



## Land tenure and biological communities in dry Chaco forests of northern Argentina



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### ABSTRACT

Environmental factors and land use control habitat quality and resources availability, thus regulating species distribution. Land tenure in general, and particularly traditional indigenous properties, strongly influence land use in forest ecosystems, but their association with biodiversity is poorly explored. We surveyed 43 forests in the Northern Argentina Gran Chaco, to (1) compare species diversity and composition of birds, mammals and trees between land tenures across a 17 million-hectares region; and to (2) compare diversity between *Wichí* indigenous properties and non-indigenous properties, within a more restricted geographic range to control for climatic and soil factors ( $n = 19$ ). Contrary to our expectations, protected areas did not include higher biodiversity, although they showed higher densities of species specifically targeted for human harvest. *Wichí* properties were the most original regime in terms of community composition of birds and trees. Every land tenure had particular indicator bird and tree species; thus a territorial conservation strategy could include a combination of all them, with a special focus on indigenous properties. Land tenure differences in biodiversity could be the complex result of different habitat quality derived from land use practices and of different geographic location.

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### 1. Introduction

The physical environment determines the overall distribution, abundance and richness of organisms (MacArthur, 1964; Pianka, 1966). At a global scale, once species overcome geological barriers, climate, soils and topography are mainly responsible of their occurrence and spread, by acting directly on species metabolism and indirectly on the habitat quality provided by the landscape (MacArthur, 1964; Pianka, 1966). At a regional scale, species abundance and distribution are mainly affected by human land use (Chapin et al., 2000; Ellis and Ramankutty, 2008; Foley et al., 2005) which modifies habitat characteristics and influence populations by hunting, cultivating, harvesting and introducing alien species. Therefore, understanding the relation between human land use and biodiversity is key to plan regional land use strategies sensitive to local biodiversity conservation.

Neotropical dry forests are characterized by their high level of transformation and deforestation rate (Hoekstra et al., 2005; Janzen, 1988). Gran Chaco dry forests represent the largest continuous dry forest remnant in South America, and during the

last decade it ranked second in terms of deforestation after the Amazonian rainforest (Aide et al., 2013), mostly due to the expansion of soybean crops and planted pastures (Clark et al., 2010; Gasparri and Grau, 2009). Despite rapid deforestation, large areas of forest in South American Gran Chaco still persist. In these areas, however, forest vegetation is often highly degraded by timber, firewood and charcoal extraction and extensive livestock grazing (Bucher and Huszar, 1999; TNC et al., 2005) since the end of 19 century and beginning of the 20, when the “*puestos*” livestock system spread over the area as part of campesinos colonization plans (Brown et al., 2006). In addition to the campesinos, there are two other important social actors in the Argentinean Chaco: indigenous communities and large properties owners. Indigenous communities have a closely dependent relation with forest resources (TNC et al., 2005; van Dam, 2011), and consequently may play an important role in native forests conservation (e.g. Nepstad et al., 2006; Schwartzman and Zimmerman, 2005). In vast areas of Latin America, indigenous communities often conserve natural vegetation cover in their management areas and their properties are vast territories with a low-density population, and a biological diversity comparable with that in protected areas (van Dam, 2011). Since the international and national statements of indigenous communities' rights, these recognitions are acquiring legal status. In Argentina this is reflected by the national laws number 23,302,

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24,071 and 26,160 (year 1985, 1992 and 2006, respectively), which together enhance the legal rights and land use access to indigenous communities. The most recent social actors in the region are large properties owners, which became important since the beginning of the 1970s as part of the process of modern mechanized agriculture expansion. In the present most of these large properties consists in soybean crops and planted pastures, intermingled with forest curtains and relatively small forest patches within a highly fragmented landscape. These social actors clearly differ in the decisions they take about the destiny of forests and their associated biodiversity (Redo, 2013).

Land tenure is recognized to influence land use efficiency. Resource overexploitation due to the process of “tragedy of the commons” provided arguments in favor of land privatization as a better choice for sustainable use in comparison to open access systems (Demsetz, 1967; Hardin, 1968). However, other assessments comparing the influence of land tenure on natural resources concluded that land tenure effects may be obscured by other more important variables, such as access to agricultural technology and to labor opportunities (Beaumont and Walker, 1996), the physical presence of the land owner and the range of mobility of the resources (Altrichter and Basurto, 2008). While these analyses typically focus on the efficiency for resource acquisition, they are also likely to be indirectly related to biodiversity conservation.

In the case of the Argentine South American Dry Chaco, the study of the influence of land tenure on forests uses became particularly important since 2007, when the Law of Minimum Standards for the Environmental Protection of Native Forests (national law number 26,331) was approved. This law aims to balance agriculture production and forest conservation by defining standards for forests protection, promoting land-use zonation of forests, and offering economic incentives for sustainable management and payment in compensations for environmental services resulting from preserving forests. Within this law, biodiversity conservation is both directly and indirectly included as a goal of land use planning. Therefore, it will become progressively more important to assess the role of land uses on biodiversity conservation. For such goal, however, basic information is scarce.

To help filling this information gap, we explored the variation in biological diversity and species composition of three groups of organisms (trees, birds, large mammals) in forests under different land tenures across the Northern Argentina Dry Chaco. We expected the highest biodiversity to be found in protected areas, where higher restriction to resources exploitation would generate better conditions for biological communities, and where little land use should result in a higher habitat quality. Large private properties would have the lowest values of biodiversity, because their forests are remnant patches within a matrix of intensive agriculture and pasturelands. We also expected that higher composition similarity would occur between small properties (hereafter, *puestos*) and indigenous communities than between other types of land tenure, because both regimes practice a subsistence exploitation of forests (Bucher and Huszar, 1999) that usually does not imply forest cover removal.

Land tenure regimes are not evenly distributed across the region; indigenous communities, for example, are mainly located at the north of the study area, so our samples are mostly in west Formosa province. In consequence, differences in biodiversity between land tenures can be the result of causal effects of tenure-controlled land uses on biodiversity but also on the different geographic distribution of land tenures. Given the particular importance of indigenous properties as conservation targets in the neotropics (Nepstad et al., 2006; Schwartzman and Zimmerman, 2005; TNC et al., 2005), we analyzed in more detail the diversity patterns of *Wichí* owned forest lands (the most abundant

indigenous community in the study area) of western Formosa in comparison with non-indigenous properties.

The research design of this study was framed to answer the following specific questions: (1) How do land tenure regimes differ in their biological diversity and community composition? (2) In west Formosa, do forests of *Wichí* properties differ in their biodiversity respect to forests under other tenure regimes?

## 2. Methods

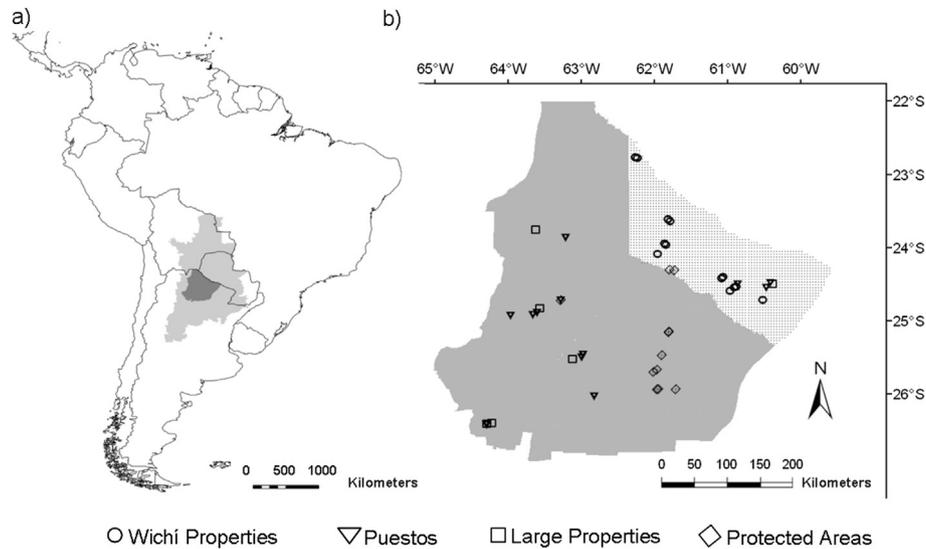
### 2.1. Study system

South American Gran Chaco covers a total area of 1.3 million of square kilometers distributed in Argentina, Bolivia and Paraguay (Bucher, 1983; Morello and Adámoli, 1968). Vegetation is characterized by a mixture of shrublands and medium-tall xerophilous forests, with the upper stratus reaching 16 m–18 m dominated by *Schinopsis lorentzii*, *Aspidosperma quebracho-blanco* and *Bulnesia sarmientoii*, and the lower layer dominated by species of genus *Acacia*, *Mimosa*, *Prosopis*, *Celtis*, *Opuntia* and *Cereus* (Bucher, 1983).

Our study was conducted over an area of 172,800 km<sup>2</sup> of the Northern Argentina Dry Chaco (Fig. 1), in a semi-arid subregion with annual rainfall ranging from 400 to 900 mm, 80% of which typically falls between November and March (Minetti, 1999). Mean temperature ranges from 20 to 23 °C and maximum extremes reach 48 °C in the summer. Northern Argentina Dry Chaco has a long history of occupation and human use associated to extensive livestock ranching and selective extraction for timber, firewood and charcoal, all of them strongly related to forests degradation (Bucher and Huszar, 1999). Land tenure is distributed among three major groups of social actors: small campesinos (*puestos* owners), indigenous communities and large properties owners. Small campesinos base their production system in the *puestos* livestock management system, normally consisting in a group of houses, farm buildings, some minor crops, a water source and relative small herds of cows and goats. The *puesto* economy is based on extensive livestock grazing, selective extraction of timber for charcoal and firewood, and hunting of vertebrate's bushmeat. *Puestos* are often located on fiscal lands. Most frequently they have some legal rights of 250 ha of land, but livestock influence reaches farther on the forest since cows and goats move freely into it (Altrichter and Basurto, 2008). Land tenures are not evenly distributed along the region, as they differ in latitude, longitude and mean annual temperature. Indigenous communities are the most distinctive tenure in terms of these geographic variables (Kruskall–Wallis and pairwise comparisons;  $p < 0.05$  for all these variables); therefore differences in biological communities could be partially explained by these factors.

Formosa province, in the north of the study area (Fig. 1b), concentrates the highest density of indigenous communities of Argentine Chaco, distributed between *Wichí* (the most abundant in the study area), *Toba Qom* and *Pilagá* communities. *Wichí* people live in communities of several families sharing forest resources. Their economy is mainly for subsistence; they practice hunting, fishing and fruits gathering, charcoal and firewood harvesting and manufacture handicrafts based on *chaguar* (a fiber processed from two species of Bromeliaceae, *Bromelia hieronymi* and *B. urbaniana*). They cultivate small crop plots and breed small herds of cows and goats (Bucher and Huszar, 1999). Additionally, some *Wichí* people provide manpower for temporary and seasonal paid labor in private properties (Paulino Ruiz pers. com.).

With agricultural frontier advancing in Northern Argentina Dry Chaco since beginning of the 70's, large properties owners became more relevant as social and economic actors. Their distinctive feature is a much higher capital and information availability, and a



**Fig. 1.** (a) Location of the study area in South American. Gran Chaco is depicted in light gray and study area in dark gray (b) Enlargement of the study area showing sampling sites location. Western Formosa province is mapped as a lighter area.

cultural setting well integrated into the national and global market economy. This characteristic allows a higher level of conversion of forest to agriculture, typically soybean crops and implanted pastures.

## 2.2. Sampling design

We surveyed 43 forest sites in Northern Argentina Dry Chaco, under four land tenure regimes (Fig. 1b): *puestos* (PU, median area of the properties of 480 ha;  $n = 13$ ) with livestock production; *Wichí* indigenous properties (WP, properties with a median area of 3000 ha,  $n = 13$ ); large private properties with livestock production (LP, median area of the properties of 2100 ha;  $n = 6$ ); and protected areas (PA, median area of 17,500 ha;  $n = 11$ ), including provincial and National Parks and one large private property with exclusion of human use for the last 10 years (only one site in Salta province, *Los Colorados*, which in practice works as a protected area). Surveys were conducted during the dry season (May to September) between 2009 and 2012, in hours of maximum activity of birds (i.e. 8:00–10:30 a.m.; Ralph et al., 1996).

Each sampling site consisted in a square plot of 900 m of side, with nine points and nine transects regularly distributed within it. At each sampling point we recorded every terrestrial bird species seen or heard during 10 min within a 30 m radio. We also recorded every tree species with a minimal height of 2 m, into a radio of 15 m; and we surveyed each  $100 \times 4 \text{ m}^2$  transect searching for traces (living individuals, carcasses, footprints and feces) of large terrestrial mammals. We only considered species of mean weight higher than 1 kg, therefore capable of leaving footprints or feces visible for a walking-watcher (i.e. small rodents and small marsupials were excluded); then, we included those species which were present in at least three sites in total (this criterion left out marsupials as *Didelphis albiventris*). For species with similar traces which we were unable to determine their identity, we classified them into groups according to their range of weight or length. In this way we defined the groups Canidae (*Cerdocyon thous* and *Lycalopex gymnocercus*), Small Dasypodiidae (*Cabassous chacoensis*, *Chaetophractus vellerosus*, *Chaetophractus villosus*, *Dasyus septemcinctus* and *Tolypeutes matacus*), Small Felidae (*Herpailurus yaguarondi* and *Oncifelis geoffroyii*) and Tayassuidae (*Catagonus wagneri*, *Pecari tajacu* and *Tayassu pecari*). The group Rabbits joined

*Pediolagus salinicola* and *Sylvilagus brasiliensis*, because they both are typically consumed as bushmeat; and so this group avoided the general criterion. Surveys were non-extractive and had the unique aim of generating comparable data between sites, not to make complete biodiversity surveys.

## 2.3. Data analysis

To analyze how land tenure regimes differ in their biological diversity and community composition (research question 1), we first calculated Inverse Simpson index ( $C_{inv}$ ) of terrestrial birds, terrestrial large mammals and trees in each surveyed site. We calculated  $C_{inv}$  adapting the following equation from Feinsinger (2003):

$$C_{inv} = \frac{1}{\sum_{i=1}^s (p_i^2)}$$

where  $p_i = SF_{ik}/N_k$

We assigned  $SF_{ik}$  to the frequency of  $i$  species in  $k$  site, and to  $N$  the sum of every species frequencies in  $k$  site. Species frequency (SF) at each site was calculated as the number of birds and trees in sampling points, or of traces of mammals in transects, in which a species was registered; so, it ranged from 0 (when the species was not recorded) to 9 (when it was found at each sampling point or transect).  $C_{inv}$  has a minimum value of 1 (for samples with just 1 species) and a maximum value that equals the total number of species when all species have exactly the same frequency in the site.  $C_{inv}$  is more sensitive to changes in equality of species than, for example, Shannon-Weaver index (Feinsinger, 2003). We performed an analysis of variance (ANOVA) and Tukey comparisons between land tenure regimes to assess differences in  $C_{inv}$ . We checked for normality and homogeneity of variance by using standard graphical methods (Di Rienzo et al., 2011). To assess community composition, we performed non-metric multidimensional scaling ordinations (NMDS, Kruskal and Wish, 1978) for each biological group. The NMDS ordination was based on a matrix of Bray–Curtis distances (Legendre and Legendre, 1998) between land tenure regimes. In computing similarity between two land tenures, the Bray–Curtis index compares the frequency of each species present. Regimes that share species with comparable frequencies are considered

more similar, and are thus closer in the multivariate space (Jogman et al., 1995). In contrast to other ordination techniques, NMDS has no assumptions about how species are distributed along environmental gradients (Kenkel and Orłóci, 1986). We performed autopilot procedures (“slow and thorough” mode) to decide the best solution (McCune and Grace, 2002). To generate acceptable ordinations, we used 3-dimensional configuration for birds and mammals ordinations, because final stress (an index of agreement between the distances in the graph configuration and the distances in the original data matrix) was 16.43 and 15.12 respectively (most ecological community data sets have solutions with stress between 10 and 20), and was different from chance (Monte Carlo: 500 runs with randomized matrix,  $p = 0.004$  for both ordinations; McCune and Grace, 2002). Mammal frequency data showed a weaker structure, and NMDS did not converge into a configuration with acceptable stress values in three or less ordination axes. Therefore, we instead conducted mammals ordinations by means of Bray–Curtis ordination procedure (Bray and Curtis, 1957), also based on a matrix of Bray–Curtis distances between land tenure regimes (Legendre and Legendre, 1998). Bray–Curtis ordination extracts ecological gradients with no assumption of a linear relationship between species (McCune and Grace, 2002). To arrange points along the diagram, Bray–Curtis ordination selects reference points and uses a distance matrix to locate the remaining points in a relative way. We used the variance-regression method (Beals, 1984). The first endpoint has the highest variances of distance to other points. This finds a point at the long end of the main cluster in species space, and it ignores outliers because their distances will be consistently higher, so resulting in a lower variance (McCune and Grace, 2002). We based NMDS and Bray–Curtis ordination on frequency of species with presence in at least 3 sites. In both NMDS and Bray–Curtis ordinations we calculated the proportion of variance represented by ordination axes at the final configurations. For NMDS we calculated the coefficient of determination ( $r^2$ ) between distances in the ordination space and distances in the original space, by the “after-the-fact” method using Bray–Curtis distance; and for Bray–Curtis ordination the proportion of variance represented was result of a built-in, considered a logical way of evaluating it with residual distances over the original ones (McCune and Grace, 2002). We used the non-parametric Kruskal–Wallis analysis to test for overall differences among land tenure regimes in terms of scores along the ordination axes. Pairwise non-parametric comparisons identified groups of land tenures along the axes. Finally, to identify which species of each group best characterize each land tenure regime, we performed an indicator species analysis (ISA, Dufrene and Legendre, 1997), which generates indicator values (IV) on basis of species frequency (SF) and relative abundance in each type of land tenure, according to the equation:

$$IV_{ij} = A_{ij} \times B_{ij} \times 100$$

$$A_{ij} = SF_{ij} / SF_i$$

$$B_{ij} = NT_{ij} / NT_j$$

Where  $A_{ij}$  is the frequency of  $i$  species in  $j$  land tenure ( $SF_{ij}$ ), on the frequency of  $i$  species in all sites ( $SF_i$ ).  $B_{ij}$  is the number of sites of  $j$  land tenure where  $i$  species is present ( $NT_{ij}$ ), over the total number of sites of  $j$  land tenure ( $NT_j$ ). IV ranges from 0% to 100%, reaching 100% when  $i$  species have their maximum frequency (i.e.  $SF_i$  is 9) at every sites of  $j$  land tenure, and it is present at none site of another tenure. We performed a Monte Carlo test (4999 permutations) to assess statistical significance of observed values.

To answer whether forests of *Wichí* properties differ in their biodiversity from those under other tenure regimes, over an area of comparatively low environmental and geographic variation (research question 2), we compared  $C_{inv}$  of both types of forests within the west Formosa province. Given that *Wichí* properties are concentrated at the lower latitudes, we performed non-parametric Wilcoxon tests for independent samples (Lehmann, 1975) including only sites of west Formosa province to control the latitude effect; we previously classified sites as belonging ( $n = 13$ ) or not ( $n = 6$ ) to *Wichí* properties.

Infostat/P (Di Rienzo et al., 2011) was used to perform ANOVA, Kruskal–Wallis and Wilcoxon analyses, Tukey and pairwise comparisons and, finally, to check normality and homogeneity of variance. ISA and ordination analyses were executed with PC-ORD 5.0 (McCune and Mefford, 1999).

### 3. Results

Diversity of birds and large mammals were similar among land tenures, while tree diversity showed some differences (Fig. 2a): the highest  $C_{inv}$  of trees was found in *puestos* and the lowest one in protected areas, while *Wichí* and large properties had intermediate values ( $F = 3.60$ ,  $p = 0.02$ ).

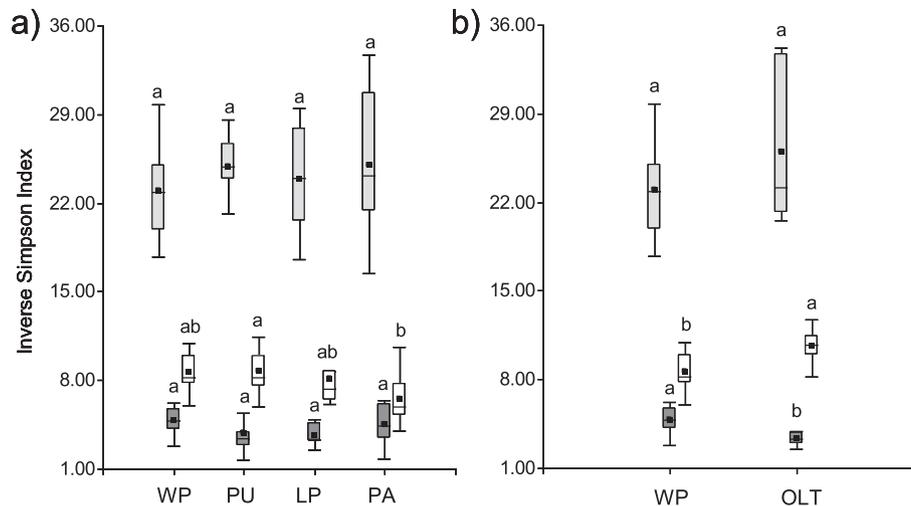
Different land tenures showed some differences in their community composition; and overall *Wichí* properties emerged as the most distinctive land tenure in terms of species composition. NMDS ordination diagram performed with bird species frequencies, segregated sites along 3 axes, representing 76% of variance (Fig. 3a, b). Axis 1 significantly (Kruskal–Wallis,  $p = 0.03$ ) separated *puestos* (low scores) from protected areas and *Wichí* properties (high scores), while large private properties had intermediate scores (Fig. 3a, b). Axis 2 clearly discriminated *Wichí* properties (low scores) from all the remaining tenure regimes (high scores;  $p < 0.001$ ; Fig. 3a). Axis 3 did not significantly discriminate between land tenure regimes ( $p = 0.20$ ; Fig. 3b).

Based on tree frequencies, NMDS also segregated sites along 3 axes representing 84% of variance (Fig. 3c, d). Axis 1 significantly separated *Wichí* properties (high scores) from the three remaining regimes (low scores; Kruskal–Wallis,  $p = 0.001$ ; Fig. 3c, d). Axis 2 did not significantly separate land tenures ( $p = 0.51$ ; Fig. 3c). Finally, axis 3 clearly discriminated *puestos* (low scores) from *Wichí* properties and protected areas (high scores,  $p = 0.005$ ), while large properties could not be discriminated from both groups (intermediate scores; Fig. 3d).

Bray–Curtis ordination of large mammals frequencies included 63% of the variance in the three main dimensions (Fig. 3e, f). However, land tenure types were not statistically different in their ordination scores.

Bird diversity in western Formosa forests did not significantly differ between *Wichí* and other land tenure regimes ( $W = 69.00$ ,  $p = 0.45$ ). Large mammal diversity was, in turn, higher in *Wichí* forests than in other land tenure forests within the Formosa province ( $W = 30.00$ ,  $p < 0.01$ ); while tree diversity showed the opposite pattern ( $W = 86.50$ ,  $p = 0.02$ ; Fig. 2b).

Indicator species analysis of the three biological groups had the highest number of species as indicator of *Wichí* properties, and the lowest (only 1 tree species, *Opuntia quimilo*) of *puestos* (Table 1; appendix A). *Wichí* properties significantly associated to *Amazona aestiva*, *Heliomaster furcifer*, *Melanerpes cactorum* and *Poospiza melanoleuca*, among 79 bird species; to *B. sarmientoi*, *Ceiba chodatii*, *Ruprechtia triflora* and *Stetsonia coryne*, within 22 tree species; and finally associated to *Procyon cancrivorus* and *Tapirus terrestris*, among 14 large mammal species or group of species. Large properties had also 4 indicator bird species, *Mimus triurus*, *Patagioenas picazuro*, *Rhinocrypta lanceolata* and *Tarphonomus certhioides*; only



**Fig. 2.** Inverse Simpson diversity indexes of birds (light gray boxes), large mammals (dark gray boxes) and trees (empty boxes). (a) Land tenure regimes of the whole study area (WP: *Wichí* properties; PU: *puestos*; LP: large properties; and PA: protected areas). (b) Land tenure regimes considered to Formosa province (WP: *Wichí* properties; OLT: other land tenures). Boxes show median and mean value (line and point inside boxes, respectively), quartiles and extreme values. Boxes with the same letter do not differ statistically ( $p < 0.05$ ) in terms of mean (panel a) or median (panel b) values.

one mammal species, *Mazama gouazoubira*; and no tree species (Table 1; appendix A). Protected areas had not bird species as indicators; they associated to one tree species, *S. lorentzii*, and two large mammals taxa, Rabbits and Dasypodidae, which respectively represent the most heavily harvested tree species in the area and mammals typically hunted as bushmeat (Table 1; appendix A).

#### 4. Discussion

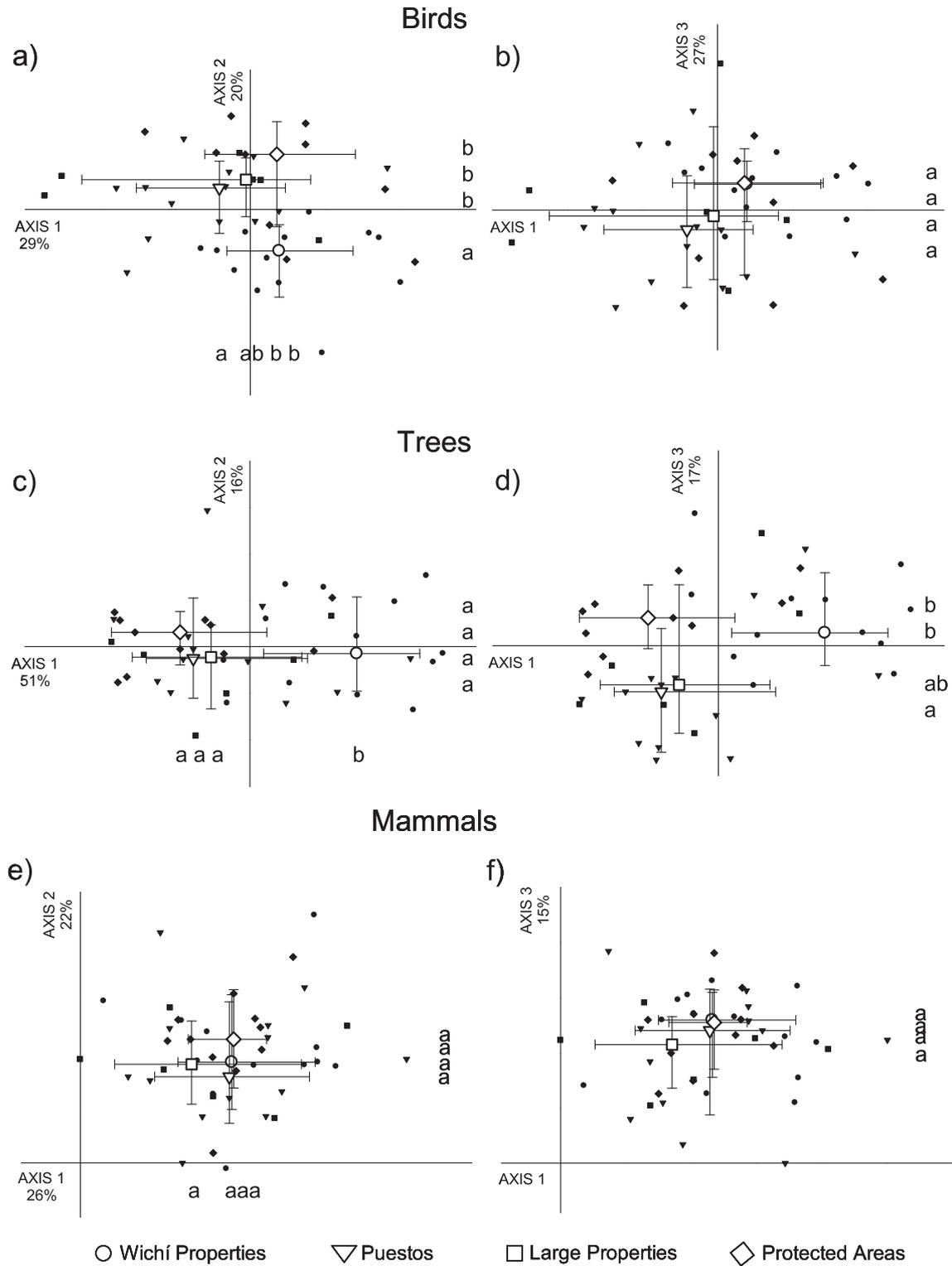
Land tenure regimes were similar in relation to their bird and large mammals indices of diversity, and differed in their tree species diversity as well as in their biological composition of all the analyzed groups. Since land tenures are not evenly distributed along the study area, which is reflected in their differences in environmental conditions, it is hard to separate the “land tenure” from the “environmental” effect which co-varies. In spite of this, our study contributes to the knowledge of the association between geographical patterns of biodiversity and land tenure, a key factor determining land use, in an area of rapid land use change and potential land use-related conflicts. As such this study can serve as basis for biodiversity conservation planning taking into account their land tenure condition.

The most important pattern found is the highest originality of the *Wichí* land tenure, reflected in the differences in the ordination axes and in the number of indicator species associated to this tenure. Even when, at the regional scale of analyses, this could be associated to the observed differences in environmental conditions (being *Wichí* properties the most different one in terms of geographic location and, particularly, mean annual temperature), this result implies that *Wichí* properties play a necessary role in regional biodiversity conservation planning given their original biodiversity. In contrast to our prediction, the highest similarities in trees and birds composition were found between *Wichí* properties and protected areas in one dimension, and between large private properties and *puestos* in other, separated from *Wichí* properties. Indicator Species Analysis of birds associated typical forest-species, as *Amazona aestiva* and *H. furcifer* (Di Giacomo and Krapovickas, 2005) with *Wichí* properties, and *H. furcifer* was almost exclusively recorded in this land tenure. Tree species associated to *Wichí* properties, as *R. triflora* and *S. coryne*, have a recorded distribution across all the study area (Demaio et al., 2002), therefore we could

interpret their segregation as attributable to land tenure and land use. Finally, *P. cancrivorus* and *T. terrestris* were indicator large mammals of this land tenure regime, and were exclusively recorded there (excepting for one record of *P. cancrivorus* in a protected area). Even when we could assign these associations to the land tenure regime and its traditional use, we think these could be coupled with historical reasons. Formosa is the province in Argentina where *T. terrestris* actually occupies the largest area, so coinciding with the location of *Wichí* properties (Chalukian et al., 2009). Formosa has also the minor loss of area historically occupied by the species (Chalukian et al., 2009), which could indicate that *Wichí* properties are acting as a barrier for the advance of the main threats, related to land use changes and hunting pressure.

When comparing only sites of west Formosa, in order to reduce the influence of the physical environment, tree diversity was lower in *Wichí* properties. This result could be related to a history of use of forests by *Wichí* people, with trees being an important source of charcoal, firewood (Bucher and Huszar, 1999) and construction material for houses (Paulino Ruiz pers. com.), and harvested for charcoal and firewood (Bucher and Huszar, 1999). It must be taken into account that regeneration of trees in dry forests can be a relatively slow ecological process in comparison with recovery of many animal populations. For mammals, in contrast, we found a higher diversity in *Wichí* than in other land tenure forests. The results of informal interviews with members of *Wichí* communities suggest they only hunt for familiar consumption and, contrary to non-traditional poaching, they have a goal of long term conservation of the bushmeat resource. This implies that, in opposition to the observed pattern for trees, traditional *Wichí* uses of forests seem to be relatively sustainable for large mammals; if adequately monitored, they could act a reserve for some large mammals population with high conservation value.

In contrast to our prediction, protected areas had not the highest biodiversity values across the region. Instead, this category had the lowest tree diversity. Only one of the five surveyed protected areas is a national park, the unique category of protected areas recognized by the literature to have a real control on the ground (Brown et al., 2006), and only one another of those areas is older than 20 years. The lower tree diversity in protected areas could be result of their location in places that had a low diversity due to historical reasons prior to the protection of the area, added to the time-lag



**Fig. 3.** (a to d) non-metric multidimensional scaling ordination of sampled forests based on species frequency of birds and trees. (e to f) Bray–Curtis ordination of forests respect to large mammal frequencies. Diagrams represent axis 1 versus 2 (a,c,e) and 1 versus 3 (b,d,f). According to the indicated land tenure, solid symbols represent sites and empty symbols, the median values of the scores. Bars represent standard deviation from the median value. Small letters along each axis show the homogenous groups resulting from Kruskal–Wallis analyses and pairwise comparisons. In all cases, percent of explained variance is shown for each ordination axis.

resulting from the slow regeneration of most dry forest trees (Araujo et al., 2007). Nevertheless, ISA positively associated protected areas to *S. lorentzii*, the economically most important and most heavily harvested tree species in Northern Argentina Dry

Chaco (Hueck, 1978). In spite of low diversity values, we believe that protected areas do play a role in regional biodiversity conservation, in particular for species specifically targeted for hunting. While bird species showed no associations to protected areas, Small

**Table 1**

Indicator values of bird, tree and mammal species (or group of species) occurring under different land tenure regimes. Bold numbers indicate maximum IV for each species. We only report species with significant indicator value (Monte Carlo test); remaining species are reported in [appendix A](#).

		Indicator values for land tenures				
		Wichí properties	Puestos	Large properties	Protected areas	
Bird species	<i>Amazona aestiva</i>	<b>45**</b>	11	5	14	
	<i>Helimaster furcifer</i>	<b>36**</b>	0	4	0	
	<i>Melanerpes cactorum</i>	<b>45**</b>	5	2	0	
	<i>Mimus triurus</i>	0	1	<b>26*</b>	1	
	<i>Patagioenas picazuro</i>	2	25	<b>36*</b>	20	
	<i>Poospiza melanoleuca</i>	<b>44**</b>	10	6	20	
	<i>Rhinocrypta lanceolata</i>	1	10	<b>31*</b>	1	
	<i>Tarphonomus certhioides</i>	0	2	<b>41**</b>	0	
	Tree species	<i>Bulnesia sarmientoi</i>	<b>35*</b>	6	0	1
		<i>Ceiba chodatii</i>	<b>37*</b>	1	12	0
<i>Opuntia quimilo</i>		7	<b>36*</b>	11	2	
<i>Ruprechtia triflora</i>		<b>48**</b>	9	6	12	
<i>Schinopsis lorentzii</i>		19	21	29	<b>31*</b>	
<i>Stetsonia coryne</i>		<b>44**</b>	4	5	3	
Mammal species		<i>Mazama gouazoubira</i>	19	14	<b>35*</b>	24
	<i>Procyon cancrivorus</i>	<b>26*</b>	0	0	1	
	Rabbits	9	7	12	<b>37*</b>	
	Small Dasypodidae	0	1	0	<b>51**</b>	
	<i>Tapirus terrestris</i>	<b>46**</b>	0	0	0	

Note: \* $p < 0.05$ ; \*\* $p < 0.01$ .

Dasypodidae and Rabbits, both large mammal taxa usually consumed as bushmeat, were indicators of this land tenure and were barely recorded in the other regimes.

According to ordination analyses, large properties were the land tenure category with the least distinctive birds community. This could be a response to the particular landscapes resulting from different crops and implanted pastures covering a large proportion of these management units. Indicator Species Analysis revealed that forests in large properties were characterized by comparatively high densities of some bird species, such as *P. picazuro*, a granivorous species commonly seen in agricultural land, and *T. certhioides*, which often inhabits degraded forests (Di Giacomo and Krapovickas, 2005) resulting from a history of cattle grazing and wood extraction (Brown et al., 2006; Bucher and Huszar, 1999). Additionally, indicator species *M. triurus* and *T. certhioides* had almost exclusive records in this land tenure category. No tree species were associated to large properties, but the ISA for mammals associated *M. gouazoubira* to large private properties; this result is the expected for this species, which typically inhabits forests or tree-covered savannas but prefer to forage in open and secondary habitats, where it finds fresh sprouts and leaves (Redford and Eisenberg, 1992; Richard et al., 1995). Alternatively, this species could be displaced by the agricultural frontier advance, so taking shelter in forests that still remain in the agricultural matrix. Under this interpretation, these patches of forests become “sinks” for *M. gouazoubira*, temporarily increasing its density and therefore its chance of detection (Richard et al., 1995). Limitations to access into better controlled private properties may also contribute to limit hunting in large private properties that favor a highly valued game species as *M. gouazoubira*. Preliminary analyses performed by us revealed that private properties double the number of land cover patches of the other land tenures, implying a highest level of fragmentation. Further analyses should explore the indirect effect of land tenure on biodiversity conservation through the changes in landscape configuration.

*Puestos* showed the highest tree diversity across the whole region. Ordination based on bird and tree species composition separated, in one axis, *Wichí* tenure and protected areas from

*puestos*, but did not discriminate this land tenure from large properties. We hypothesize that, even when both land tenures have great differences in their land management, these differences are not discrete but rather are spread along a gradient of situations with different land use types and intensities. In spite of this clear segregation in the ordination space, generated by a distinctive species composition, no bird or mammal species was associated to *puestos* in the ISA, and only one tree species was.

Rather than identifying which single land tenure regime is the most appropriate for biodiversity conservation in the area, our overall results suggest that each land tenure is associated to a better habitat quality for some particular species, therefore all land tenures could be part of an inclusive strategy to protect regional biodiversity. At this scale of the analysis, protected areas had not higher biodiversity than other land tenure regimes, but were important for specific species targeted for hunting. In agreement with literature reports (Nepstad et al., 2006; Schwartzman and Zimmerman, 2005), our analyses of large mammals in *Wichí* properties support the presumed relation between indigenous people and forest resources; but the opposite pattern was found with trees, implying that conservation strategies may vary among different biological groups. Although the studied *Wichí* forests represent only a small proportion of the great indigenous diversity in Formosa, their high mammal diversity suggest they are important to the protection of this particular group.

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## Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jaridenv.2014.06.005>.

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