programs that promote biodiversity-friendly production systems.

Non-forest land uses prevail in the eastern portion of the study area, where the matrix is dominated by medium (50–200 ha.) and small (< 50 ha.) scale productive activities (Chifarelli, 2010; Furlan et al., 2015). Although many farmers still retain significant remnants of native forest in their land (Furlan et al., 2015), the presence of people living in farms may have indirect effects on the native fauna associated with extractive activities or the presence of domestic animals (cattle, dogs) that may negatively affect wildlife (Cassano et al., 2012, 2014; Ribeiro, Nichols, Morato, Metzger, & Pardini, 2019; Vieira et al., 2009; Zapata-Ríos & Branch, 2018). In fact, another important anthropogenic variable that is directly associated with poaching (Ferreguetti et al., 2018) and have negative consequences on populations of large mammals in the Atlantic Forest (Di Bitetti et al., 2008; Galetti et al., 2017; Paviolo et al., 2009, 2018) was the cost of human access, a variable that was present in the best ranked models.

Another important anthropic pressure is the vegetation disturbance caused by selective logging and/or by edge effects in the forest fragments (Laurance et al., 2007; Laurance, 2008). The changes in mammal species composition along a gradient of vegetation could be explained as a result of differences in the response of species depending on their feeding or refuge requirements (Pardini et al., 2005). This vegetation change results in a decrease in abundance of some medium-size habitat-specialist species, such as the black-eared opossum (Cruz, Iezzi et al., 2019) and the Azara's agouti, that are more affected by the loss of structural complexity of the understory vegetation and an increase in the abundance of the larger and/or habitat-generalist ones (e.g., the crab-eating fox and the gray brocket deer, that are more frequently recorded in the most degraded fragments; Andrade-Núñez & Aide, 2010; Cassano et al., 2012; Iezzi et al., 2018; Timo, Lyra-Jorge, Gheler-Costa, & Verdade, 2014).

## 5. Final conclusions and applications

Habitat fragmentation involves changes in the amount, configuration and quality of the available habitat for the species in a landscape (Bennett & Saunders, 2010). In the Atlantic Forest of Argentina, the relatively large proportion of forest that still remains certainly favors landscape connectivity and sustains a large proportion of its mammal richness and composition. However, fragmentation is clearly affecting the mammal assemblage in this area, the degradation of the environment being one of its most important consequences. In particular, the most important effects of fragmentation were derived from the proportion of remaining forest in the landscape, the type of productive matrix, and the degree of vegetation disturbance. However, landscape configuration is not irrelevant since the presence and proximity to large protected areas are very important factors that also affect mammal richness. Therefore, to mitigate the impacts of the less permeable productive land uses, it is necessary to improve connectivity to large population sources through the effective protection of corridors and riparian forests, promoting fauna-friendly agroecological systems, and encouraging the restoration of degraded fragments.

Scenarios of future habitat loss and transformation should be taken into account for the conservation of mammal assemblages in threatened

landscapes as the Atlantic Forest. This is the first study to evaluate the effect of forest replacement by productive activities on mammal assemblages in an area with a relatively high proportion of remaining forest, not only offering a good scenario to understand the processes behind their detrimental effects, but also allowing us to generate recommendations to develop appropriate strategies for biodiversity conservation in the face of an unceasing process of habitat loss. In this work, we detected some of the relevant variables that affect the richness and composition of mammal assemblages in the forest fragments immersed in a productive matrix. Additionally, we modeled and mapped these effects, which can be used as spatially explicit planning and conservation tools. These tasks of identifying and understanding the specific factors derived from the transformation of different landscapes is essential to face and counteract the effects of habitat fragmentation.

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## Data availability

The datasets analyzed during the current study are partially available in the Supplementary Material of Iezzi et al. (2018) and in Lima et al. (2017). The complete datasets are available on request from the corresponding author.

## Declaration of Competing Interest

None.

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