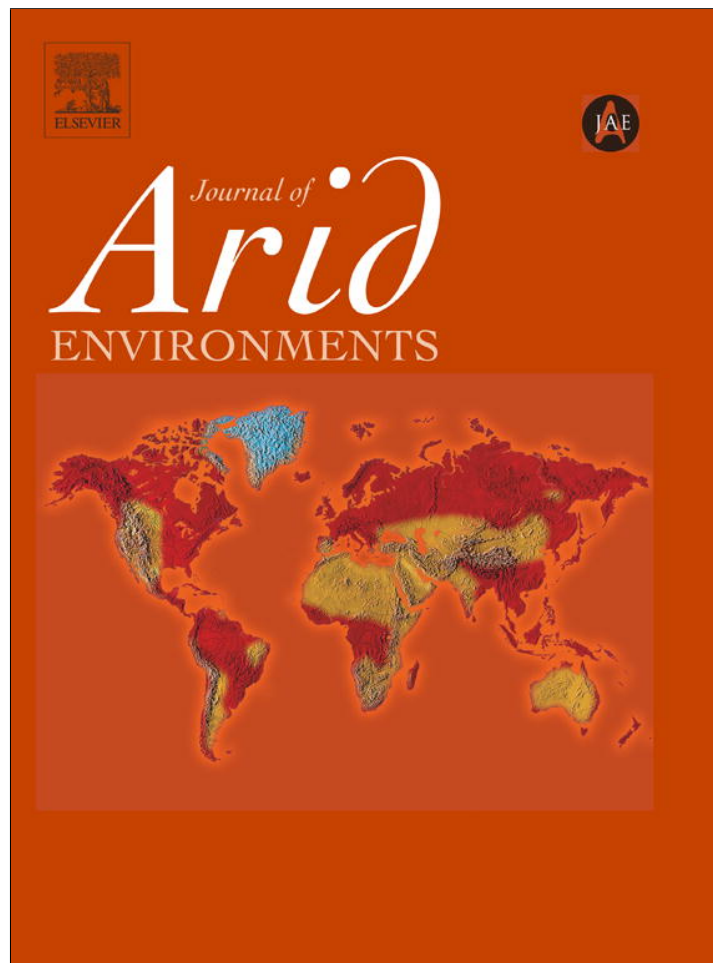


Provided for non-commercial research and education use.  
Not for reproduction, distribution or commercial use.



(This is a sample cover image for this issue. The actual cover is not yet available at this time.)

This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

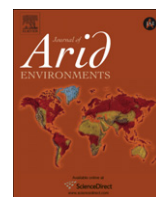
Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/copyright>

Contents lists available at [SciVerse ScienceDirect](http://SciVerse.ScienceDirect.com)

## Journal of Arid Environments

journal homepage: [www.elsevier.com/locate/jaridenv](http://www.elsevier.com/locate/jaridenv)

# Piospheres in the dry Chaco. Contrasting effects of livestock *puestos* on forest vegetation and bird communities

L. Macchi\*, H.R. Grau

CONICET – Instituto Ecología Regional (IER), Universidad Nacional de Tucumán, Casilla de Correo 34, 4107 Yerba Buena, Tucumán, Argentina

## ARTICLE INFO

## Article history:

Received 30 March 2011  
 Received in revised form  
 6 June 2012  
 Accepted 7 June 2012  
 Available online xxx

## Keywords:

Bird guilds  
 Livestock gradient  
 Neotropical dry forest

## ABSTRACT

In arid and semiarid ecosystems, the congregation of livestock around water sources gives rise to a utilization gradient termed the “piosphere pattern”. We evaluated piospheres surrounding the *puestos* livestock management system in the Chaco dry forests of Argentina. We sampled vegetation and bird communities around eighteen *puestos* and we fitted curves to describe the responses of vegetation and bird community variables to the distance from the *puestos*. We used Partial Canonical Correspondence Analysis to evaluate the organization of bird guilds constrained by vegetation variables and the distance from the *puestos*. Vegetation structure increased with the distance from the *puestos*. In contrast, the abundance of most bird's guilds decreased with distance from the *puestos*, likely in response to the gradient in resources associated to the water source, food and changes in vegetation. Rare or low abundance bird species peaked at intermediate or long distances from the *puestos*. Our results concur with studies characterizing the *puestos* as a focus of vegetation degradation, but the analysis of the avian community shows that the nature of this piosphere is more complex, as is a favorable habitat for some ecological groups.

Published by Elsevier Ltd.

## 1. Introduction

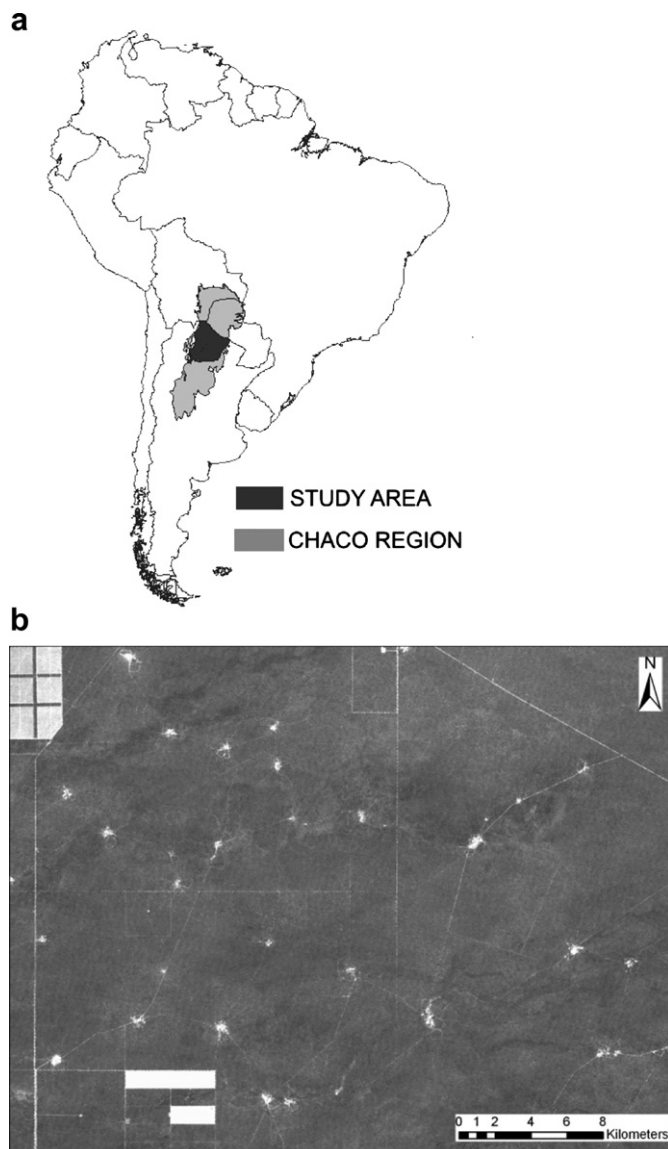
In order to meet its physiological needs, livestock moves between places used for feeding and places used for drinking. In arid and semiarid environments, where water sources are scarce, these movements generate particular landscapes patterns. The localization of impacts associated with the congregation of animals around sites with water and the declining grazing pressure with distance from them gives rise to a utilization gradient termed the “piosphere pattern” (Thrash and Derry, 1999). “Piospheres” are the result of a gradient in stocking pressure, which is greatest near the water source and decreases with distance from it (Andrew, 1988). As such, “piospheres” represent a rather paradoxical landscape pattern, where the supply of the key limiting factor in an ecosystem (water, in this case) results in biomass reduction and overall ecosystem degradation. In the dry Chaco forests of Argentina, traditional livestock management is based on the “*puestos*” system, which consists on a group of houses, farm buildings, and minor local crops nearby an artificial water source aimed to supply water during the dry season. In the core of the *puesto* area, there is an extreme reduction in vegetation cover and a high proportion of bare soil. Vegetation degradation gradually decreases with distance

from the *puesto*, as grazing and wood collection decreases. In the dry Chaco of Argentina, *Puestos* are spread across a landscape of several million hectares of forest generating a distinctive landscape configuration (Fig. 1).

Tropical and subtropical dry forests are among the most threatened ecosystems globally (Hoekstra et al., 2005). In Argentina, the forests of the Chaco region cover an area of approximately 23 million hectares and represent the southernmost subtropical dry forests in America. Despite being severely affected by forest degradation and deforestation (Grau et al., 2008) the Chaco forests represent the largest remaining continuous area of Neotropical Dry forests. The importance of the *puesto* system in the landscape patterns of the Chaco has been recognized in early research (e.g. Morello and Saravia Toledo, 1959). Given the obvious effects on vegetation and easy detection by remote sensing, *puestos*' density or distance from the *puesto* have been used as proxy for environmental degradation in the region (Adámoli et al., 1990; Grau et al., 2008). This categorization was reinforced by studies on large mammals affected by hunting (peccaries and jaguars), which show decreasing abundance with *puestos* density or time since *puesto* establishment (Altricher and Boaglio, 2004). However, quantitative descriptions of vegetation in relation to *puestos* are limited, and, in particular, studies on faunal groups not directly affected by human presence are lacking. The large number of *puestos* spread across millions of hectares is a distinctive landscape pattern in the dry Chaco (Fig. 1), making the piosphere concept

\* Corresponding author. Tel.: +54 381 4255174.

E-mail address: [leandrom\\_84@hotmail.com](mailto:leandrom_84@hotmail.com) (L. Macchi).



**Fig. 1.** Study area. (a) Location of the dry Chaco in South America (light gray), and the North Argentinian dry Chaco where the *puestos* are widespread (dark gray) (b) Landsat TM satellite scene showing the pattern of the *puestos* (scattered bright points) on the Chaco landscape. Large squared bright areas are zones deforested for agriculture, and linear features are roads.

particularly relevant since a semiarid climate with a long and severe dry season makes water availability a key limiting factor in the ecosystem. Similar patterns are also found in other dry ecosystems of the world, for example Botswana (Moleele, 1994), Zimbabwe (Rodríguez, 1995), Australia (Landsberg et al., 2003), South Africa (Stokes and Yeaton, 1994), and Mojave, USA (Brooks et al., 2006).

The response of the vegetation to the piosphere depends on several interacting factors such as competition, soil types, water availability, and life history of plant species along the gradient of livestock pressure (Landsberg et al., 2003). More generally, numerous studies have shown that livestock affects vegetation composition (Milchunas and Lauenroth, 1993) and structure (Molina et al., 1999). In the Argentine Chaco dry forest different authors have suggested that livestock may reduce seed germination and seedling establishment through trampling and soil compaction, increased seed dispersal of forage species, enhanced resprout

of some species, and by acting as a selective force of plant species composition due to their differential palatability (Guevara et al., 2006; Morello and Saravia Toledo, 1959). Livestock grazing is expected to reduce the competitive ability of herbaceous plants in favor of woody and spiny succulent species; and this may reduce fire frequency by the removal of fine fuels. As a result, livestock introduction in the Chaco since the beginning of the 20th century has been hypothesized as a major ecological change in relation to the pre-European landscape (Adámoli et al., 1990; Morello and Saravia Toledo, 1959).

In turn changes in vegetation are expected to affect animal communities due to the effects on habitat structure and food availability (Gonnet, 2001). In the case of bird communities, habitat structure plays a key role on the provision of sites for deployment of courtship, nesting, protection from predators, food availability, and environmental conditions for reproduction (Wiens and Rotenberry, 1981). Studies in North America showed that livestock grazing promotes the replacement of entire sets of grassland birds (Bock and Bock, 1988) and the disappearance of the most sensitive species, usually replaced by generalist birds with wider distribution ranges (Zalba and Cozzani, 2004). Some avian groups could be favored around the *puestos* by the presence of an open canopy, water bodies and grain supply for livestock; whereas others that require a more complex forest structure or are more sensitive to disturbance would respond negatively. In the Monte desert of Argentina, a drier ecosystem, livestock showed a negative effect on granivore birds through a reduction of seed availability (Gonnet, 2001). Different studies on Chaco avifauna showed that birds respond to changes in habitat, both natural and caused by human activity, as avian richness and abundance is higher in primary forest and increases with increasing forest structural complexity. Different avian guilds showed different patterns, with bark insectivores and short flight insect hunters being more abundant in the forest interior, and long flight insect hunters, frugivores, terrestrial insectivores and granivores being more abundant in forest edges (Codesido and Bilenca, 2004; Lopez de Casenave et al., 1998).

Most studies assessing the ecological effects of piospheres focus on plant communities, with particular emphasis on grasses, and their relationship with livestock (Landsberg et al., 2003); whereas studies on birds have tended to focus on a few focal species (Fontaine et al., 2004). Here, we assessed the effect of piosphere on whole bird community and its association with changes in vegetation structure in a semiarid system. We present the results of a detailed survey of vegetation and avian community along a gradient of distance from 18 *puestos* located in the Chaco forest of northwestern Argentina, in order to answer the following research questions (1) what is the relative importance of the variation of vegetation attributes and birds community explained by the piosphere gradient (intra *puestos*) and by the variation between the *puestos* (inter *puestos*), (2) what is the response of the structure and composition of the forest vegetation to the distance from the *puestos* and how is this related to grazing pressure?, (3) do bird guilds vary with the distance from the *puestos* in terms of composition and abundance? (in particular, we were interested in assessing if birds show a pattern of density and diversity in the *puestos* similar to the one observed for vegetation and large mammals), and (4) to what degree are the changes in avian guilds abundance explained by changes in vegetation along the gradient?

## 2. Methods

### 2.1. Study area

The study was conducted on the western or “dry” Chaco of Argentina (Fig. 1a). Dry forests and savannahs are the second largest

biome in South America after the Amazonian rainforest. The Cerrado and Chaco are the two largest continuous units of this biome. The Chaco ecoregion covers a total area of c.1,200,000 km<sup>2</sup>, in Argentina, Bolivia and Paraguay. The Dry Chaco has a subtropical seasonal climate. In the study area mean annual temperature ranges between 20 and 23 °C, with average temperatures of 28 °C and 16 °C for the hottest (January) and coldest (July) months, respectively. Argentinian Dry Chaco has absolute maximum temperatures above 48 °C, being one of the hottest areas in South America. Annual rainfall ranges between 400 and 900 mm, with a strong pattern of monsoonal precipitation seasonality in which c. 80% of the rainfall falls between November and March and the winter and early spring are characterized by water deficit (Minetti, 1999).

Vegetation is characterized by semi-deciduous xerophytic forests and shrublands, that represents a breeding habitat for many Neotropical and Nearctic birds, and provides food resources such as insects, seeds, grains, and in the rainfall season flowers and fruits (Codesido and Bilenca, 2004). In the middle of 20th century, there were more than 200 species of birds cited for this region (Olog, 1963). This ecoregion has a long history of human use associated to extensive livestock ranching since the beginnings of the 20th century (Bucher and Huszar, 1999). Extensive livestock management is based on the *puestos* system. Each *puesto* consists on a group of houses, farm buildings, minor local crops (e.g. a few hectares of corn, sorghum, and other annual grains used mostly for forage supplement), a water source (that typically becomes dry by end of the winter), and herds of cows and goats grazing freely in the landscape. Observational studies suggest that livestock walks as far as 5 km of the water source searching for forage, but as the dry season proceeds, they gradually restrict their movements closer to the *puesto*, thus increasing the grazing pressure. As a consequence, in the surroundings of the *puestos* there are typically several hectares of bare soil (Grau et al., 2008; Morello and Saravia Toledo, 1959). In 13.4 million hectares of forest within the study area, there were 1100 *puestos* in 2001; the area within 5 km of distance of the closest *puesto* represented c. 40% of the total area (Grau et al., 2008). We sampled *puestos* in the Central North of Argentinian Chaco (Fig. 1). Field work was conducted between May and April 2010.

## 2.2. Sampling design

We surveyed 18 *puestos* that were at least 10 km apart from another to avoid ambiguity in the identification of the closest focal *puesto*. At each *puesto* we set sampling sites for vegetation and bird community at six distances: 0, 250, 500, 1000, 2000 and 4000 m, located along a north-direction straight line from the water source. The zero distance was located next to the water pond, where animals are freely dispersed. Birds sampling was done during the first two hours after dawn considering changes in birds activity along the day (Ralph et al., 1996).

Vegetation surveys focused on dominant tree composition and abundance, vertical structure, and tree size. Vertical structure was described using the point quadrat method (Bullock, 1996). At each sampling site, we sampled ten point counts along a 30 m transect perpendicular to the radial distance from the water source. Each point count consisted on counting the numbers of touches of bare ground, grass, shrub and trees by a stick graduated on the following intervals: 0–20, 21–40, 41–100, 101–200, 201–400 and 401–600 cm. Along the same transect we quantified the density of the eight most abundant tree species and the Diameter at breast height (DBH) of all tree species on a 15-m radius of each point. Along the same 30-m transect, we counted the number of cow feces (the most abundant livestock in terms of biomass) over a strip 4 m

wide, as an indicator of livestock density. We assumed that patterns of grazing of other domestic animals (e.g. goats, horses) were similar to those of cows and we did not analyze them.

To characterize the bird community, at each sampling site we conducted 12-min birds point's counts, during the first two daylight hours of the morning, the period with highest birds activity. For each site we quantified bird abundance on a radius of 20 m, considering only diurnal forest birds. We selected the May–April period because summer migrant's species are still present in the region and it is the end of the rainy season, which facilitates road access to the sample points.

This design generated a total of 108 sampling sites (18 *puestos* by 6 distances) based on which we used a Two-way ANOVA analysis to quantify the relative contribution (research question 1) of the distance from the *puestos* (i.e. within *puestos*) and among the different *puestos* to the variance on the followings parameters: Vegetation Structure Shannon's diversity (H), Tree species richness (S), Trees Shannon's diversity (H), DBH Median, Cow Feces abundance, Birds communities richness (S) and Bird community Shannon's diversity (H). We tested the ANOVA assumptions using the Shapiro–Wilk test for normality and Bartlett test for homoscedasticity using the package *car* (<http://CRAN.R-project.org/package=car>), software R Development Core Team (2010).

## 2.3. Vegetation analysis

For each sampling site we considered the abundance of the six dominant trees species in the study area: *Aspidosperma quebrachoblanco*, *Caesalpinia paraguariensis*, *Prosopis nigra*, *Ruprechtia triflora*, *Schinopsis lorentzii*, *Ziziphus mistol*, which represent 80% of all individual trees sampled. Other tree species had low densities and in few cases we were unable to identify them. We computed the richness and Shannon's diversity, and the Median and Standard Deviation of DBH of all trees species present at each sample site as size structure, including the tree species we were unable to identify. Using the point quadrat data we considered the frequency of touches of trees, shrubs and grasses of each vertical height category (% trees touch, % shrub touch, % grass touch and % bare ground touch) and we used Shannon's diversity Index of frequency of touches of trees–shrubs–grass at each vertical interval as an index of vertical structural complexity.

In order to describe how vegetation parameters vary with the distance from the *puesto* (research question 2), we classified the response in four categories following Landsberg et al. (2003): Increasers (variables that increase towards the *puestos*), Middle distance trend (that peak at intermediate distances, taking lower values both near and far from the *puesto*), Decreasers (which increase with distance from the *puesto*), and Extremists (that have comparatively higher values both near and far from the *puesto*, which for example could result from the fact that people leave some trees for shadow cover next to the *puestos* and they use trees for firewood with decreasing intensity away from the *puesto*). Each of these categories could be described by more than one possible function (Fig. 2): constant (no distance effect), linear (positive for Decreasers and negative for Increasers), quadratic (positive reflects Middle distance trend, negative reflect Extremists trend), exponential (positive for Decreasers trend and negative for Increasers trend), and saturation (positive or negative trends, with a maximum parameter). Models were fitted to data in the R Development Core Team (2010) using maximum likelihood estimator (MLE) package (<http://lib.stat.cmu.edu/R/CRAN/web/packages/bbmle/>) to adjust the functions of each distance value of the eighteen replicates (*puestos*). The probabilistic component of the model varied according to the nature of each variable: for the abundance of each tree species, the number of





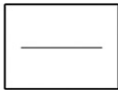

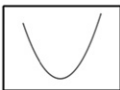
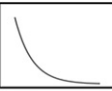
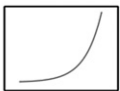
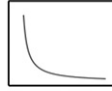

MODEL	Increasesers Highest abundance near the <i>puestos</i>	Decreasers Highest abundance far from the <i>puestos</i>	Medial trend Highest abundance at middle distances	Extremists Highest abundance at each extreme	No pattern
LINEAR $y=a+b*x$					
QUADRATIC $y=a+b*x+c*x^2$					
EXPONENTIAL $y=a*exp(-b*x)$					
SATURATION $y=a*(1-exp(-b*x))$					

Fig. 2. Classification scheme used for determining vegetation and bird guilds responses to the distance from the *puestos*. The nature and significance of their response trends were determined by fitting linear, quadratic, exponential, and saturation models (Modified from Landsberg et al., 2003).

touches of each vertical strata, and trees richness we used the Poisson distribution; for DBH and diversity measures we used the Normal distribution (Bolker, 2008). Then we used the corrected Akaike Information Criterion (AICc) to select the best fitting function, comparing the differences of the AICc values ( $\Delta AICc$ ) between the models with the lower AICc, where AICmim is the AICc value for the best-fitting model. Models with  $\Delta AICc > 2$  were considered as good descriptors of vegetation along the gradient (Burnham and Anderson, 2002). We tested the significance of the best fitting model using the Likelihood ratio test, comparing with the AICc value of the constant model (Appendix Table 2). We included a goodness of the fit measure using the non-linear least-squares estimates of the parameters, package nls2 in R (<http://lib.stat.cmu.edu/R/CRAN/web/packages/nls2>; Huet et al., 2004; Appendix Table 2).

To explore the relationship between livestock pressure and vegetation structure we regressed density of cow feces with the Vertical structure Shannon's diversity index.

#### 2.4. Analysis of bird community

To address research question 3, along the gradient of distance from the *puestos* we analyzed overall bird community's richness, abundance, evenness diversity index, and Fisher  $\alpha$  diversity index (is independent of sample size). Using MLE we fitted curves of the response of the abundance of each guild to the distances from the *puestos* in the same way we did for vegetation variables; and we used the functions to classify avian guilds response into Increasesers, Medial, Decreasers and Extremist (Fig. 2). In this case we considered Extremists cases possible because some guilds can respond to different resources along the gradient, such as forest cover or vertical structure and water. For the statistical analysis we considered only species that were present in at least five sampling sites. As for vegetation we considered  $\Delta AICc > 2$  to select a model over others. For bird species recorded in four or less sites (restricted species; 25 over a total of 73) we did not fit any curve, and instead

we used a simple guild classification criterion whereby species were designated: restricted increasesers if they occurred only at distance 0 and/or 250 m; restricted decreaseers, if they occurred only at distance 2000 or 4000 m; and restricted medials, if they occurred only at distance 500 and 1000 m (Table 3).

We classified 73 bird species into eleven guild assemblages defined by diet composition and foraging sites, following previous studies in the area (Codesido and Bilenca, 2004; Lopez de Casenave et al., 1998) and our own field observations. We considered the following guilds: Arboreal granivores (AG), Foliage insectivores (FI), Bark insectivores (BI), Short flight insect hunters (SF; mean attack distance 0.85 m), Long flight insect hunters (LF; mean attack distance 5.48 m), Terrestrial granivores (TG), Terrestrial insectivores (TI), Terrestrial omnivores (TO), Terrestrial and foliage granivores insectivores (TFGI), Arboreal omnivores (AO) and Carnivores (CAR), (Fig. 4). Frugivores and nectivores guilds were not included because we did not sample enough individuals.

#### 2.5. Association between vegetation and birds communities

We used Partial Canonical Correspondence Analysis (PCCA) to evaluate if the changes in avian guilds abundance were explained by changes in vegetation variables, considering the effects of distance from the *puestos* in both components (research question 4). Canonical Correspondence Analysis (CCA) is an eigenvector ordination technique that produces direct gradient analysis. In PCCA the sum of canonical eigenvalues is a measure of the amount of variation in the species data that is explained by the environmental variable set. When the analysis includes covariables, the effect of these variables is partialled out, and the sum of the canonical eigenvalues represents the variance in the community explained by the environmental variables after accounting for the covariable (Ter Braak and Smilauer, 2002). Thus using PCCA we could disentangle the variation in birds guilds abundance that was determined by the distance from the *puestos* and by the changes in vegetation attributes. For this analysis we considered the 108

**Table 1**  
Two-way ANOVA output considering the effects of the different *puestos* (“among”) and the distance from each *puesto* (“within”) to different avian community and vegetation variables.

	Distance				<i>Puestos</i>			
	df	F	p	r <sup>2</sup>	n	F	p	r <sup>2</sup>
Structure diversity (H)	5	43.91	<0.01	0.69	17	0.87	0.6	0.05
Trees richness (S)	5	14.23	<0.01	0.36	17	2.41	<0.01	0.21
Trees diversity (H)	5	11.05	<0.01	0.30	17	2.53	<0.01	0.23
DBH median	5	9.35	<0.01	0.28	17	2.12	0.01	0.21
Feces	5	10.04	<0.01	0.30	17	2.04	0.02	0.20
Birds diversity (H)	5	2.27	0.05	0.09	17	1.55	0.09	0.21
Birds richness (S)	5	4.07	<0.01	0.14	17	2.26	<0.01	0.27

sites (18 *puestos*, 6 sites per *puesto*) based on guilds abundances for each site. We standardized the environmental variables to compare them at the same scale (median equal zero, standard deviation equal 1). To select the vegetation variables we performed a stepwise-forward selection of the environmental variables, adding only those that were significantly associated ( $p < 0.05$ ) to bird species scores (Leps and Smilauer, 2003). We made a general CCA, and accounted for the total variation (inertia) considering distance and vegetation attributes. Then we used the PCCA considering the distance from the *puestos* as a covariable of birds guilds abundance and vegetation attributes as the environmental variables. We followed the same procedures using the vegetation variables as covariables and distance as the environmental constraint. We recorded the sum of canonical eigenvalues and the percentage of birds guilds abundance explained. We used Monte Carlo permutations to test the statistical significance of the axes in CCA and to test if distance and vegetation attributes significantly influence birds ordination in PCCA. Ordination analyzes were performed with CANOCO 4.52 software (Ter Braak and Smilauer, 2002).

### 3. Results

#### 3.1. Within and among *puestos* variation

The different distances from the *puestos* were statistically different in terms of structure diversity, tree richness, tree diversity, DBH median, feces density, birds communities diversity and richness; and the variation explained by distances from *puestos* was on average approximately 50% higher than the variance explained among *puestos*; and vegetation structure diversity and birds diversity did not show statistically significant differences among *puestos* (Table 1). In contrast, the variation in birds species richness (S) was twice as high among *puestos* in comparison to distances from the *puestos* both being highly statistically significant (Table 1).

#### 3.2. Vegetation response along the gradient

Two of the tree species responded as Decreasers (i.e. had a lower density nearby the *puestos*): *A. quebracho-blanco* was best described by a saturation curve ( $\Delta\text{AICc} = 1.8$ ) and *Ruprechtia apetala* by a linear positive model, but in this case the difference with respect to the constant and the exponentials models was too low to select a model ( $\Delta\text{AICc} = 0.6$ ). The abundance of *C. paraguayensis* ( $\Delta\text{AICc} = 4.1$ ), *Schinopsis balansae* ( $\Delta\text{AICc} = 1.9$ ), and *Z. mistol* ( $\Delta\text{AICc} = 13.5$ ) were better described by a quadratic model (i.e. middle trend). The abundance of *P. nigra* showed no response along the gradient (constant model,  $\Delta\text{AICc} = 0.7$ ), a value too low to allow model selection (Appendix Table 2).

The frequency of trees and shrubs touches responded as Decreasers, best described by a saturation curve ( $\Delta\text{AICc} = 4$  and 16.5 respectively). The same model fitted for the cases of vertical complexity indices, Structure Shannon's diversity (H) ( $\Delta\text{AICc} = 31.7$ ) and Structure richness (S) ( $\Delta\text{AICc} = 5.8$ ). The frequency of grass touches responded to a Middle trend model ( $\Delta\text{AICc} = 13.6$ ), and the frequency of bare ground touches responded as an Increaser fitting a negative exponential curve ( $\Delta\text{AICc} = 13.8$ ) (Fig. 3).

The DBH Median ( $\Delta\text{AICc} = 1.3$ ) and DBH Standard Deviation ( $\Delta\text{AICc} = 1.1$ ) of all trees species had a Decreasers response along the gradient fitting to saturation curve. Tree species richness (S) had a Medial increasers response described by a quadratic model and also by a saturation and linear positive models ( $\Delta\text{AICc} = 0.3$ ) (Fig. 3 and Appendix Table 2).

Most decrease-type saturation curves reached saturation at the distances of less than 1 km from the *puestos*, implying a strong effect at relatively short distances of the gradient (Fig. 3).

The density of feces diminished exponentially with the distance from the *puesto* and there was a negative correlation ( $r = -0.51$ ,  $p < 0.01$ ) between density of feces and vegetation structural complexity as represented by Structure Shannon's diversity (H) (Table 1).

#### 3.3. Birds response along the gradient

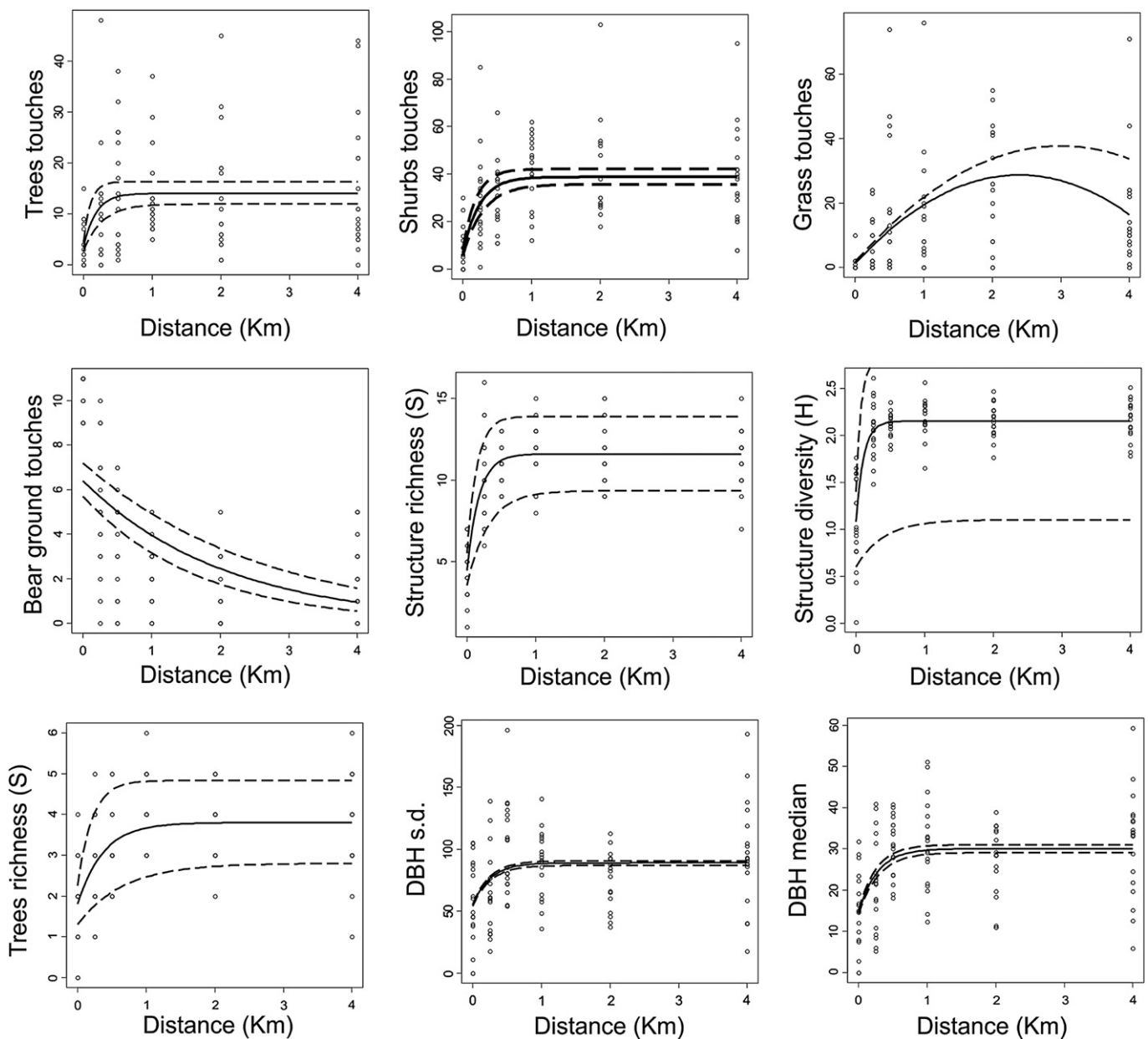
Bird abundance decreased markedly with distance from the *puestos*, to approximately 50% at 4000 m (Kendall's Tau =  $-0.54$ ,  $p < 0.01$ ). Species richness also decreased slightly along the distance gradient, but this decrease in richness was not significant and is likely to be mostly an effect of the changes in density, since Fisher's  $\alpha$  diversity index (a measure of species diversity independent from density) showed the lowest values at the nearest distances (0 m). Evenness did not show a response along the gradient (Table 2).

Five guilds showed an Increasers response, all of them best described by a saturation curve in which the largest difference occurs in the first hundreds of meters from the *puesto*: Arboreal omnivores ( $\Delta\text{AICc} = 25.7$ ), Long flight insect hunters ( $\Delta\text{AICc} = 31.3$ ), Terrestrial and foliage granivores insectivores ( $\Delta\text{AICc} = 10.1$ ), Terrestrial granivores ( $\Delta\text{AICc} = 25.9$ ), and Arboreal granivores ( $\Delta\text{AICc} = 13.3$ ). Terrestrial insectivores abundance decrease in the first 500 m, but was also described by a quadratic and a saturation model ( $\Delta\text{AICc} = 0.2$ ). One guild, Bark insectivores, responded as Extremist, fitting a positive quadratic function ( $\Delta\text{AICc} = 2.4$ ). Two guilds presented a medial distance response, adjusting best to a negative quadratic function: Foliage insectivores ( $\Delta\text{AICc} = 3.1$ ) and Short flight insect hunters ( $\Delta\text{AICc} = 3.4$ ). Carnivores and Terrestrial omnivores did not show changes in their abundances along the gradient, fitting a constant function ( $\Delta\text{AICc} = 2.1$  and 0.1, respectively) (Fig. 4 and Appendix Table 2).

Of the eight guilds in which we grouped the 25 restricted species (i.e. those with four or less observations), five were classified as medials, two as decrease, and one showed no trend (Table 3).

#### 3.4. Vegetational association with birds patterns

The total variation in birds guilds explained by environmental variables was 16% (total inertia = 1.18). The first axis was constrained by vegetation attributes and the distance from the *puestos* (Pearson correlation Spp-Env = 0.72) explained 14% of this variation and was the only significant axis according to the Monte Carlo test (eigenvalue = 0.17,  $p = 0.01$ ) (Fig. 5a). The vegetation variables that were added to the model by the stepwise-forward selection were DBH median, Trees richness (S), and vertical structure



**Fig. 3.** Vegetation variables response to the distance from the *puestos*, expressed as the total values of the vegetation variables at each distance for the eighteen *puestos*. Solid lines represent the best fitting function according to MLE and selected by AICc criteria, dotted lines represented the confidence intervals of each of these models.

complexity (H). The first axis of the PCCA using the distance from the *puestos* as a covariable and the vegetation variables as the environmental component significantly explained 6.8% of birds guild abundance (eigenvalue = 0.08,  $p = 0.01$ ). For the second PCCA

we used vegetation attributes as covariables and the distance as the environmental constrain in PCCA. The first axis of this ordination explained the 5.4% of the variation (eigenvalue = 0.06,  $p < 0.01$ ). The rest of the variation explained by the canonical axe (1.8%) corresponded to a mixed effect of distance and vegetation that was not possible to separate (Fig. 5b).

**Table 2**  
Sum of total birds communities richness and cattle feces for each distance (in meters) from the *puestos*. Median values and Standard deviation of birds abundance, Fisher's  $\alpha$ , evenness indexes, and cow feces at each distance.

	0	250	500	1000	2000	4000
Richness	76	74	71	61	64	69
Abundance	46 ± 17	35 ± 14	34 ± 13	27 ± 11	33 ± 12	25 ± 16
Fisher's $\alpha$	9.9 ± 4.6	13.5 ± 6.6	11.9 ± 6	12.5 ± 5.3	11.4 ± 4.6	12.1 ± 8
Evenness	0.7 ± 0.1	0.8 ± 0.1	0.8 ± 0.1	0.8 ± 0.1	0.7 ± 0.1	0.8 ± 0.1
Median n° feces	23 ± 13	14 ± 19	6 ± 5	6 ± 4	7 ± 6	5 ± 5

Kendall's correlations analysis between guild's abundance and CCA scores for axis one revealed seven significant correlations. Bark insectivores, Long flight insect hunters, Arboreal omnivores, Terrestrial and Foliage granivores insectivores, Terrestrial insectivores and Arboreal granivores were negatively associated to axis one (Table 4). Foliage insectivores was the only guild positively associated to axis one. Carnivores, Short flight insect hunters, Terrestrial granivores and Terrestrial omnivores were located at the middle of the gradient. Only two guilds were correlated to axis two: Bark insectivores and Terrestrial omnivores (Table 4).

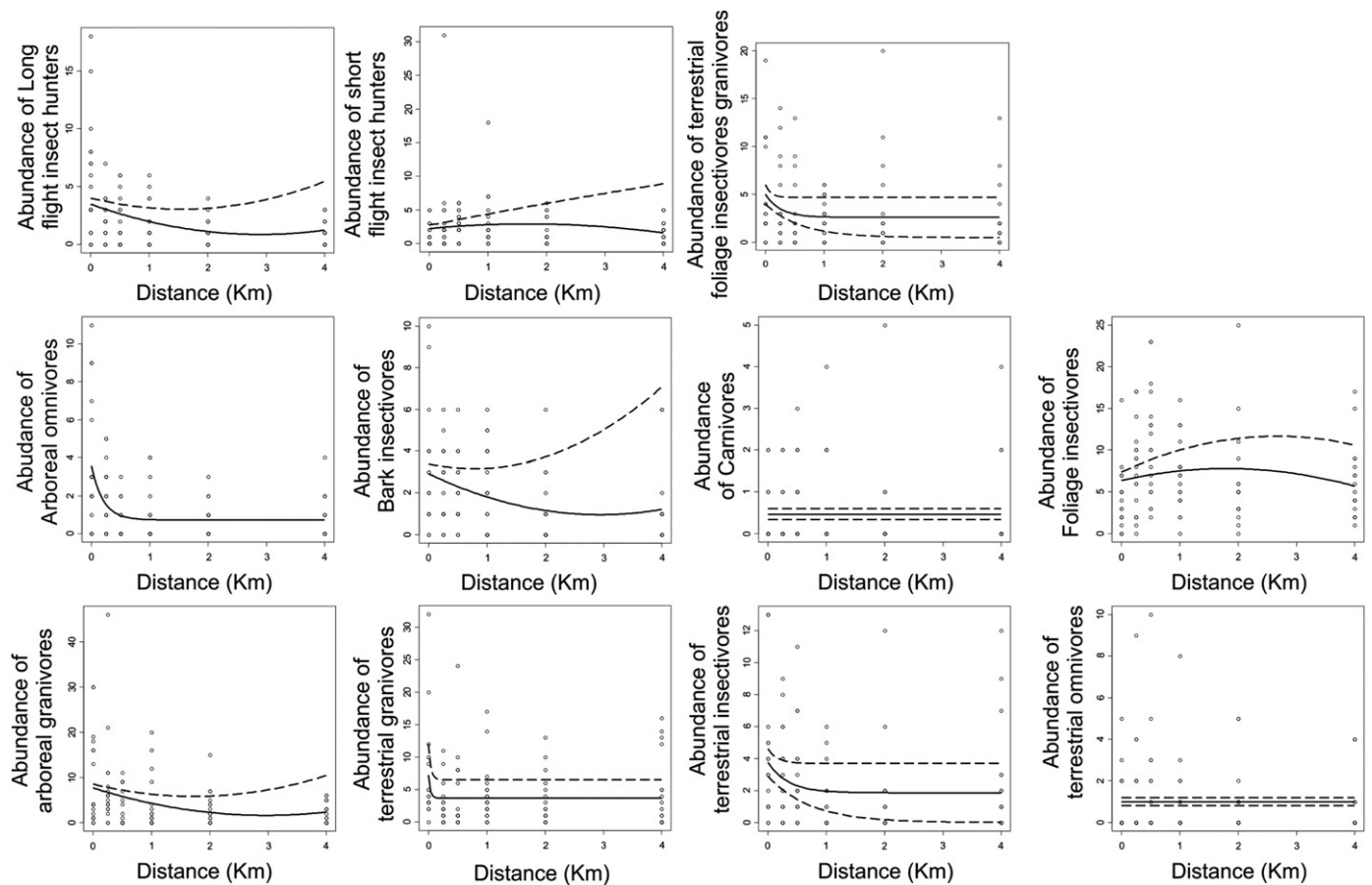


Fig. 4. Avian guild's response to the distance from the *puestos*, expressed as the total abundance values of each guild along the distance gradient for the eighteen *puestos*. Solid lines represent the best fitting function according to MLE and selected by AICc criteria, dotted lines represented the confidence intervals of each of these models.

4. Discussion

In this study we assessed the piospheres pattern on vegetation, bird communities and their relationships in the semi-arid Chaco of Argentina. The existence of piosphere patterns in several other arid and semi-arid ecosystems in the world (e.g. Derry, 2004; Graetz and Ludwig, 1978) makes these results relevant for a general framework of dryland landscape ecology beyond this case study. The local scale gradient of distance from each of the *puestos* involved more variation in the vegetation descriptors than the differences among *puestos* distributed across an area of 12 million hectares; implying that the piosphere effect plays a major role in defining vegetation

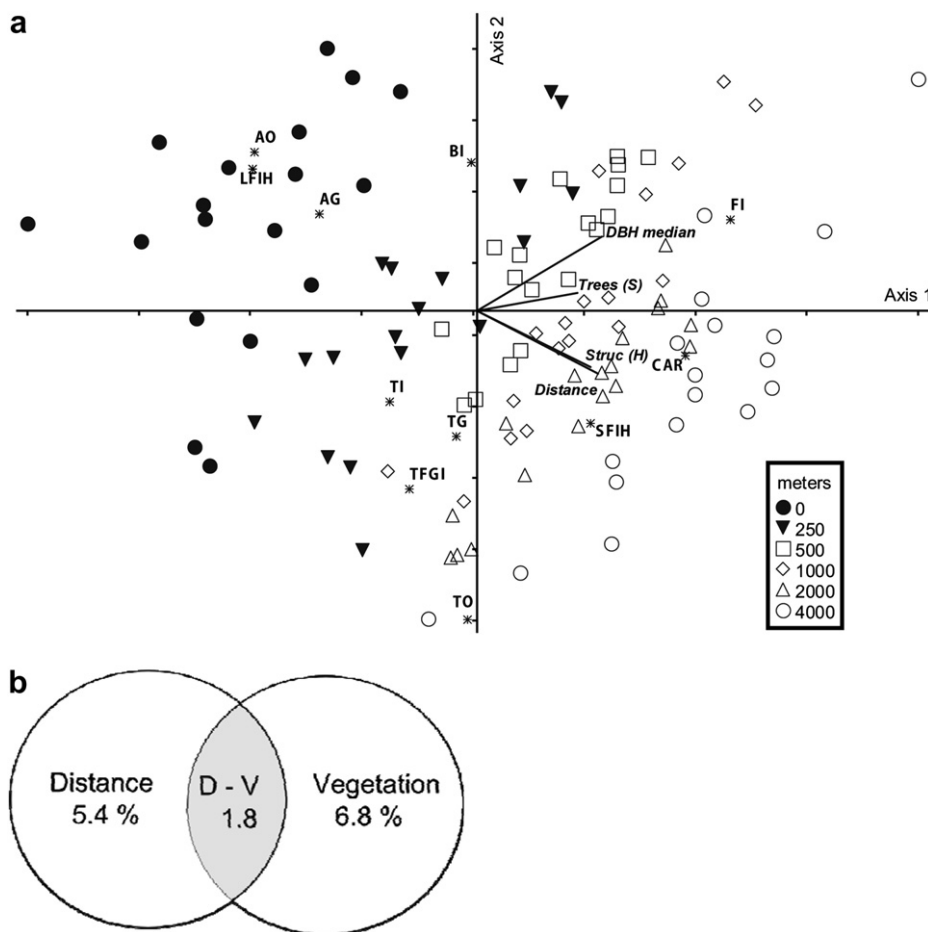
landscape patterns in this ecoregion. In contrast, bird community richness and diversity were more influenced by the inter-*puestos* variation likely due to the higher mobility of birds and their capacity to adjust their abundance at a coarser spatial scale (García et al., 2009).

As predicted by the “piosphere” model both plants and birds reflected statically significant trends in relation to the distance from the *puestos*, resulting from changes in livestock pressure. However, their trends along the distant gradient are opposite. Vegetation attributes reflecting structural complexity, diversity and biomass (research question 2) increase with the distance from the water source (Fig. 3), making the *puestos* a focus of vegetation degradation as has been indicated by previous observations in the area (Adámoli et al., 1990; Grau et al., 2008). In contrast, the abundance of most bird's guilds (research question 3) decreased with distance from the *puestos* (Fig. 3, Table 2), likely in response to a combination of resources like water, seeds and grains, insects and changes in vegetation structure around the *puestos*. In semi-arid regions, different resources increase nearby with water bodies, including insects taxa related to water such as Odonata, Ephemeroptera, Thicoptera, Diptera, Heroptra, Coleoptera, Anostraca, Notostraca, Conchostraca (Codesido and Bilenca, 2004; Williams, 1996; Zacharias et al., 2007), and parasitoids associated to livestock feces (Zalba and Cozzani, 2004). In addition to feces, direct access to livestock grain supplies may represent a valuable resource to be found by birds that are no sensible to human presence (Gonnet, 2001). In contrast, rare or low abundance bird species showed higher densities away from *puestos* peaking at long or intermediate distances, similarly to the vegetation attributes. This differential

Table 3  
Response of restricted guilds to the distance from the *puestos*.

Species	Trend	N° species
Carnivores	Middle trend	2
Arboreal omnivores	Middle trend	3
Foliage insectivores	Decreasers trend	6
Terrestrial insectivores	Middle trend	2
Short flight insects hunters	Middle trend	3
Long flight insects hunters	Decreasers trend	1
Terrestrial and foliage granivores insectivores	No trend	6
Terrestrial granivores	Middle trend	1
<b>Total</b>		<b>8</b>
<b>Total increasers</b>		<b>0</b>
<b>Total deceasers</b>		<b>2</b>
<b>Total medials</b>		<b>5</b>
<b>Total no trend</b>		<b>1</b>
<b>Total extremist</b>		<b>0</b>





**Fig. 5.** Partial Canonical Correspondence Analysis ordination diagram based on birds guilds abundance, vegetation attributes and the distance from the *puestos*. (a) Each point represents one sampling point of the six distance of the eighteen *puestos*. Straight lines indicates the joint plot of the principal environmental variables related to the ordination. (b) Partitioning of variance of guilds composition.

pattern reflects the varying capacity of different taxes to respond to managed systems according to their requirements, and the importance of evaluating them simultaneously to compare their relationships.

The response of woody vegetation to piospheres is highly variable among regions with differences in climate, soil, vegetation and

management (Derry, 2004). In our study the composition and structure of vegetation followed the expected pattern reflecting a degradation gradient, where both the abundance of trees and complexity of the forest increased with the distance from the *puestos*. As a result of our detailed field work, we were able to quantitatively describe several properties of the response of different vegetation attributes along the gradient. The abundance of dominants tree species, the structure of shrubs and trees, tree diversity and size resulted in a common pattern: increasing from very low values around the *puestos* and stabilizing at medium (500 m) and long distances (2000–4000 m). Similar results have been found in other works related to the effect of piospheres patterns, suggesting a “sacrifice zone” near the water bodies, and a sigmoidal increase in vegetation along the gradient, e.g: Australian chenopodian and acacias shrublands (Graetz and Ludwig, 1978; Landsberg et al., 2003), and drylands of Botswana (Molelele, 1994), Zimbabwe (Rodriguez, 1995), and South Africa (Stokes and Yeaton, 1994). In the case of Mojave Desert of USA, native vegetation increased with the distance, while alien vegetation was more abundant next to the water (Brooks et al., 2006). In our study, the highest grass cover occurred at intermediate distances (c. 1000–2000 m), probably because these distances combine comparatively low grazing pressure (which selectively removes grasses) with less forest canopy cover (which limits grass growth). In the Chaco region woody vegetation appears to be less variable at intermediate and long distances from the *puestos*, where partially

**Table 4**  
Guild richness, abundance of the 108 sampling sites. Kendall's Tau correlation coefficients of the guilds and vegetation variables with the axis one of the PCCA.

Guilds	Richness	Abundance	Axis 1
Arboreal granivores	4	131	-0.30**
Bark insectivores	6	85	-0.22*
Carnivores	2	7	0.04
Foliage insectivores	13	600	0.20*
Long flight insect hunters	6	398	-0.40**
Short flight insect hunters	8	336	-0.03
Arboreal omnivores	7	169	-0.37**
Terrestrial and foliage granivores insectivores	10	307	-0.24**
Terrestrial granivores	5	356	-0.19
Terrestrial insectivores	8	252	-0.26**
Terrestrial omnivores	4	109	0.06
Structure diversity (H)			0.73**
Distance			0.80**
DBH Median			0.84**
Tree species richness (S)			0.61**

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

degraded forests do not differ markedly. This is possibly related to prolonged human use of the Chaco forest, with intense wood extraction during the last century for different purposes (Bucher, 1987). Studies in other systems have explored the piosphere effects at longer distances (between 10 and 15 km, Landsberg et al., 2003). This is not practical to do in the Chaco region, since the high *puestos* density makes difficult to find locations in the landscape at more the 5 km of the closest one.

Most bird's guilds responded positively to the presence of *puestos*. The main changes in guilds abundance were observed between the *puesto* core and the 250 m sampling site; whereas at longer distance, communities were comparatively more similar to each other. This pattern of response of the avian community not only differ from the trends in vegetation, but also with those in game animals such as peccaries and jaguars hunted for bushmeat and for livestock protection (Altricher and Boaglio, 2004). In particular, Long flight insect hunters and Arboreal granivorous were significantly more abundant nearby the *puestos*. Around the *puestos* generally there are a few big remaining trees, and Long flight insect hunters have no difficulty to fly from the perch in the absence of the middle stratum (Lopez de Casenave et al., 1998). Arboreal granivores and Arboreal omnivores are expected to benefit from grain supplies for cattle near the *puesto* (e.g. corn or sorghum plantations) on which they can feed either directly from the ground or from livestock feces. This guild, which includes doves, cowbirds and sparrows are hardly affected by human disturbances (Zalba and Cozzani, 2004; and personal observations.).

In the analysis of avian community patterns constrained by vegetation and the distance from the *puestos*, we found low explanatory effect of these environmental components (research question 4). In spite of this, we were able to separate the effects of vegetation and distance on avian communities. Vegetation structure and distance from the *puesto* have a separate effect on birds guilds, which adds up as one complex gradient of variation from the center of the *puestos*. Besides the three guilds (LFIH, AG, and AO) that were abundant near the *puestos*, there were others guilds such as Bark insectivores, Terrestrial and Foliage granivores insectivores, Terrestrial insectivores, and Terrestrial granivores that also increased their abundance near the *puestos*. In the PCCA ordination diagram these groups were located at intermediate values of axis one, both near the *puestos* and at intermediate distances along the gradient expressed in axis one (Fig. 5). Considering the high vagility of birds, it is possible that these groups make use of the water bodies but also require a more developed and complex forest structure, responding to resources as food, protection from predators, and places suitable for courtship and nest sites during the breeding season (Wiens, 1989). Foliage insectivores and Short flight insect hunters were more abundant at intermediate distances from the *puestos* (1000–2000 m); both guilds may be responding to the need of a well-structured forest to hunt for insects and nest building, coinciding with our vegetation increasing variables along the. We found no response for Terrestrial omnivores and Carnivores along the gradient. Both of these guilds are characterized by large body size, possibly with lower density than the birds of others guilds. Terrestrial omnivores include species that are hunted for food by *puestos* inhabitants such as *Crypturellus tataupa*, *Eudromia formosa*, *Ortallia canicollis* and *Chunga burmeisteri*; therefore this group may need to compromise the advantages (resources) and disadvantages (hunting risk) of the *puesto*. Carnivores guild is composed by species with wider distribution ranges, and is possible that the scale of selection of habitat use is coarser than the studied gradient.

The dominant trend in the avian community (i.e. increasing abundance at short and intermediate distances from the *puestos*) does not hold for the restricted species, which can be considered

rare either by their low abundance, high habitat specificity or high sensitivity to disturbances (Wiens, 1989). These species peaked at medium and long distances from the *puestos*, suggesting they tend to be more dependent on resources related to less disturbed forests. Given the higher conservation value of these species due to their scarcity, this pattern has important implications for biodiversity management in this region; and more research, including higher sampling sizes, is needed to better understand their life history and habitat needs. During the summer season (prior to the sampling of this study) some avian guilds (e.g. frugivores and nectarivores) could have different behavior in relation to the piosphere as a consequence of a greater availability of water in the landscape, flowers, fruits, and insects in the forest interior; and to the requirements related to reproduction (Codesido and Bilenca, 2004).

While the patterns of vegetation and nutrients related to piospheres systems have been well studied (Craig et al., 1999), the effect on native fauna is less understood. There are numerous studies of the response of groups of birds to the presence of cattle, reporting negative effects (e.g. Taylor, 1986), positive effects (Medin and Clary, 1989), and no effects (Medin, 1986). But studies on the effects of artificial water bodies to the native fauna are largely restricted to large mammals such as kangaroos and elephants (Chamaillé-Jammes et al., 2007), zebras and lions (Owen-Smith, 1996), and mammals interactions such as competition and predation (Owen-Smith, 1996). With regard to birds most studies has been done in Australia, where many species have expanded their geographical distribution and abundance increased by the provision of artificial water (James et al., 1999). To our knowledge this would be the first quantitative analysis of the response of bird communities in the context of piospheres in South America, and in particular in the dry Chaco, where piospheres excerpt a strong influence on landscape patterns over millions of hectares (Fig. 1).

In conclusion, our study reinforces the idea that *puestos* represent a salient landscape pattern with strong influences of the functioning of biotic communities in the Argentine Chaco and other arid lands by generating strong local environmental gradients. But, in contrast to previous studies, our results emphasize that this gradient is complex with non-linear effects in community composition that vary according to the group of species considered. In particular, plant and bird communities respond to this gradient in opposite ways. The study of other organisms likely to respond differently to this gradient by their different relationship with water resources, livestock and hunting pressure (e.g. insects, amphibians, small mammals) is needed to provide a complete understanding on how human-made water surplus scattered across the landscape affects the patterns and processes in this water-limited neotropical forest ecosystems.

## Acknowledgments

Financial support for this research was provided by grant PICT 2006 #1693 'Cambios y eficiencia de uso del territorio en el Chaco Argentino' and additional funds from grant 26-G420 from CIUNT. Provincial Park rangers Mariana Welter and Luis Molina helped us in the field. People of the eighteen *puestos* were always welcoming and willing to help, providing local assistance both in terms of information and basic logistical support. Pedro Blendinger commented an earlier manuscript and gave us key information on birds biology; Agustina Malizia, Ezequiel Araoz, Natacha Chacoff and Juan Manuel Morales helped with the statistical analysis, and Ignacio Gasparri collaborated with satellite image analysis for Fig. 1. The comments of three anonymous reviews greatly improved the organization and quantitative analysis of this paper.

## Appendix

## Appendix Table 1

List of sampled bird species indicating its respective guild. Nomenclature consider of the classification of the bird species of South America (<http://www.museum.lsu.edu/~remsen/saccbaseline.html>).

Bird species	Guilds	Family
<i>Amazona aestiva</i>	Arboreal granivores	Psittacidae
<i>Aratinga acuticaudata</i>	Arboreal granivores	Psittacidae
<i>Myopsitta monachus</i>	Arboreal granivores	Psittacidae
<i>Patagioenas cayennensis</i>	Arboreal granivores	Columbidae
<i>Cacicus solitarius</i>	Arboreal omnivores	Icteridae
<i>Cyanocorax chrisops*</i>	Arboreal omnivores	Corvidae
<i>Icterus cayanensis</i>	Arboreal omnivores	Icteridae
<i>Melanerpes cactorum</i>	Arboreal omnivores	Picidae
<i>Pheucticus aureoventris</i>	Arboreal omnivores	Cardinalidae
<i>Phytotoma rutila*</i>	Arboreal omnivores	Cotingidae
<i>Piranga flava*</i>	Arboreal omnivores	Cardinalidae
<i>Thraupis bonariensis</i>	Arboreal omnivores	Thraupidae
<i>Thraupis sayaca</i>	Arboreal omnivores	Thraupidae
<i>Turdus amaurochalinus</i>	Arboreal omnivores	Turdidae
<i>Campephilus leucopogon</i>	Bark insectivores	Picidae
<i>Campylorhamphus trochilrostris</i>	Bark insectivores	Furnariidae
<i>Melanerpes candidus</i>	Bark insectivores	Picidae
<i>Picumnus cirratus</i>	Bark insectivores	Picidae
<i>Veniliornis mixtus</i>	Bark insectivores	Picidae
<i>Xiphocolaptes major</i>	Bark insectivores	Furnariidae
<i>Coragyps atratus*</i>	Carnivores	Cathartidae
<i>Falco sparverius</i>	Carnivores	Falconidae
<i>Glaucidium brasilianum</i>	Carnivores	Strigidae
<i>Spizapterix circumcinctus*</i>	Carnivores	Falconidae
<i>Asthenes baeri</i>	Foliage insectivores	Furnariidae
<i>Cranioleuca pyrrhophia</i>	Foliage insectivores	Furnariidae
<i>Cyclarhis gujanensis</i>	Foliage insectivores	Vireonidae
<i>Parula pitiayumi</i>	Foliage insectivores	Parulidae
<i>Phacellodomus ruber</i>	Foliage insectivores	Furnariidae
<i>Polioptila dumicola</i>	Foliage insectivores	Poliopitidae
<i>Poospiza melanoleuca</i>	Foliage insectivores	Emberizidae
<i>Stigmatura budytoides</i>	Foliage insectivores	Tyrannidae
<i>Tapera naevia</i>	Foliage insectivores	Cuculidae
<i>Taraba major</i>	Foliage insectivores	Thamnophilidae
<i>Thamnophilus caerulescens</i>	Foliage insectivores	Thamnophilidae
<i>Troglodytes aedon</i>	Foliage insectivores	Troglodytidae
<i>Vireo olivaceus</i>	Foliage insectivores	Vireonidae
<i>Anairetes flavirostris*</i>	Foliage insectivores	Tyrannidae
<i>Anumbius annumbi*</i>	Foliage insectivores	Furnariidae
<i>Coccyzus cinereus*</i>	Foliage insectivores	Cuculidae
<i>Hemitriccus margaritaceiventer*</i>	Foliage insectivores	Tyrannidae
<i>Synallaxis albescens*</i>	Foliage insectivores	Furnariidae
<i>Synallaxis frontalis*</i>	Foliage insectivores	Furnariidae
<i>Empidonomus aurantioatrocristatus</i>	Long flight insect hunters	Tyrannidae
<i>Empidonomus varius*</i>	Long flight insect hunters	Tyrannidae
<i>Myarchus tyrannulus</i>	Long flight insect hunters	Tyrannidae
<i>Myiodynastes maculatus</i>	Long flight insect hunters	Tyrannidae
<i>Pyrocephalus rubinus</i>	Long flight insect hunters	Tyrannidae
<i>Tyrannus melancholicus</i>	Long flight insect hunters	Tyrannidae
<i>Tyrannus savana</i>	Long flight insect hunters	Tyrannidae
<i>Camptostoma obsoletum</i>	Short flight insect hunters	Tyrannidae
<i>Knipolegus aterrimus</i>	Short flight insect hunters	Tyrannidae
<i>Knipolegus striaticeps</i>	Short flight insect hunters	Tyrannidae
<i>Lathrotriccus euleri*</i>	Short flight insect hunters	Tyrannidae
<i>Myiophobus fasciatus*</i>	Short flight insect hunters	Tyrannidae
<i>Nystalus maculatus</i>	Short flight insect hunters	Bucconidae
<i>Pachyrhamphus polychopterus*</i>	Short flight insect hunters	Tityridae
<i>Pitangus sulphuratus</i>	Short flight insect hunters	Tyrannidae
<i>Serpophaga subcristata</i>	Short flight insect hunters	Tyrannidae
<i>Sublegatus modestus</i>	Short flight insect hunters	Tyrannidae
<i>Suiriri suiriri</i>	Short flight insect hunters	Tyrannidae
<i>Agelaioides badius</i>	Terrestrial and foliage granivores insectivores	Icteridae
<i>Coryphospingus cucullatus</i>	Terrestrial and foliage granivores insectivores	Emberizidae
<i>Guira guira</i>	Terrestrial and foliage granivores insectivores	Cuculidae
<i>Lophospingus pusillus*</i>	Terrestrial and foliage granivores insectivores	Emberizidae
<i>Molothrus bonariensis</i>	Terrestrial and foliage granivores insectivores	Icteridae
<i>Molothrus rufoaxillaris</i>	Terrestrial and foliage granivores insectivores	Icteridae
<i>Paroaria coronata</i>	Terrestrial and foliage granivores insectivores	Thraupidae
<i>Passer domesticus*</i>	Terrestrial and foliage granivores insectivores	Passeridae
<i>Poospiza torquata*</i>	Terrestrial and foliage granivores insectivores	Emberizidae

(continued on next page)

Appendix Table 1 (continued)

Bird species	Guilds	Family
<i>Saltator aurantiirostris</i>	Terrestrial and foliage granivores insectivores	Insertae sedis
<i>Saltator coerulescens*</i>	Terrestrial and foliage granivores insectivores	Insertae sedis
<i>Saltatricula multicolor</i>	Terrestrial and foliage granivores insectivores	Insertae sedis
<i>Sicalis flaveola</i>	Terrestrial and foliage granivores insectivores	Emberizidae
<i>Sporophila caerulescens*</i>	Terrestrial and foliage granivores insectivores	Emberizidae
<i>Sporophila nigriollis*</i>	Terrestrial and foliage granivores insectivores	Emberizidae
<i>Thamnophilus doliatus*</i>	Terrestrial and foliage granivores insectivores	Thamnophilidae
<i>Zonotrichia capensis</i>	Terrestrial and foliage granivores insectivores	Emberizidae
<i>Columbina picui</i>	Terrestrial granivores	Columbidae
<i>Cyanocopsa brissonii*</i>	Terrestrial granivores	Cardinalidae
<i>Leptotila verreauxi</i>	Terrestrial granivores	Columbidae
<i>Patagioenas maculosa</i>	Terrestrial granivores	Columbidae
<i>Patagioenas picazuro</i>	Terrestrial granivores	Columbidae
<i>Zenaida auriculata</i>	Terrestrial granivores	Columbidae
<i>Anthus chii*</i>	Terrestrial insectivores	Motacillidae
<i>Coryphistera alaudina</i>	Terrestrial insectivores	Furnariidae
<i>Drymornis bridgesii</i>	Terrestrial insectivores	Furnariidae
<i>Furnarius cristatus</i>	Terrestrial insectivores	Furnariidae
<i>Furnarius rufus</i>	Terrestrial insectivores	Furnariidae
<i>Machetornis rixosa</i>	Terrestrial insectivores	Tyrannidae
<i>Mymorchilus strigilatus*</i>	Terrestrial insectivores	Thamnophilidae
<i>Pseudoseisura lophotes</i>	Terrestrial insectivores	Furnariidae
<i>Rhinocrypta lanceolata</i>	Terrestrial insectivores	Rhinocryptidae
<i>Vanellus chilensis</i>	Terrestrial insectivores	Charadriidae
<i>Chunga burmeisteri</i>	Terrestrial omnivores	Cariamidae
<i>Crypturellus tataupa</i>	Terrestrial omnivores	Tinamidae
<i>Eudromia formosa</i>	Terrestrial omnivores	Tinamidae
<i>Ortalis canicollis</i>	Terrestrial omnivores	Cracidae

Appendix Table 2

Curve fitting of vegetation and birds guilds response to the distance from the *puestos*. AICc values, ΔAICc, correlation coefficient and significance values.

Variables	Response	AICc					ΔAICc	r	p
		Saturation	Lineal	Constant	Medial	Exponential			
<i>Ziziphus mistol</i>	Medial	571	546	549	<b>530</b>	547	13.5	0.24	<0.01
<i>Caesalpinia paraguariensis</i>	Medial	184	182	181	<b>176</b>	182	4.1	0.10	0.08
<i>Schinopsis lorentzii</i>	Medial	373	371	372	<b>369</b>	372	1.9	0.16	0.22
<i>Aspidosperma quebracho-blanco</i>	Decreaser	<b>517</b>	539	591	518	550	1.8	0.40	<0.01
<i>Ruprechtria triflora</i>	Decreaser	227	<b>225</b>	226	–	226	0.6	0.13	0.32
<i>Prosopis</i> sp.	Constant	509	507	<b>506</b>	508	507	0.7	0.06	0.41
Tree's touch	Decreaser	<b>1239</b>	1313	1405	1243	1333	4	0.26	<0.01
Shrub's touch	Decreaser	<b>1520</b>	1720	2128	1536	1808	16.5	0.47	<0.01
Grass's touch	Medial	1861	1915	2421	<b>1848</b>	2066	13.6	0.39	<0.01
Bear ground touch	Increaser	517	511	2421	468	<b>454</b>	13.8	–0.74	<0.01
Structure diversity (H)	Decreaser	<b>30</b>	104	150	62	110	31.7	0.60	<0.01
Structure richness(S)	Decreaser	<b>492</b>	524	573	597	531	5.8	0.63	<0.01
DAP median	Decreaser	<b>818</b>	823	841	819	825	1.3	0.42	<0.01
DAP S.D.	Decreaser	<b>1077</b>	1078	1086	1078	1079	1.1	0.30	0.01
Tree's richness (S)	Medial/Decreaser	368	369	383	<b>367</b>	371	0.3	0.52	<0.01
Arboreal granivores	Increaser	<b>987</b>	1019	1094	1022	1000	13.2	–0.26	<0.01
Bark insectivores	Extremist	416	414	429	<b>409</b>	412	2.4	–0.28	<0.01
Carnivores	Constant	218	216	<b>214</b>	218	216	2.1	0.00	0.35
Foliage insectivores	Medial	798	796	795	<b>792</b>	796	3.1	–0.06	0.22
Long flight insect hunters	Increaser	<b>457</b>	504	541	489	493	31.3	–0.32	<0.01
Short flight insect hunters	Medial	596	594	595	<b>591</b>	594	3.4	–0.09	0.13
Arboreal omnivores	Increaser	<b>359</b>	401	422	385	393	25.7	–0.28	<0.01
Terrestrial and foliage granivores insectivores	Increaser	<b>708</b>	719	725	718	718	10.1	–0.12	0.01
Terrestrial granivores	Increaser	<b>840</b>	873	874	866	873	25.9	–0.06	0.13
Terrestrial insectivores	Increaser/Extremist	<b>572</b>	785	786	<b>572</b>	784	0.2	–0.10	<0.01
Terrestrial omnivores	Constant	391	<b>388</b>	<b>388</b>	389	<b>388</b>	0.1	–0.09	0.31

References

Adámoli, J., Senhauser, E., Acero, J.M., Rescia, A., 1990. Stress and disturbance: vegetation dynamics in the dry Chaco region. *Journal of Biogeography* 17, 491–500.

Altricher, M., Boaglio, G.I., 2004. Distribution and relative abundance of peccaries in the Argentine Chaco: associations with human factors. *Biological Conservation* 116, 217–225.

Andrew, M.H., 1988. Grazing impact in relation to livestock watering points. *Trends in Ecology and Evolution* 3, 336–339.

Bock, C.E., Bock, J.H., 1988. Grassland birds in southeastern Arizona: impacts of fire, grazing and alien vegetation. In: *Ecology and Conservation of Grassland Birds*. International Council for Bird Preservation, Technical Publication. 7, pp. 43–58.

Bolker, B.M., 2008. *Ecological Models and Data* in R. Princeton University Press, Princeton, New Jersey, United Kingdom.

Brooks, M.L., Matchett, J.R., Berry, K.H., 2006. Effects of livestock watering sites on alien and native plants in the Mojave Desert, USA. *Journal of Arid Environments* 67, 125–147.

Bucher, E.H., 1987. Herbivory in arid and semi-arid regions of Argentina. *Revista Chilena de Historia Natural* 60, 265–273.

Bucher, E.H., Huszar, P.C., 1999. Sustainable management of the Gran Chaco of South America: ecological promise and economic constraints. *Journal of Environmental Management*, 57–99.

Bullock, J., 1996. In: Sutherland, W.J. (Ed.), *Ecological Census Techniques*. Cambridge University Press, pp. 111–138.

Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Multimodal Inference: a Practical Information-theoretic Approach*, second ed. Springer-Verlag, New York, NY, US.



- Chamaillé-Jammes, S., Valeix, M., Fritz, H., 2007. Managing heterogeneity in elephant distribution: interactions between elephant population density and surface-water availability. *Journal Applied Ecology* 44, 625–633.
- Codesido, M., Bilenca, D., 2004. Variación Estacional de un Ensemble de Aves en un Bosque Subtropical Semiárido del Chaco Argentino. *Biotropica* 36, 544–554.
- Craig, J., Landsberg, J., Morton, S.R., 1999. Provision of watering points in the Australian arid zone: a review of effects on biota. *Journal of Arid Environments* 41, 87–121.
- Derry, J.F., 2004. Piospheres in Semi-arid Rangeland: Consequences of Spatially Constrained Plant-herbivore Interactions. PhD thesis. University of Edinburgh, UK.
- Fontaine, A.L., Kennedy, P.L., Johnson, D.H., 2004. Effects of distance from cattle water developments on grassland birds. *Journal of Range Management* 57, 238–242.
- García, D., Chacoff, N.P., Herrera, J.M., Amico, G.C., 2009. In: Medel, R., Aizen, M.A., Zamora, R. (Eds.), *Ecología y evolución de interacciones planta-animal: conceptos y aplicaciones*. Editorial Universitaria, Santiago, Chile.
- Gonnet, J.M., 2001. Influence of cattle grazing on population density and species richness of granivorous birds (Emberizidae) in the arid plain of the Monte, Argentina. *Journal of Arid Environments* 48, 569–579.
- Graetz, R.D., Ludwig, J.A., 1978. A method for the analysis of piosphere data applicable to range assessment. *Australian Rangeland Journal* 1, 126–136.
- Grau, H.R., Gasparri, N.I., Aide, T.M., 2008. Balancing food production and nature conservation in the Neotropical dry forests of northern Argentina. *Global Change Biology* 14, 985–997.
- Guevara, J.C., Estevez, O.R., Stasi, C.R., 2006. Vegetation response in a grazing intensity gradient in Mendoza, Argentina. *Multequina* 15, 27–36.
- Hoekstra, J.M., Boucher, T.M., Ricketts, T.H., 2005. Confronting a biome crisis: global disparities of habitat loss and protection. *Ecology Letters* 8, 23–29.
- Huet, S., Bouvier, A., Gruet, M.A., Jolivet, E., 2004. *Statistical Tools for Nonlinear Regression: a Practical Guide with S-Plus Examples Series*. In: Springer Series in Statistics. Springer-Verlag.
- James, C.D., Landsberg, J., Morton, S.R., 1999. Provision of watering points in the Australian arid zone: a review of effects on biota. *Journal of Arid Environments* 41, 87–121.
- Landsberg, J., James, C.D., Morton, S.R., Muller, W.J., Stol, J., 2003. Abundance and composition of plant species along grazing gradients in Australian rangelands. *Journal of Applied Ecology* 40, 1008–1024.
- Leps, J., Smilauer, P., 2003. *Multivariate Analysis of Ecological Data Using CANOCO*. Cambridge University Press, Cambridge.
- Lopez de Casenave, J., Pelotto, J.P., Caziani, S.M., Mermoz, M., Protomastro, J., 1998. Responses of avian assemblages to a natural edge in a Chaco semiarid forest in Argentina. *The Auk* 115, 425–435.
- Medin, D.E., 1986. Grazing and passerine breeding birds in a Great Basin low-shrub desert. *Great Basin Naturalist* 46, 567–572.
- Medin, D.E., Clary, W.P., 1989. *Small Mammal Populations in a Grazed and Ungrazed Riparian Habitat in Nevada*. United States Department of Agriculture, Intermountain Research Station, No. INT-413. Ogden, UT.
- Milchunas, D.G., Lauenroth, W.K., 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs* 63, 327–366.
- Minetti, J.L., 1999. *Atlas climático del Noroeste Argentino*. Laboratorio Climatológico Sudamericano. Fundación Zon Caldenius, Tucumán.
- Moleele, N.M., 1994. *Ecological Change and Piospheres: Can the Classical Range Succession Model and its Modification Explain Changes in Vegetation and Soil Around Boreholes in Eastern Botswana*. Unpublished MSc. Thesis, University of Canberra, Australia.
- Molina, S.I., Valladares, G.R., Gardner, S., Cabido, M., 1999. The effects of logging and grazing on the insect community associated with a semi-arid Chaco forest in central Argentina. *Journal of Arid Environments* 42, 29–42.
- Morello, J., Saravia Toledo, C., 1959. El bosque chaqueño I: paisaje primitivo, paisaje natural y paisaje cultural en el oriente de salta. *Revista Agronómica del Noroeste Argentino* 3, 5–81.
- Olog, C.C., 1963. Lista y distribución de las aves argentinas. *Opera Lilloana* 9, 1–377.
- Owen-Smith, N., 1996. Ecological guidelines for waterpoints in extensive protected areas. *South African Wildlife Research* 26, 107–112.
- R Development Core Team, 2010. *R: a Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0. URL <http://www.R-project.org>.
- Ralph, J.C., Geupel, G.R., Thomas, P.P., Martin, E., Desante, D.F., Mila, B., 1996. *Manual de métodos de campo para el monitoreo de aves terrestres*. Forest Service, U.S. Department of Agriculture.
- Rodríguez, S.J., 1995. *Artificial Waterholes: a Study of Day-time Utilisation of Artificial Waterholes by Large Mammals and the Subsequent Impact on Vegetation in Gonarezhou National Park, Zimbabwe*. Durrell Institute of Conservation and Ecology, University of Kent, Canterbury. Unpublished report.
- Stokes, C.J., Yeaton, R.I., 1994. A line-based vegetation sampling technique and its application in succulent karoo. *African Journal of Range Forage Science* 11, 11–17.
- Taylor, D.M., 1986. Effects of cattle grazing on passerine birds nesting in riparian habitats. *Journal of Range Management* 39, 254–258.
- Ter Braak, C.J.F., Smilauer, P., 2002. *CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (Version 4.5)*. Microcomputer Power, Ithaca, NY, USA, 500 pp.
- Thrash, I., Derry, J.F., 1999. The nature and modelling of piospheres: a review. *Pretoria. Koedoe* 42, 73–94.
- Wiens, J.A., 1989. *The Ecology of Bird Communities*. In: *Foundations and Patterns*, vol. 1. Cambridge Univ. Press, Cambridge, England.
- Wiens, J.A., Rotenberry, J.T., 1981. Habitat associations and community structure of birds in shrub-steppe environments. *Ecological Monographs* 51, 21–42.
- Williams, Dudley, 1996. Environmental constraints in temporary fresh waters and their consequences for the insect fauna. *Journal of the North American Benthological Society* 15, 634–650.
- Zacharias, I., Dimitriou, E., Dekker, A., Dorsman, E., 2007. Overview of temporary ponds in the Mediterranean region: threats, management and conservation issues. *Journal of Environmental Biology* 28, 1–9.
- Zalba, S.M., Cozzani, N., 2004. The impact of feral horses on grassland bird communities. *Animal Conservation* 7, 35–44.