# Tree monocultures in a biodiversity hotspot: Impact of pine plantations on mammal and bird assemblages in the Atlantic Forest

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## ARTICLE INFO

## ABSTRACT

Forest plantations of fast-growing exotic species constitute an important economic activity in tropical and temperate regions of developing countries. Large areas of native forests and grasslands are being turned into tree plantations without assessing their impacts on natural communities. We evaluated the effects of replacing native forests by non-native pine (*Pinus taeda*) plantations on the diversity and composition of assemblages of terrestrial mammals and ground-dwelling and understory birds, in a forest productive landscape of the Upper Paraná Atlantic Forest of Misiones, Argentina. Camera-trap stations were deployed in three different "environments": 53 in a continuous forest, 69 in forest fragments, and 62 in tree plantations. The evaluation focused on the effect of the environment, the structural complexity of the vegetation, the cost-distance (distance weighted by connectivity) to the continuous forest, the percentage of native forest within different radii, and the cost of human access (as a proxy for hunting pressure) on both mean species richness per station and species composition. Alpha diversity of the assemblages of each environment was estimated using Hill numbers (effective number of species): $q_0$ = richness, $q_1$ = number of common species and $q_2$ = number of dominant species. Changes in community composition were evaluated by comparing the assemblages of the three environments using three similarity indices: Sorensen ($q0$ = similarity in species identity), Horn ($q1$ = similarity in common species), and Morisita-Horn ($q2$ = similarity in dominant species). For mammals and birds, richness was significantly higher in forest stations (both continuous and fragmented) than in those located in plantations. For both taxa, it also decreased with the distance to the continuous forest (but with a negative quadratic term in birds). Tree plantation stands contained biased and impoverished subsets of the original assemblages. Mammal composition was affected by the environment, the distance to the continuous forest, the proportion of native forest in the landscape, and human access. The bird assemblages of plantations were seriously affected, and their composition was also influenced by changes in vegetation structure. Alternative management practices (e.g. pruning, thinning) and landscape features can partially mitigate the negative effect of tree plantations on mammal and bird assemblages. Large areas of forest that function as population sources and forest fragments immersed in the matrix of plantations are strictly necessary to preserve the original native mammal and bird assemblages in the productive landscape. Promoting connectivity and improving hunting controls will also support their conservation.

## 1. Introduction

Tropical and subtropical forests contain a large share of the terrestrial biodiversity (Myers et al., 2000). Worldwide, these forests are increasingly being replaced by monoculture plantations (Kremen and Miles, 2012), including tree plantations (Keenan et al., 2015), which results in the simplification of the vegetation structure and composition, and in the loss of a large portion of the native species (Barlow et al., 2007; Brockerhoff et al., 2008). Therefore, species richness is often lower in tree plantations than in natural forests (Bergner et al.,

2015; Lantschner et al., 2011; Zurita et al., 2006), but the extent of this decline varies considerably across a range of management intensities and taxa (Bergner et al., 2015; Brockerhoff et al., 2013, 2008; Trentini et al., 2017).

Species well adapted to mature, climax-forest communities and with narrow niche breadths are usually the most affected in agro-forested landscapes (Newbold et al., 2014; Pryde et al., 2016; Zurita et al., 2017) that usually retain the generalist species which sometimes thrive in human-modified environments (Azhar et al., 2013; Estavillo et al., 2013; Lindenmayer et al., 2008). Particularly, mammals and birds are
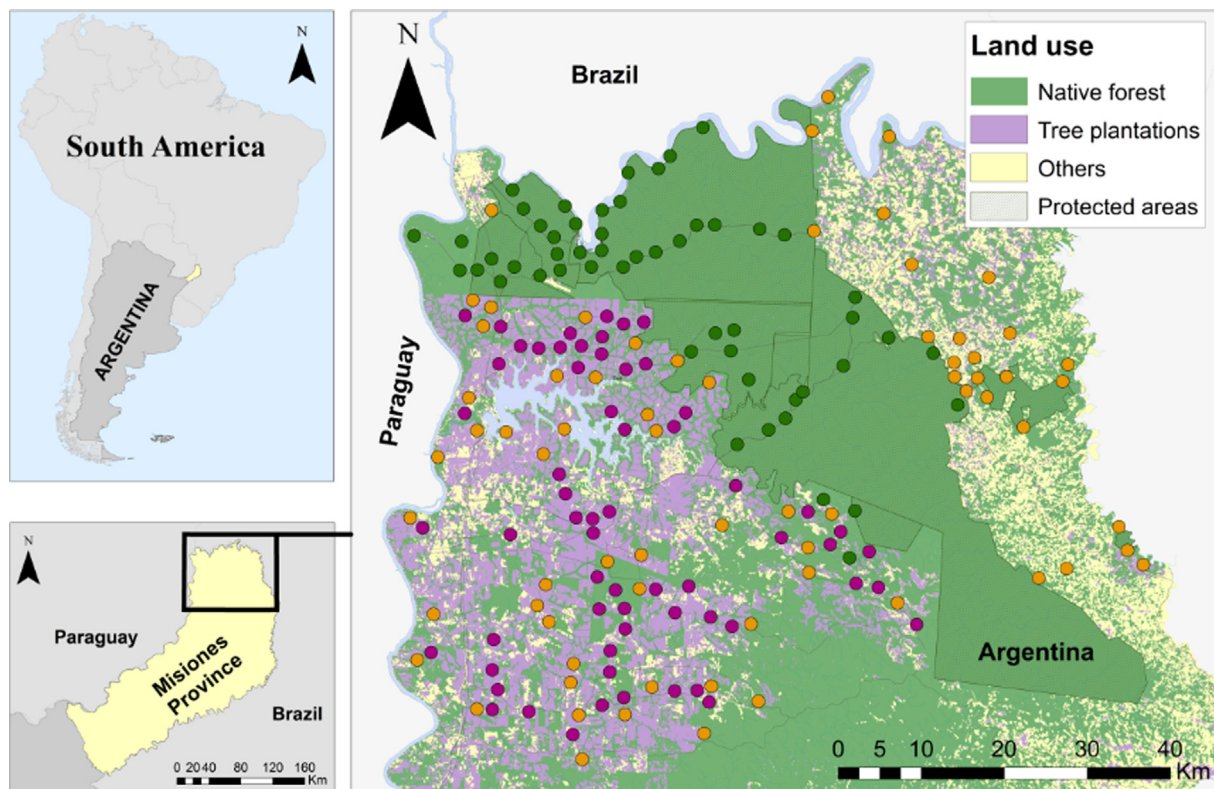
**Fig. 1.** Location of the study site and camera-trap stations in the Atlantic Forest of Misiones province, Argentina. Green points correspond to continuous forest stations (53), orange points to native forest fragments (69), and violet points to tree plantations (62).

sensitive to human-modified ecosystems (Barlow et al., 2007), and the richness and composition of their assemblages are negatively affected by the replacement of forests with commercial tree plantations (Barlow et al., 2007; Irwin et al., 2014; Mortelliti and Lindenmayer, 2015; Zurita et al., 2017, 2006).

However, there are several features of productive landscapes that can mitigate the negative impacts of plantations on biodiversity. For instance, planted forest stands may become alternative, albeit not optimal, habitats for native species through specific management practices (Brockerhoff et al., 2013, 2008; Fonseca et al., 2009; Pietrek and Branch, 2011). Tree plantations that promote the growth of understory vegetation, for example, can provide food and shelter for birds and mammals, supporting higher levels of biodiversity (Azhar et al., 2013; Bergner et al., 2015; Simonetti et al., 2013). However, the native species that use productive stands as alternative or temporal habitats usually depend on patches of natural habitat that serve as population sources (Lindenmayer and Hobbs, 2004).

Very large forest patches of natural habitat are critical as population sources of mammal and bird species in productive landscapes (Núñez-Regueiro et al., 2015; Yue et al., 2015). The conservation and restoration of wide areas of forest immersed or buffered by the productive landscape are essential for the persistence and resilience of the original assemblages in the landscape (Brockerhoff et al., 2013; Lindenmayer and Hobbs, 2004). Consequently, the richness and occupancy of some species decline as the distance to the native forest increases (Edwards et al., 2010; Sunarto et al., 2012; Yue et al., 2015). Moreover, mammal and bird species abundances are usually higher in connected forest fragments compared to isolated ones (e.g. Magioli et al., 2016; Mortelliti et al., 2014; Pardini et al., 2005). Therefore, ensuring the connectivity of the forest remnants with large expanses of well-preserved habitat can constitute an important mechanism for native species conservation in productive landscapes.

Besides their contribution for maintaining habitat connectivity, relatively small remnants of native forest immersed in the productive

areas can contribute to landscape heterogeneity (Brockerhoff et al., 2013; Lindenmayer et al., 2008) and may create the conditions for the existence of population sources of species with low spatial requirements, thus maintaining the richness and composition of the native assemblages (e.g. Beca et al., 2017; Felton et al., 2010; Lindenmayer et al., 2008, 1999; Zurita and Bellocq, 2009). Native vegetation patches and strips of riparian vegetation, even those relatively small or narrow, may be critically important, since they could be used by many native animals to traverse productive areas (Di Bitetti et al., 2011; Heer et al., 2015; Pietrek and Branch, 2011).

Although the form of tree plantation stands and landscape management practices affect biodiversity conservation, they may interact with other anthropic pressures associated with landscape transformation. For example, the conversion of forests to plantations usually implies the deploy of a network of roads that facilitate the access of people to previously remote areas, which in turn may increase extractive activities, such as hunting, on previously inaccessible forests. Poaching can have strong effects on the abundance of some particular species (Benítez-López et al., 2017), causing changes in the composition of mammal and bird assemblages (Peres and Palacios, 2007). In tropical forests, large mammals such as ungulates and big carnivores are the most negatively affected species by poaching (Di Bitetti et al., 2008; Jerozolimski and Peres, 2003; Paviolo et al., 2009; Peres and Palacios, 2007), and these are the species with the biggest impact on ecological processes and biodiversity through top-down regulation (Estes et al., 2011).

The Atlantic Forest is not only considered a hotspot of biodiversity (Mittermeier et al., 1998; Myers et al., 2000), but also one of the most threatened forests in the world with only 11–16% of its original cover remaining (Ribeiro et al., 2009). One of the larger portions of continuous Atlantic Forest persists in Misiones province, Argentina (Ribeiro et al., 2009), where forest loss has been mainly caused by its conversion to crop and extensive non-native tree plantations for fiber production (Izquierdo et al. 2008). In northern Misiones province, the matrix of

tree plantations contains forest remnants of different shapes and sizes, and it is contiguous to a large forest fragment dominated by protected areas (Fig. 1). This offers a good scenario to understand the role of tree plantations, their spatial configuration and management practices on biodiversity conservation at a landscape level.

The aim of this study was to quantify the effects of the replacement of portions of the Atlantic Forest of Misiones province by non-native pine (*Pinus taeda*) plantations on the richness and composition of terrestrial mammal and ground-dwelling and understory bird assemblages. The specific aim was to test the following main hypotheses with their corresponding predictions: (1) Tree plantation stands negatively affect terrestrial mammal and bird assemblages. Consequently, they will have lower alpha diversity and greater differences on species composition when compared to native forest remnants, and generalist species will dominate them. (2) The Atlantic Forest has a structurally complex understory vegetation and a high diversity of plant species on which many mammal and bird species depend for protection, nesting, finding food, etc. As a result, species richness will decrease and species composition will change with a reduction in the structural complexity and diversity of the vegetation. (3) Large areas of native forest are the main population sources of native birds and mammals, especially of forest specialist species. Thus, the richness and the similarity of species composition will decline with the distance to the continuous forest. (4) The extension of forest in the surroundings of a plantation stand positively affects the diversity and composition of its mammal and bird assemblages. We expect that the richness and the similarity to the original assemblage will increase with the relative proportion of forest vs. plantation in the landscape. (5) Poaching negatively affects populations of large mammals and birds. As a consequence, the richness and the similarity of species composition (compared to that of relatively inaccessible native forest) will decline with human accessibility.

## 2. Material and methods

### 2.1. Study area

We conducted this study in the northern part of Misiones province, Argentina (an area of approximately 5005 km$^2$ centered at 54.258° W, 25.931° S; Fig. 1). The study area encompasses a large portion of the largest continuous fragment of Upper Paraná Atlantic Forest, a semi-deciduous subtropical forest with a high diversity of plants and animals that still contains the complete regional native mammal and bird assemblages (Galindo-Leal and Gusmão Câmara, 2003). In Misiones, fast-growing monospecific plantations of the non-native genus *Pinus* (mostly *Pinus taeda*), totaling 40,5824 ha, have partially replaced and fragmented the originally continuous native forest (MA, 2015). Thus, the study area comprises three main portions. To the southwest, a matrix of tree plantations that contains riparian woodlands and forest strips and fragments of different sizes dominates the landscape. To the northeast, a matrix of small scale (10–200 ha) farmlands devoted mainly to cattle, yerba mate, tobacco, maize and manioc plantations surrounds small-to-medium-sized forest remnants. A forest block of Upper Paraná Atlantic Forest lies between these areas (Fig. 1).

### 2.2. Sampling design

To study the assemblage of terrestrial mammals and ground-dwelling and understory birds (canopy birds, although rarely recorded, were excluded from the analyses), we conducted a camera-trap survey between May 2013 and December 2014. We deployed 184 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 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 49.8 days (range: 12–123 days),

amounting to a total effort of 9171.8 camera-days. A > 1-h period had to pass for two successive pictures of the same species to be considered independent records.

We located the stations in three main situations (from now on, we will refer to them as "environments"): continuous forest, forest fragments and plantations (Fig. 1). We defined the continuous forest stations (53 camera-trap stations) as those located in the largest continuous native forest block (a single block of 352,116.5 ha, including Brazilian forest) 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 forest fragments (69 stations) were those placed in native forest remnants outside the continuous forest, mostly immersed in a pine-plantation or agriculture matrix, including isolated fragments and riparian forests. We also included in this category a few stations contiguous to the large forest block, but surrounded by < 75% of forest cover. Stations located in plantations (62 stations) were those immersed in 4–14 year-old pine plantations stands. We randomly distributed stations within each environment using a grid of 2 × 2-km cells, with no more than one station in each cell. Cells were selected on an accessibility basis (those situated further than 500 m away from a road or trail were not accessible for us and therefore were not considered for locating cameras).

### 2.3. Estimation of independent variables

We quantified 4 independent variables at each station to evaluate their effect on the richness and composition of mammal and bird assemblages: (1) structural complexity of vegetation ("vegetation"); (2) distance to the continuous forest block border ("distance"); (3) percentage of native forest in a concentric radius around the station ("% of forest"); (4) estimated time for a human to reach the station from the closest town or city; a variable that indirectly measures the level of human pressure and hunting ("cost of access").

We measured vegetation complexity at each station with surveys of typical understory species and the density of understory cover. For this purpose, we estimated the relative abundances (on a scale from 0 to 3) of some of the dominant understory species or genera (Table S1) at 10 m distance from the camera-trap, towards the four cardinal points (N = 4 points). At each of these four points we also estimated the understory vegetation density by the punctual interception method (Mueller-dombois and Ellenberg, 1974) with a 4 m rod positioned vertically. Finally, we counted the number of *Syagrus rommanzoffiana* and *Euterpe edulis* adult palms present in an area equivalent to ¼ ha centered at the camera trap station. These features were summarized using Principal Components Analysis (PCA). We used the values of the stations on the first principal component axis, which corresponds to a gradient from locations with less understory vegetation cover and higher abundance of grasses to locations with denser and more structurally complex understory vegetation dominated by mature forest species (Table S1).

We estimated variables 2–4 from a Geographic Information System (GIS). A least-cost functional connectivity model (Adriaensen et al., 2003; Epps et al., 2007) that takes into account the heterogeneity and friction effect of the landscape matrix was used to estimate the variable "distance". For that purpose, we created a grid assigning movement costs to each landscape element for a generic medium and a large native animal following Adriaensen et al. (2003) and Gurrutxaga et al. (2011) (Table S2). We used the Cost-Distance function to estimate the accumulated costs through the least-cost paths as the animal moves away from the native forest block, taking into account the distance (in km) from its border. Thus, a station located in the forest block border had a cost value equal to zero and continuous forest stations had negative values. We evaluated the variable "% of forest" at six different radii (500, 1000, 2000, 5000, 7000, and 10,000 m), centered on the camera-trap stations, in order to detect community responses at different scales (e.g. Nagy-Reis et al., 2017; Zurita et al., 2017). Radii ≥ 5000 m were

excluded for the analysis, because they were highly correlated (> 0.7) with the distance from continuous forest (Table S3). The variable "cost of access" was created following De Angelo et al. (2011), and represents the human accessibility cost measured as the hours needed to access the focal cell from the nearest town or city. In this model, the speed of human movement inside protected area borders was halved, so the variable incorporates the deterrence of poaching inside protected areas (Table S2). In order to define the extent of the continuous forest and estimate variables 2–4, we used a land-use vector layer (pixels of $30 \times 30$ 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

In order to test our hypotheses, we analyzed the effects of the above mentioned variables on the richness, alpha diversity, and on the composition of the assemblage of terrestrial mammals and ground-dwelling and understory birds separately. For these analyses, records of the small (< 200 g) sigmodontine rodents were categorized as "sigmodontines" because of the impossibility of identifying them at species level.

#### 2.4.1. Species richness per station

For testing our hypotheses regarding species richness, we used generalized linear models (GLM), including the number of observed species per station as a response variable, and the environment and variables 1–4 as fixed effects. As we expected a potential edge effect, which could lead to a higher richness near the border of the continuous forest block, we included the interaction between distance and environment as well as a quadratic term for distance in the full models. Since survey efforts varied among stations, the number of days that each camera remained active was included as an offset term. Mammal richness models were assumed to have a Poisson distribution with a log link. Bird richness models were assumed to have a Negative Binomial distribution because the number of species was an over-dispersed count variable. Best models explaining species richness were selected using a multiple-hypothesis model-selection approach (Anderson et al., 2000; Franklin et al., 2001; Johnson and Omland, 2004). We used a stepwise backward selection procedure based on the minimization of the Akaike's Information Criterion with small sample size correction (AICc). For each full model, we tested all possible combinations of the explanatory variables. From those models showing the lowest AIC (ΔAIC ≤ 2), we chose only those containing all variables with a strong effect (whose 95% intervals did not include zero, Arnold, 2010). The selection started from 3 different full models for each taxon, each corresponding to a different radius used to estimate the percentage of native forest (Table S6). The significance of the effect of the explanatory variables was assessed by the 95 percent confidence intervals of the parameter. We used one-tailed tests in all cases, except for the quadratic term of distance and the environment "fragments", for which we did not have a directional hypothesis. We used Tukey-Kramer multiple comparisons to test for differences among environments.

Moran's I index of spatial autocorrelation (Moran, 1950) was calculated on the residuals of the best models using ArcGIS 10.3.1 (Spatial Statistic Tools) to test for possible spatial autocorrelation not accounted by the models. Moran's I value indicated no spatial autocorrelation of the final models neither for mammals nor for birds (z = 0.76, p = 0.44; z = 1.3 p = 0.19 respectively). We generated models, model selection, and contrasts in R ver. 3.2.2, with packages "MASS" (stepAIC function, Ripley et al. 2016) and "multcomp" (Hothorn et al., 2016). The distributions of residuals were analyzed with package "DHARMa" (Hartig, 2017) and figures were produced with package "visreg" (Breheny and Burchett, 2016).

#### 2.4.2. Alpha diversity

We estimated true alpha diversity ($^{q}D_{\alpha}$) per environment using incidence data (presence – absence of records of each species) for mammals and birds. We used Hill numbers (Hill, 1973), which represent the "effective number of species within a specific community" (Jost, 2007). The values of q are referred to as the "order" of the diversity measure. $^{0}D_{\alpha}$ represents the species richness, $^{1}D_{\alpha}$ the number of common species, and $^{2}D_{\alpha}$ the number of dominant species in a community (Jost, 2007). As every environment had a different number of stations, we performed coverage-based rarefaction curves to estimate sampling completeness at each station (Chao et al., 2014). Coverage refers to the proportion of the total abundance or frequency of individuals in an assemblage that belongs to species represented in the sample (Chao and Jost, 2012). We compared the values of $^{q}D_{\alpha}$ among environments using the 95% confidence intervals at the same coverage level (the minimum one). Evenness was estimated as $^{2}D_{\alpha}/^{0}D_{\alpha}$ (Jost, 2010). All the curves, sampling completeness and Hill numbers were generated in R ver. 3.2.2, with "iNext" package (Hsieh et al., 2016).

#### 2.4.3. Species composition and indicator species

For the analysis of species composition and indicator species we used the relative frequency of records, estimated as the number of independent records of each native mammal and bird 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 environments and stations. Comparisons were made using three similarity indices from a general multiple-assemblage overlap measure $C_{qN}$ (Chao et al., 2008; Jost et al., 2011): the multi-assemblage Sørensen's index, that measures similarities in species identities (q = 0); the generalized Horn index for similarities in common species (q = 1) (Horn, 1966); and the generalized multi-assemblage Morisita-Horn index for similarities in dominant species (q = 2).

To estimate the degree of change in species composition between environments, we compared the $C_{qN}$ between environments at different orders of q, with 95% confidence intervals estimated from bootstrapping at 1000 random iterations. Differences in species composition was estimated by subtracting $C_{qN}$ from 1 (Chao et al., 2012), where a value of 1 corresponds to two completely different communities and 0 to two identical ones.

In order to determine if differences in species composition were higher among environments than within them, and if the dissimilarities were affected by variables 1–4, we compared $C_{qN}$ values of all pairwise comparisons between stations using One-Way PERMANOVA (Anderson, 2001) with 9999 permutations. In order to test for differences among environments and to evaluate the effect of the variables, we used the pseudo-F statistic (Anderson, 2001). The order of the variables included in the models was changed in all possible ways with the aim of evaluating the effect of each variable on the variation that was not explained by all the other ones. In order to control a potential spatial effect, we initially added latitude and longitude (X and Y) in models. We created 3 different models for each radius of percentage of native forest and calculated AIC values to select the radius which best explained the variation in species composition (Table S7).

In order to visualize the differences in community composition among sites, we performed non-metric multidimensional scaling (NMDS, Kruskal, 1964; Minchin, 1987) using the three similarity measures. We excluded from these analyses those sites with no records or with records that we could not identify to species level (except for "Sigmodontines"; 3 sites for mammals and 71 for birds). Similarity matrixes were generated in R 3.2.2 with package "vegetarian" (Charney and Record, 2012). PERMANOVAs and NMDS were performed with R package "Vegan"(Oksanen et al., 2007) and PERMANOVA contrasts with the software Past ver. 3.08. Finally, in order to identify the indicator species of each environmental condition, we used the Indicator value analysis (IndVal) proposed by Dufrene & Legendre (1997). This analysis was performed in R 3.2.2 using package "labdsv" (Roberts, 2016).

**Table 1**

Total number of species (Total spp.) and mean number of species per station (Spp. p/station; SD within brackets) of mammals and understory birds observed in three environments (continuous forest, native forest fragments and tree plantations) in the Atlantic Forest, Misiones, Argentina. Sampling completeness (SC) and mean effort per station (in days) are also indicated.

| Environment | # stations | Mammals | | | Birds | | | Mean effort per station (SD) |
|---|---|---|---|---|---|---|---|---|
| | | Total spp. | Spp. p/station | SC | Total spp. | Spp. p/station | SC | |
| Continuous Forest | 53 | 30 | 7.92 (2.5) | 0.99 | 18 | 2.62 (2.09) | 0.97 | 49.04 (17.18) |
| Fragments | 69 | 30 | 5.98 (2.46) | 0.99 | 20 | 2.49 (2.23) | 0.97 | 50.47 (19.9) |
| Plantations | 62 | 26 | 3.53 (1.88) | 0.98 | 9 | 0.58 (0.82) | 0.86 | 49.82 (20.44) |

## 3. Results

We obtained 4735 independent records of 57 species (34 mammals and 23 birds, Tables S4 and S5). Only 13.7% (n = 649) of the records were obtained in stations located in tree plantations, even though these represent 34% of the stations that sum up 34% of the camera trap effort. We excluded from the analysis those records that were impossible to identify at species level (634 records, except "sigmodontines") and records of 3 exotic mammal species (domestic dog, 19 records; domestic pig, 4 records; and cattle, 4 records). The range of the number of species recorded per camera was 0–15 species for mammals (mean = 5.71, SD = 2.87) and 0–11 species for birds (mean = 1.88 species, SD = 2.04). For both mammals and birds, stations located in continuous forest had the highest mean richness per station, followed by those located in forest fragments. The lowest mean richness per station was observed in the tree plantations (Table 1).

Two variables affected the species richness of mammals and birds: the environment and the distance to the continuous forest. For both mammals and birds, stations located in plantations had a much lower richness than those located in native forest, either in the continuous block or in fragments (Table 2 and Table S6). The distance to the border of the continuous forest also affected species richness in mammals and birds, but in different ways. In mammals, species richness decreased with the distance to this border, with an average of 1 species lost per 10 cost units (comparable to 10 linear km of forest) (Table 2, Fig. 2). In birds, species richness reached a maximum in stations located near the border of the forest block, since it decreased with the squared distance (Table 2, Fig. 2). Other independent variables had no effect on mammal or bird richness.

The effective species richness ($^0D_\alpha$) per environment was also lower in plantations but without any significant differences with the native forest. However, plantations had a significantly lower effective number of common species ($^1D_\alpha$) and dominant species ($^2D_\alpha$), and had the lowest evenness for both taxa (Fig. 3). Differences were higher for birds, for which the effective number of common and dominant species in plantations was almost half as much as in fragments (Fig. 3).

For both mammals and birds species composition did not differ significantly among environments due to large confidence intervals. Differences in species composition for both taxa were higher when comparing continuous forest vs. plantations and lower when comparing continuous forest vs. fragments. A change in patterns was observed between taxa (Fig. 4). Differences in mammal species composition were higher when dominant species were compared between plantations and continuous forest (Fig. 4a). Meanwhile, for birds, there is no clear trend since confidence intervals overlap extensively (Fig. 4b).

For mammals, pairwise similarities in effective species identities (Sørensen's index), common species (Horn index), and dominant species (Morisita–Horn index) differed among environments (Table 3, Table S7). In addition to environmental differences, similarities were also affected by the distance to the native forest block, the percentage of native forest in a radius of 500 m, and the cost of human access (Table 3 and Fig. 5). Mammal indicator species associated to the continuous forest were the Azara's agouti *Dasyprocta azarae*, the black-eared opossum *Didelphis aurita*, the red brocket deer *Mazama americana*, the lowland tapir *Tapirus terrestris*, the ocelot *Leopardus pardalis*, the brown four-eyed opossum *Metachirus nudicaudatus*, and the "sigmodontine" rodents. The species associated to forest fragments were the nine-banded armadillo *Dasypus novemcinctus*, the South American coati *Nasua nasua*, the white-eared opossum *Didelphis albiventris*, and the crab-eating raccoon *Procyon cancrivorus*. The crab-eating fox *Cerdocyon thous* and the gray brocket deer *Mazama gouazoubira* were associated to pine plantations (all p < 0.05, Table S4).

There were no differences among environments in bird species composition and only the understory vegetation complexity had an effect on species identities and common species similarities (Table 3). Bird indicator species associated with continuous forest were the gray-fronted dove *Leptotila rufoaxilla*, the brown tinamou *Crypturellus obsoletus*, and the white-shouldered fire-eye *Pyriglena leucoptera*. Those

**Table 2**

Variables that affect the mammal and understory bird richness per station (per day) in the Atlantic Forest of Misiones, Argentina. Beta values, standard errors, and 95% confidence intervals were obtained from the best weighted generalized linear models. 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 |
| *Mammals* | | | | |
| **Distance (cost units)** | **−0.011** | 0.003 | **−0.017** | **−0.006** |
| Tukey contrasts | | | | |
| Fragments vs. Continuous forest | −0.094 | 0.087 | −0.238 | 0.048 |
| **Plantations vs. Continuous forest** | **−0.58** | **0.102** | **−0.785** | **−0.385** |
| **Fragments vs. plantations** | **0.49** | **0.083** | **0.326** | **0.655** |
| *Birds* | | | | |
| **Distance$^2$ (cost units)** | **−6.331 E$^{-4}$** | **1.850 E$^{-7}$** | **−9.95 E$^{-4}$** | **−2.69 E$^{-4}$** |
| Tukey contrasts | | | | |
| Fragments vs. Continuous forest | 0.103 | 0.168 | −0.225 | 0.432 |
| **Plantations vs. Continuous forest** | **−1.354** | **0.228** | **−1.730** | **−0.979** |
| **Fragments vs. plantations** | **1.600** | **0.244** | **1.190** | **2.000** |
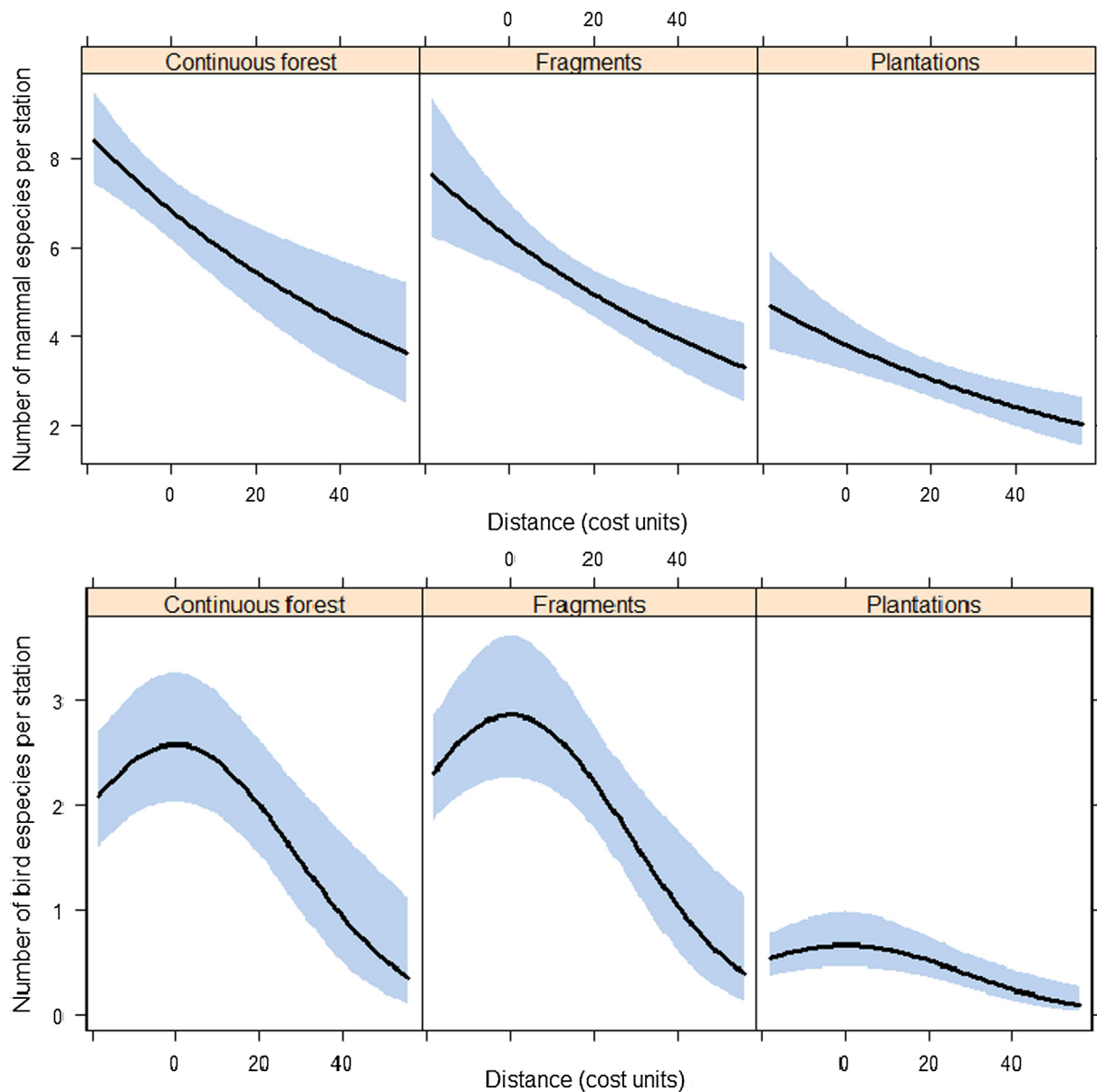
**Fig. 2.** Representation of the best models for mammal and understory bird richness per station: the number of species in relation to distance (in cost units, 1 cost unit ≈ 1 linear km inside forest) to the native forest block border in the three environmental conditions in the Atlantic Forest, Misiones, Argentina. The black line corresponds to the parameter estimates with the 95% confidence interval represented by the grey area.
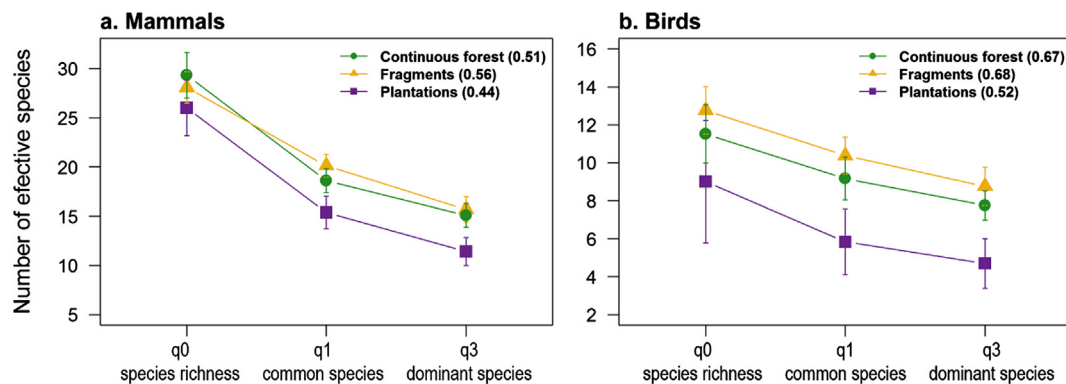


**Fig. 3.** Alpha diversity ($^qD_\alpha$) at the minimum coverage (SC = 0.982 for mammals and SC = 0.862 for birds) in the continuous forest, in native forest fragments, and in tree plantations of mammal (a) and understory bird (b) assemblages in the Atlantic Forest, Misiones, Argentina. Error bars depict 95% confidence interval of each parameter obtained from bootstrapping of the original data. Numbers in parenthesis correspond to the evenness for each environment ($q_2/q_0$).
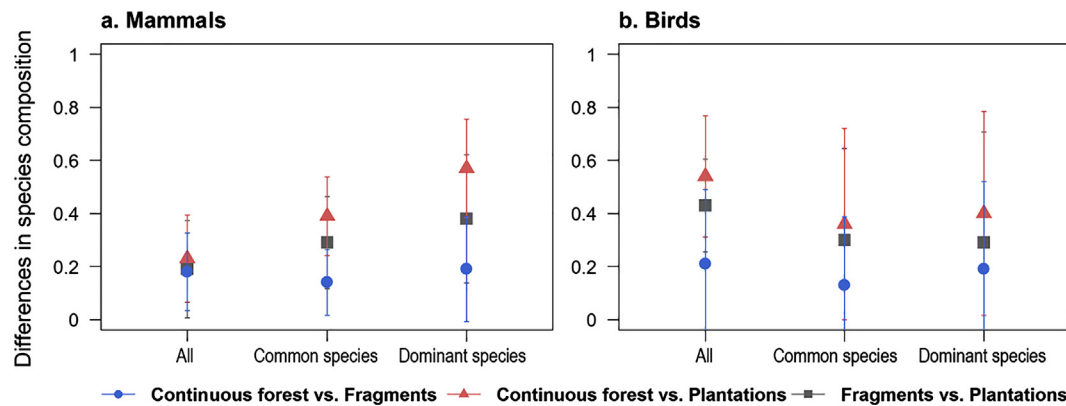
**Fig. 4.** Differences in species composition (1-$C_{qN}$) of mammals (a) and understory birds (b) among the three environments (continuous forest, forest fragments, and tree plantations) for all species (q = 0), common species (q = 1) and very abundant/dominant species (q = 2). Error bars depict 95% confidence interval of each parameter obtained from bootstrapping of the original data.

**Table 3**
Pairwise mammal and understory bird assemblages' comparisons of $C_{qN}$ values (PERMANOVA test) among 181 camera-trap stations for mammals and 113 for birds, distributed along three environments (continuous forest, forest fragments and tree plantations) in the Atlantic Forest, Misiones, Argentina. In all models, latitude and longitude were initially added to control for a potential spatial effect.

| Variable | Df | Sørensen's index (all species) | | Horn index (common species) | | Morisita-Horn index (dominant species) | |
|---|---|---|---|---|---|---|---|
| | | $F_{pseudo}$ | P | $F_{pseudo}$ | p | $F_{pseudo}$ | p |
| *Mammals* | | | | | | | |
| Environment: | 2 | 2.27 | 0.001* | 2.04 | 0.029* | 1.79 | 0.050* |
| *Fragments* vs. *Continuous forest* | | 14.41 | 0.001* | 17.39 | 0.001* | 14.63 | 0.001* |
| *Plantations* vs. *Continuous forest* | | 26.7 | 0.001* | 30.71 | 0.001* | 28.56 | 0.001* |
| *Fragments* vs. *Plantations* | | 9.85 | 0.001* | 9.34 | 0.001* | 8.06 | 0.001* |
| Distance | 1 | 4.08 | 0.001* | 4.96 | 0.001* | 4.42 | 0.001* |
| % of Forest (500 m) | 1 | 2.25 | 0.037* | 2.56 | 0.025* | 2.66 | 0.018* |
| Cost of access | 1 | 2.62 | 0.016* | 3.43 | 0.005* | 3.19 | 0.006* |
| Vegetation | 1 | 1.31 | 0.250 | 1.61 | 0.152 | 1.31 | 0.257 |
| Residuals | 172 | | | | | | |
| *Birds* | | | | | | | |
| Environment | 2 | 1.66 | 0.15 | 0.12 | 0.951 | 0.18 | 0.724 |
| Distance | 1 | 1.04 | 0.409 | 0.84 | 0.482 | 0.23 | 0.682 |
| % of Forest (500 m) | 1 | 1.06 | 0.393 | 0.92 | 0.452 | 0.49 | 0.545 |
| Cost of access | 1 | 0.89 | 0.498 | 1.13 | 0.355 | 0.79 | 0.397 |
| Vegetation | 1 | 3.34 | 0.006* | 3.10 | 0.037* | 3.2 | 0.079 |
| Residuals | 104 | | | | | | |

associated with forest fragments were the slaty-breasted wood rail *Aramides saracura*, the short-tailed antthrush *Chamaeza campanisona*, the tataupa tinamou *Crypturellus tataupa,* and the ruddy quail-dove *Geotrygon montana*. There were no significant indicator bird species for plantations (all p < 0.05, Table S5).

## 4. Discussion

The native mammal and bird assemblages of the Atlantic Forest in Argentina were affected by the replacement of the forest by pine monocultures. This is indicated by the drastic decrease in the number of species in tree plantations and by the substantial difference in species

composition in this environment when compared with the continuous forest and the native forest fragments. Pine plantations are a structurally and compositionally simplified environment as compared to the native forest. Therefore, they would be expected to contain poorer communities of native animals in general. Even though we observed this pattern, our results showed that those changes in species richness and composition do not depend only on forest replacement by a monoculture, but also on landscape features and management practices that determine the distance to the sources of native species, the amount of forest remaining in the landscape, the threats posed by humans on the native species, and the vegetation structure.

### 4.1. Effects of tree plantations

As predicted by our first hypothesis, pine plantation stands contain lower mammal and bird alpha diversity than the native forest environments. The mean number of mammal species recorded per station was the lowest in tree plantations. However, the overall richness did not show a significant effect because most of the species appeared at least once in plantations, which was expected since plantations are not strict barriers for most species inhabiting the contiguous native forest. Tree plantations also lost a remarkable number of understory bird species, not only per station but also as a whole (see also Zurita et al., 2006). Nevertheless, this decrease in species richness in pine plantations is lower in relation to the one observed when the native forest is replaced by annual crops (Filloy et al., 2010). Due to methodological constraints we worked with a small number of bird species; therefore, future surveys of canopy birds may find different patterns to those reported here.

As expected, differences in the composition of mammal and bird assemblages were higher when comparing tree plantations to the native forest. For both taxa, almost no species appeared exclusively in tree plantations, with no real species turnover but rather a sharp reduction in the relative abundances of most species in this environment, something that is expected for disturbed areas (e.g. Corley et al., 2006; Santoandré, 2017). For example, the higher differences in bird community composition (Fig. 4b) is likely due to the fact that the assemblage found in the plantations is an impoverished subset of the continuous forest (Jost et al., 2011). The effects of the environment, and particularly of pine plantations, in mammal composition were notorious (Fig. 5). In contrast to what we observed with mammals, the differences in composition for birds were not evident among the three environments (Table 3, Fig. 5).

Despite tree plantations being depauperate environments, we frequently recorded a few mammal species, such as the brocket deer (*Mazama* spp., 3 species), the nine-banded armadillo, and the crab-eating fox (see Table S4). However, only the grey brocket and the crab-eating fox resulted indicator species of pine plantations. As expected,
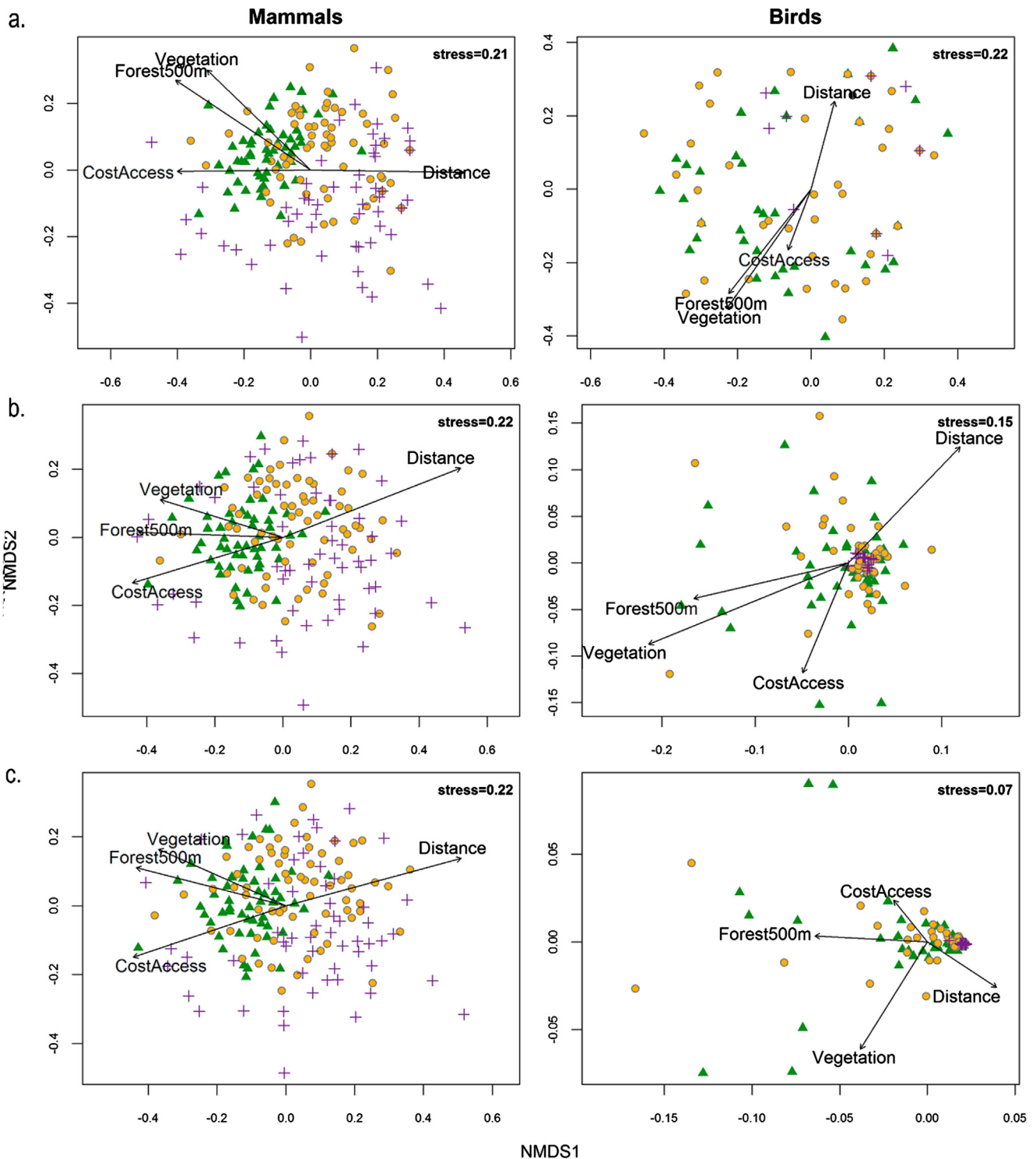
**Fig. 5.** Non-metric multidimensional scaling (axes NMDS1 vs. NMDS2) using similarity distances for mammal (left) and bird (right) assemblages surveyed with camera-traps in continuous forest (green triangles), native forest fragments (orange circles), and tree plantations (violet crosses) in the Atlantic Forest, Misiones, Argentina. Distances were estimated using 1- Sørensen– proportion of unshared species (a), 1-Horn– proportion of unshared common species (b); 1- Morisita–Horn– proportion of unshared very abundant/dominant species (c). Vectors show the correlation of variables 1–4 to the assemblage composition.

most of these are generalist species (Eisenberg and Redford, 2000) that are able to exploit open or disturbed areas (Andrade-Núñez and Aide, 2010; Cassano et al., 2012; Timo et al., 2014). At the other extreme, the relatively small- and medium-sized rodents and marsupials (e.g. Sigmodontines, Azara's agouti, the paca *Cuniculus paca*, the opossums *Didelphis* sp., and the brown four-eyed opossum) were more affected by plantations than the larger mammal species (see Table S4), probably as

a result of their sensitivity to the vegetation structure (Lantschner et al., 2011) or their lower dispersal abilities (Bowman et al., 2002). This relative change in the abundance of small mammals could bring about changes in prey selection by mesocarnivores (Lantschner et al., 2012; Moreira-arce et al., 2015). Future studies should focus on the relationship between species traits and environmental variables in order to better predict which species would be affected by the conversion of

forests to tree plantations (e.g. performing the RLQ analysis or the Fourth Corner Analysis, Dray et al., 2014; Dray and Legendre, 2008; Legendre et al., 1997). We found no indicator bird species in tree plantations. The white-tipped dove (*Leptotila verreauxi*) and the rusty-margined guan (*Penelope superciliaris*) were the only species with a relatively high frequency of records (> 10) in this environment, although much lower than in the native forest (Table S5).

### 4.2. Effect of understory vegetation

Contrary to the predictions of the second hypothesis, we found no effect of the vegetation structure on the richness and composition of the mammal assemblage. This lack of an effect could partially result from the role of the variable "environment" in explaining most differences in vegetation structure. Most of the pine plantations surveyed were planted for pulp production with neither thinning nor pruning practices, which lead to a striking simplification and homogenization of the vegetation structure and diversity in the understory (Trentini et al., 2017). This may explain why we did not observe the differences in richness and composition associated to dissimilarities in the understory in pine plantations described in other studies (e.g. Simonetti et al., 2013).

Contrary to its negligible effect on mammal assemblages, vegetation structure was, as expected, the most important variable for explaining bird species composition in this landscape. The change in bird species composition along a gradient of vegetation complexity could be explained as a result of differences in the response of species belonging to foraging guilds (Azhar et al., 2013), by the appearance of generalist species, or species adapted to disturbance regimes (e.g. de Lima et al. 2012; Pryde et al., 2016), and by the reduction of forest specialists in sites with a simplified vegetation structure (Bergner et al., 2015; Jacoboski et al., 2016; Lees and Peres, 2008).

It is possible that, irrespective of the taxa considered, smaller species are more affected than larger ones by the loss of structural complexity of the understory vegetation. Pine plantations – with less fallen logs, hollow trees, and understory vegetation – have fewer niches for refuge, breeding, and feeding for small- and medium-sized bird and mammal species than native forests (e.g. Lantschner et al., 2011). Further studies should be undertaken on the effects of different management practices and the structural complexity of the environment upon vertebrates of different body size and trophic guilds.

### 4.3. Effect of the distance and connectivity to the major continuous forest block

As hypothesized, the continuous forest is probably acting as a source for most mammal and bird populations in the landscape. The diversity of both taxa and the composition of mammal assemblages were remarkably affected by the distance and connectivity to the continuous forest, something consistent with our predictions and with the results of previous studies (Lees and Peres, 2008; Yue et al., 2015).

Responses of species richness to distance differed among taxa. Mammals showed lower number of species in farther sites and the highest number in areas of continuous native forest far removed from its edge. For birds, the highest number of species was recorded in stations near the border of the continuous forest block. This could be explained by an increase in the number of bird species adapted to open or disturbed areas (de Lima et al., 2012; Pryde et al., 2016) or edge species (Kroodsma, 1982; Zurita et al., 2012) in the forest block border.

### 4.4. Effect of the extension of native forest in the landscape

As predicted by the fourth hypothesis, the proportion of native forest remaining in the landscape (within 500 m of a surveying station) had an important effect in the composition of the mammal assemblage. The change in species composition can be accounted for by differences

in habitat specialization and requirements. The larger mammals seem to use the complete mosaic of native forest and plantations, using the tree plantations mostly to move between forest fragments (e.g. Sunarto et al., 2012). The smaller rodents and marsupials may perceive the plantations as barriers, and require a high proportion of forest in the landscape to persist (e.g. Bernard et al., 2009; Estavillo et al., 2013). Finally, generalist species that are able to live in disturbed areas may not be dependent on the proportion of native forest in the surroundings (Andrade-Núñez and Aide, 2010; Cassano et al., 2012).

### 4.5. Effect of the cost of human access

The cost of human access had no effect on species richness but had a significant effect in the composition of mammal assemblages. This is consistent with one of the predictions of our last hypothesis. Populations of large mammals in the Atlantic Forest are being negatively affected by poaching, an extractive activity that is correlated with accessibility and protection (Di Bitetti et al., 2010, 2008; Galetti et al., 2017). Part of the observed changes in the composition of the mammal assemblage may result from indirect cascading effects of poaching (e.g. mesopredator release as a consequence of a reduction in the abundance of top predators, Crooks and Soulé, 1999).

### 4.6. Main conclusions and recommendations

Although tree plantations had a negative effect on mammal and bird assemblages, different management practices and landscape features also contribute to the observed changes in species richness and composition. Depending on these different conditions, the tree plantation stands in the Atlantic Forest can partially mitigate their negative impact and contribute to sustain high levels of biodiversity at the landscape level (Brockerhoff et al., 2013, 2008). Some forest management recommendations emerge from our results that may promote mammal and bird diversity and conservation. At a landscape scale, it is important to remark the importance of maintaining the integrity of the big continuous forest block, as it seems to act as the main mammal and bird population source. Even though a large proportion of this forest block is composed of protected areas, including the Iguazú National Parks of Argentina and Brazil, there are still opportunities to improve the connectivity (De Angelo et al., 2013; Martinez Pardo et al., 2017) and protection level of these areas (e.g., improving anti-poaching measures, Di Bitetti et al. 2008; Paviolo et al. 2016). It is also important to conserve the forest fragments, since they preserve most of the species of the continuous forest, and the proportion of native forest remaining in the landscape affects the composition of mammal assemblages. Promoting the connectivity of forest remnants to the protected areas may also facilitate the movement of animals across the landscape, particularly of the small mammals that seem to avoid the plantations and thus, prevent the local extinction of their populations in isolated patches. It is also important to control poaching at the landscape level because it is an activity that has a negative effect on several mammal populations, with edge effects that are notorious even within the protected areas (Fig. 2, Woodroffe amd Ginsberg, 1998; Paviolo et al., 2016). At the level of plantation stands, it is desirable to promote the growth of understory vegetation, since this has negative effects on mammal and understory bird assemblages (Simonetti et al., 2013). Thinning and pruning can radically alter the understory light regime, with positive effects on the structure, composition and dynamics of the ecosystem (Lindenmayer and Hobbs, 2004; Trentini et al., 2017).

Monoculture tree plantations have negative impacts on biodiversity at stand and landscape levels. However, the forestry landscapes of the Atlantic Forest of SE Brazil and NE Argentina offer opportunities for biodiversity conservation, since several of the forestry companies operating in the region are FSC certified, own private protected areas, and are increasingly open to implement forest management schemes that promote biodiversity. In our study area, jaguars, tapirs, and other

endangered large mammals are frequently recorded in plantations stands, especially if they are not located far from the large block of protected areas and if poaching is controlled. This does not occur in other types of plantations or land uses. Even if plantation stands contain biased and impoverished subsets of the original assemblages, we have shown that integrated management practices at stand and landscape level may promote the conservation of the native assemblages, including several critically endangered species at national or regional level (e.g., jaguars, Paviolo et al., 2016; lowland tapirs, Cruz et al., 2014 bush dogs, Dematteo et al., 2014).

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## Declarations of interest

None.

## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2018.04.049.

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