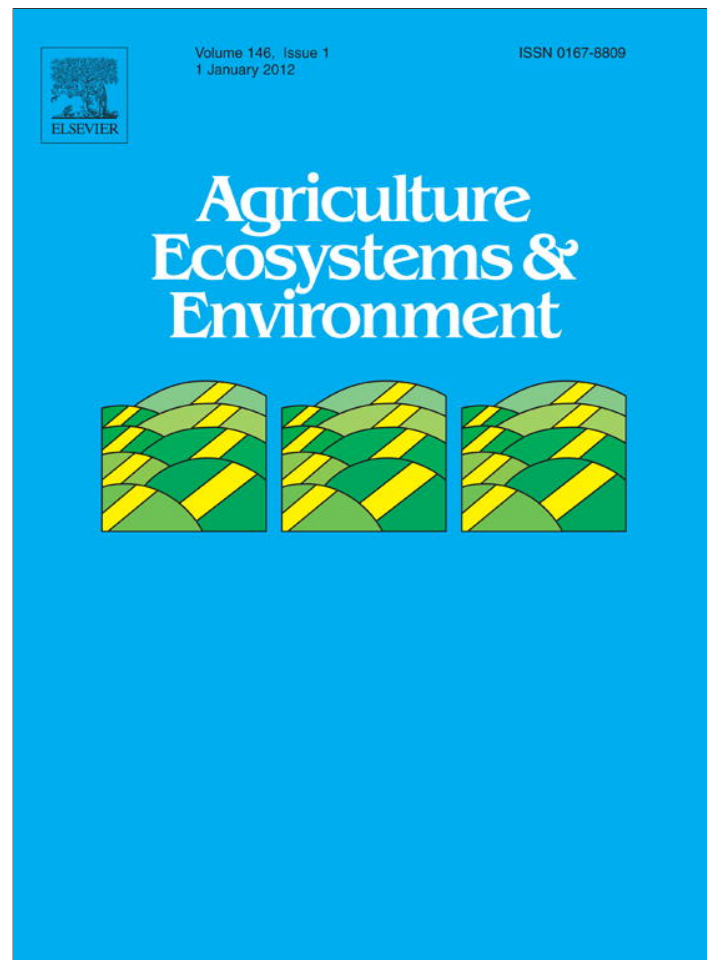


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Trade-offs between land use intensity and avian biodiversity in the dry Chaco of Argentina: A tale of two gradients



Leandro Macchi*, H. Ricardo Grau, Patricia V. Zelaya, Sofía Marinaro

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

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ABSTRACT

Studies to assess the relationship between agriculture production and biodiversity conservation usually focus on one gradient ranging from a natural reference land cover type (typically forest) to an intensive productive land use. However, many semi-arid ecoregions such as the dry Chaco are characterized by a mosaic of different land covers, including natural grasslands and woody vegetation with different degrees of transformation, frequently aimed at meat production. We analyzed the associations between avian biodiversity and meat productivity of forest, natural grasslands, three types of livestock production systems, and soybean crops in northern Argentina dry Chaco; an area of c. 19 million ha characterized by high conservation value and rapid land use change. A Generalized Lineal Model analysis of reports and publications quantified a meat productivity range in which soybean (the less diverse land cover type) doubles the most efficient livestock systems, and is eight times more productive than the widespread *puestos* system. A multidimensional scaling ordination identified two independent gradients of bird's response to increasing land use intensity, respectively from protected forests and from natural grasslands, to highly transformed systems. Along both gradients avian richness and density sharply declined in the transition from semi-natural land covers to planted pastures and similarity to native grasslands and protected forests decreased exponentially. Along the "grasslands gradient", bird richness and density presented a unimodal response. Maximum likelihood-fitted curves of bird's guilds response to the productivity gradients showed that in the "forest gradient" most guilds decreased exponentially or linearly, whereas in the "grasslands gradient" most guilds peaked at intermediate levels of meat yield. Our results suggest that land sparing strategies can be more efficient to balance agriculture production with the conservation of forest avian diversity, but also that the prevailing "forest oriented" conservation schemes (e.g. Argentine Forest Law) do not capture the complexity of the system and both forests and grassland gradients should be considered in land use planning, possibly including a combination of conservation strategies.

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1. Introduction

As human population and food consumption (particularly meat) continue to grow (Alexandratos, 2008; Bruinsma, 2009), the pressures of land use expansion and intensification increasingly affect biotic communities via habitat loss, degradation and fragmentation (Dirzo and Raven, 2003; Fahrig, 2003). Declines in wildlife populations related to land use intensification has been reported all over the world, but particularly in the tropics (Gardner et al., 2010). Tropical and subtropical dry forest ecosystems are one of the biomes with higher proportion of land transformed into agriculture and one of the least included in conservation

schemes (Hoekstra et al., 2005; Portillo-Quintero and Sánchez-Azofeifa, 2010). South American dry Chaco is the largest remaining continuous dry forest unit in the continent (Eva et al., 2004), one of the fastest expanding agriculture frontiers (Gasparri et al., 2008; Clark et al., 2010; Aide et al., 2012), and one of the least protected ecoregions in Argentina (Izquierdo and Grau, 2009; Marinaro et al., 2012).

Quantifying the contribution of different land uses to both food production and biodiversity conservation is a necessary step to evaluate their trade-offs and to promote land use schemes that minimize such conflict (Sekercioglu, 2006). Two contrasting management options framed this debate as: "land sparing" vs. "land sharing". Land sparing (LSP) favors the spatial separation of high yield productive areas (e.g. modern mechanized agriculture) with low biodiversity value that allows to "save" relatively undisturbed habitats with high biodiversity. In contrast, land sharing (LSH) farming favors locally biodiversity-friendly land uses, with a spatial

* Corresponding author. Tel.: +54 3814255174.

E-mail address: leandromacchi@gmail.com (L. Macchi).

coexistence of production and wildlife conservation. Since “wildlife friendly” systems usually attain lower per unit area agriculture yields, they require more land to meet production targets. Thus, LSH implies less undisturbed land but more biodiversity conservation in the productive systems (Green et al., 2005; Fischer et al., 2008). Most empirical studies to assess the comparative value of these strategies have been conducted in tropical rainforest biomes, alternatively supporting LSP (e.g. Aratrakorn et al., 2006; Phalam et al., 2011) and LSH (e.g. Dorrrough et al., 2007; Clough et al., 2011) strategies. These studies were based on one dominant gradient from a natural reference land cover type (typically forest) to a highly transformed use (e.g. intensive agriculture). However, complex ecosystems are characterized by a mosaic of different land covers, typically including both grasslands and woody vegetation, which in turn differ in their human land use, animal communities and species sensitivity to human disturbances. The dry Chaco in South America, for example, includes such heterogeneity of natural environments including forests and grasslands, as well as several types of human land uses (Adámoli et al., 1990). Therefore, balances between food production and biodiversity may involve more than one dimension or “gradient”.

Green et al. (2005) proposed the theoretical framework to assess the LSH vs LSP dichotomy based on the assumption that the ecological and biological characteristic of each species determine the shape of its response along the productive gradients. Species which populations decrease markedly with small increases in yield (convex function) would benefit from LSP since they require undisturbed habitats for their population maintenance. Conversely species little affected by low and intermediate levels of human transformation (concave function) would benefit with LSH strategies as moderately productive systems can sustain high population densities. This species-centered approach could be replaced by focusing on higher levels of biodiversity. Wiens et al. (2008) suggested that a useful approach for conservation management would be to identify functional groups or “guilds” of species with similar responses to landscape structure that facilitate the understanding of the ecological changes. Avian guilds are classified based on their functional and ecological characteristic, and on how these characteristics are affected by LULCC (land use land cover changes, Sekercioglu, 2006). Birds are considered good indicators of changes in habitat quality (Rodrigues and Brooks, 2007) due to their high ecological diversity, relatively easy identification and quantification, and high vagility; which allows adjusting their abundance in response to resource supply of the landscape (Wiens, 1992). At a local scale bird communities are regulated by food availability, habitat structure, and/or environmental factors (Wiens and Rotenberry, 1981; Wiens, 1992). Local patterns of avian richness may reflect local heterogeneity, and intermediately disturbed sites could present higher values of richness even in comparison with undisturbed habitats (Butsic et al., 2012). Therefore, in order to assess the effect of land use on components of biodiversity, in addition to local patterns of diversity, we need to quantify the similarity of transformed ecosystems with non-productive ecosystems (DeFries et al., 2004). Studies on Chaco avifauna have shown that avian richness and abundance are higher in primary forest and decrease with decreasing forest structural complexity (Lopez de Casenave et al., 1998; Codesido and Bilenca, 2004). In the dry Chaco avian guilds showed different patterns response to changes in forest conditions. For example, bark insectivores and short flight insect hunters are more abundant in the forest interior, whereas long flight insect hunters, frugivores, terrestrial insectivores and granivores are more abundant in forest edges (Lopez de Casenave et al., 1998; Codesido and Bilenca, 2004; Macchi and Grau, 2012).

In addition to agriculture yields and biodiversity responses to it, strategies for land optimization are constrained by local socio-economic and political realities. The dry Chaco has a prolonged

history of human land use, characterized by extensive cattle ranching, selective logging, charcoal and firewood extraction since the end of the 19th century (Morello et al., 2007). Land cover transformation accelerated since the 1970s as mechanized agriculture expanded (Grau et al., 2005) and present day vegetation is a mosaic of woodlands and grassland with different levels of degradation, and different types of production systems that vary in intensity from extensive ranching to implanted pastures and crops; and that reflect in the social actors managing the landscape (Gasparri and Baldi, 2013; Grau et al., 2008). In response to the growing concern about the conservation of the Chaco in the context of rapid agriculture expansion, in 2007 the territory was zonified by the Law 26.331 “Ley de Presupuestos Mínimos de Protección Ambiental de los Bosques Nativos” (“Forest law”; Dirección de Bosques, Secretaría de Ambiente y Desarrollo Sustentable de la Nación 2008), which classifies the territory into three levels of allowed forest management and transformation, but implicitly ignores natural grasslands as a conservation target (Cardozo et al., 2011). Emerging international initiatives such as REDD+ (reducing emissions from deforestation and forest degradation) also promote conservation schemes in which biodiversity is a “co-benefit” of carbon sequestration, largely associated to woody vegetation (UNFCCC, 2010).

The effects of land use on community diversity and composition differ among taxonomic groups (Alberti, 2005). Given the growing importance of the dry Chaco for both conservation and productive land uses, recent studies have started to assess the interactions between productive systems and wildlife. Based on the much higher productivity of soybean in comparison with extensive livestock ranching, Grau et al. (2008) suggested that intensive agriculture could play a key role in balancing agriculture production and nature conservation under a LSP conservation strategy. Due to the methodological approach focusing on historical land use assessments, however, this study did not consider land use types becoming more important in the recent past, such as planted pastures and silvopastures. More recently, Mastrangelo and Gavin (2012) compared bird communities of different livestock production systems with nearby forest. Relatively large differences in livestock productivity between low intensity and intermediate-intensity silvopastoral systems (implanted pastures with canopy above, meat production: 100–140 kg ha/year) were accompanied by little change in birds diversity, but and a sharp decline in bird diversity occurred along with minor or no productivity gains between intermediate-intensity systems (silvopastures) and implanted pastures without canopy. Based on these results, the authors suggest that silvopasture systems (a type of LSH approach) may efficiently compromise conservation and production.

However, this study had three important limitations: (i) it was restricted to a comparatively small portion of the Argentine dry Chaco (approximately 2 million ha); (ii) it did not include natural grasslands (an important natural environment) thus assuming that land use essentially can be ordered in a monotonic gradient from forests, and (iii) it did not consider intensive agriculture production, the most rapidly expanding and most productive land use in the region (Grau et al., 2008). Here, we overcome these limitations by expanding the scale of analysis to an area of c. 19 million ha and by including the description of avian communities in natural grasslands and soybean fields. Diversity patterns were related to environmental changes at a regional scale (Wiens and Rotenberry, 1981; van Rensburg et al., 2002; Hortal et al., 2008) in order to discriminate the effects originated in differences of land use from those controlled by geographic environmental gradients scale. Specifically, this study was framed to pursue the following research objectives: (1) to quantitatively compare the meat production yields of the most important land use/cover types in the northern Gran Chaco ecoregion: natural grasslands, extensive livestock in woodlands, silvopastures, implanted pastures, and soybean

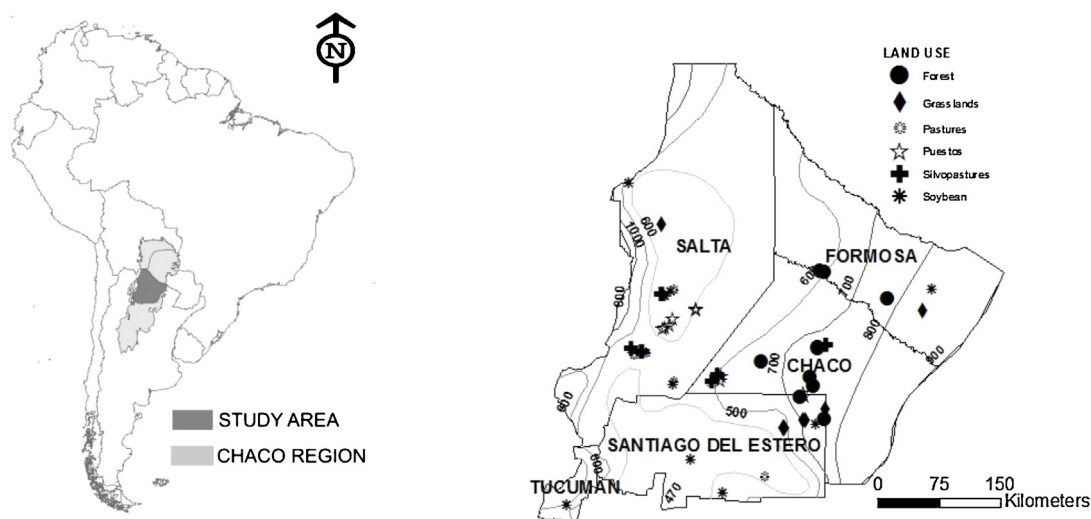


Fig. 1. (a) Location of the study area in South America. (b) Details of samples distribution, provinces border lines and isolines of annual rainfall.

crops; (2) to characterize the avian composition of the different land uses of the region and their similarity relationships in a multivariate analysis; thus identifying main community gradients that can be related to production gradients; controlling from the effects of geographic environmental factors; and (3) to describe birds response (species composition and diversity, and functional guilds) along the gradients of agriculture yield identified in (1) and (2), thus providing the basis to assess the trade-off between meat production and avian diversity.

2. Methods

2.1. Study area and sampling design

The Gran Chaco ecoregion covers a total area of c.120 million ha in Argentina, Bolivia and Paraguay. This study was conducted on the Northern dry Chaco of Argentina (22° S to 27° S; 59.5° W to 65° W), considered as part of the semiarid sub-region of the Argentine Chaco. The area includes the west of Formosa and Chaco provinces, the east of Salta province, and the north of Santiago del Estero province; spanning over of c. 19 million ha (Fig. 1a). The area has a subtropical seasonal climate. 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. Annual rainfall ranges between 500 and 900 mm, with a strong pattern of monsoonal precipitation seasonality in which c. 80% of the rain falls between November and March; and the winter and early spring are characterized by water deficit (Minetti, 1999).

Woody vegetation is characterized by semi-deciduous xerophytic forest and shrub lands with different levels of conversion by human activities. Dominant tree species include *Schinopsis lorentzii*, *Aspidosperma quebracho-blanco*, *Bulnesia sarmientoi*, *Ziziphus mistol*, *Caesalpinia paraguayensis*, *Prosopis alba* and *Prosopis nigra*, *Acacia* spp., *Geoffroea decorticans* (Prado, 1993). Natural grasslands are dominated by *Elyonorus* cf. *adustus* (espartillo or aibe) when they occur in sandy soils of paleocaucuses, and by *Trichloris crinita*, *Gouinia latifolia*, *Setaria macrostachya* when they are generated by fire on other soil types (Tálamo et al., 2012).

Extensive livestock management is based on the *puestos* system, the most widespread land use of the region (Adámoli et al., 1990; Grau et al., 2008). Each *puesto* consists on a group of houses, farm buildings, minor local crops, a water source, and herds of cows and goats grazing freely in the landscape. The development of

intensive livestock farming through deforestation and introduction of pastures in the dry Chaco began in the 1970s, associated with the introduction and interbreeding of more productive (e.g. Hereford and Angus) and better adapted (e.g. Brahman) livestock breeds. Currently, the most used planted pasture in the study region is the dwarf variety of *Panicum maximum* (Gatoon Panic) (Glatzle, 2005). In recent years the silvopastures systems have expanded, in which livestock production is conducted in plantation of exotic pastures growing under the partial shade of remaining canopy trees that help preserving soil fertility, provide shelter and shade, improve forage digestibility in the dry season, and keep higher biomass stocks (Lin et al., 2001; Udawatta and Jose, 2011). The most rapidly expanding land use type in the region is mechanized agriculture (Grau et al., 2008; Clark et al., 2010), which is dominated by soybean and is mostly exported to be used for pork and chicken feed (Grau et al., 2005; Zak et al., 2008).

Chaco dry forest provides habitat for more than two hundred species of birds; mainly represented by the Furnariidae family, but also well represented by other families such as Tyrannidae (including some neotropical migrants), Icteridae and Emberizidae. There are many emblematic species of the region, including the Black-legged Seriema (*Chunga burmeisteri*), Quebracho Crested-Tinamou (*Eudromia formosa*), Blue-fronted Amazon (*Amazona aestiva*), Red-crested Cardinal (*Paroaria coronata*), Black-bodied Woodpecker (*Dryocopus schulzi*), and crowned eagle (*Harpyhaliaetus coronatus*). Birds associated to natural grasslands have been well documented for the humid Chaco were land use changes are threatening the most sensible species (Azipiroz et al., 2012), but little research has focused on the grassland bird communities of the dry Chaco.

For each LUC category (forest, grasslands, *puestos*, silvopastures, implanted pastures, and soybean) we sampled avian communities in ten plots. Plots of all land uses were spread across the whole study area (approximately 19 million ha) to capture geographic variation of the complete northern Argentine Chaco region (Fig. 1b). We used a land cover map (Gasparri et al., 2008) to select plot location, surrounded by the same land use at least in a 1 km radius to eliminate border effects. Each plot consisted in 1 km × 1 km, within which we surveyed nine birds' point counts. Each count lasted 10 min during which we recorded the presence of bird species and computed the relative frequency of that species in each plot (from zero to nine). We considered all individuals that were seen or heard inside the 20 m of radius of each point and that were

using that space; flying- through individuals and high-flight species (e.g. Families Hirundinidae and Apodidae) were not considered.

We classified bird species into fourteen guilds defined by diet composition and foraging sites, following previous studies in the area (Macchi and Grau, 2012) and our own field observations: Aquatic (AQ), 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), Carnivores (CAR), Scavengers (SCA), and Nectarivores (NEC) (see Table S1, Supporting information). Density of frugivores increases during the wet season in response to greater fruit availability (migrant's arrivals and changes in diet; Codesido and Bilenca, 2004); since our surveys were in dry season we did not classify species as strict frugivores.

Supplementary Table S1 associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agee.2013.04.011>.

2.2. Meat productivity patterns

We estimated the forage production of each land use type (Objective 1) based literature records of the dry Chaco (Table S2, Supporting information). Most estimates were based on systematic forage harvest expressed as dry matter for one year. Protected forests were assumed to have zero production although in some case there is very low density of livestock within the national parks and reserves. Although there are other livestock productions (e.g. goats in the puesto system), cattle production is by far the principal regional and national meat product, representing 65% of all livestock for the year 2009 (Rearte, 2010), therefore we assumed all the forage production was directed to cattle meat production. Meat production of the different livestock land uses was computed as:

$$\text{Secondary production (SP)} = 0.08 \times 0.6 \times \text{FB}$$

where SP = meat production ($\text{kg ha}^{-1} \text{yr}^{-1}$); 0.08 = conversion rate from vegetable to cattle meat (Deregibus, 1988; Martin, 2005); 0.6 = proportion of the plant consumed by cattle (Deregibus, 1988; Martin, 2005); forage biomass (FB) = $\text{kg ha}^{-1} \text{yr}^{-1}$.

Supplementary Table S2 associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agee.2013.04.011>.

In the case of soybean we considered a conversion rate of 5.5 from kilograms of soybean to kilograms of pork meat (Smil, 2000, 2013); a standard conversion utilized in previous studies. To estimate the soybean yield we used data from the national government (<http://www.siaa.gov.ar>), considering the annual harvest of the last eleven years (period 2000/2010) for the provinces of Chaco (mean = $1900 \pm 0.5 \text{ kg ha}^{-1} \text{yr}^{-1}$), Santiago del Estero (mean = $2100 \pm 0.6 \text{ kg ha}^{-1} \text{yr}^{-1}$), Formosa (mean = $1900 \pm 0.5 \text{ kg ha}^{-1} \text{yr}^{-1}$) and Salta (mean = $2500 \pm 0.4 \text{ kg ha}^{-1} \text{yr}^{-1}$). Argentina is the third world exported of soy grain, mostly destined to feed pork's and chickens; soybean is also used for flours and oils production, destined to the European Union, China and India (Lapitz et al., 2004). We decided to consider pork meat due to: (1) Pork fed is the number one use of soybean. (2) In contrast with chicken (the second most important use of soybean) from both culinary and nutritional (calories, proteins, fat) point of view pork is fairly similar to beef. (3) It is intermediate in terms of food-meat transformation efficiency, with a conversion factor of 5, is about twice as efficient as cattle, and approximately half as efficient as chicken (Smil, 2013). For comparative purposes, we also made analyzed the response of

bird's richness and similarity to productive patterns considering cattle and chickens meat production efficiency (Fig. S1, Supporting information).

Supplementary Fig. S1 associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agee.2013.04.011>.

2.3. Statistical analysis

We used bibliographic data (Table S2, Supporting information) to compare per-hectare meat productivity between the different land use types (Objective 1) by means of a generalized linear model (GLM). Normality and homoscedasticity were checked using standard graphical methods (Quinn and Keough, 2002). To determine the statistical significance of the differences in meat production between land uses we used the LSD a posteriori test of multiple comparisons. To control for the effect of regional changes in precipitation we used the 2000/2010 mean annual rainfall as a co-variable of the sites where productivity values were reported or the nearest locality using data from the national government (<http://www.siaa.gov.ar>). Grau et al. (2005) showed that soils are less important than rainfall in limiting deforestation expansion. Based on the Atlas of soils of the national government (GeoINTA, 2004) we estimated the area not appropriated for agriculture expansion considering the following restrictions: alkaline soils above 50 m, saline soils and flooded soils. Since 82% of the surface of the study area has agricultural potential (i.e. it did not fall within these limitations) we decided to exclude soils types of the production patterns model.

To describe the relationships of similarity among land uses in terms of bird communities (Objective 2) we used the Non Metric Multidimensional Scaling ordination method (NMDS, Kruskal and Wish, 1978) based on a matrix of Sorensen's distances of the species composition (as frequency data) of each sampling site; considering axes that describe most of the variation of birds composition. To evaluate for difference in composition between forest and grasslands we compared their scores in the ordination axes by means of a non parametric Mann–Whitney *U*-test. We correlated the centroids' scores (mean value of the scores for each land use) with the mean of the yields of each land use (from Objective 1) to describe the relationship between the ordination diagram and the production patterns. To analyze if the patterns of land use ordination in the NMDS were affected by the effects of the physical environment on the community ordination we run non-parametric Spearman's correlations between the scores of the NMDS axes one and two with the following variables: latitude as a proxy of temperature, and annual precipitations obtained from the WorldClim database (Hijmans et al., 2005).

We estimated the mean values of richness, Shannon's diversity, and total number of individuals for each land use category. To test for differences on avian richness and Shannon's diversity between land uses we used the non-parametric Kruskal–Wallis analysis, and pairwise non-parametric Mann–Whitney's *U*-test to identify homogeneous groups of land uses. We used the Bray–Curtis dissimilarity index (Bray and Curtis, 1957) to quantify the compositional dissimilarity between the land uses and the two "reference" land cover types (protected forest and natural grasslands); and we estimated the mean value of the similarity index $[(1 - \text{dissimilarity}) \times 100]$. We evaluated the particular effects of the land uses over the richness, total individuals, and similarity along the forest and the grasslands gradients (Objective 3). For this we estimated the slope or average per-unit change of the biodiversity attributes (richness, total individuals, and similarity) between successive land use types along the productivity gradients. We also explored the evenness of each land use assemblages using rank abundance curves (Fig. S2, Supporting information).

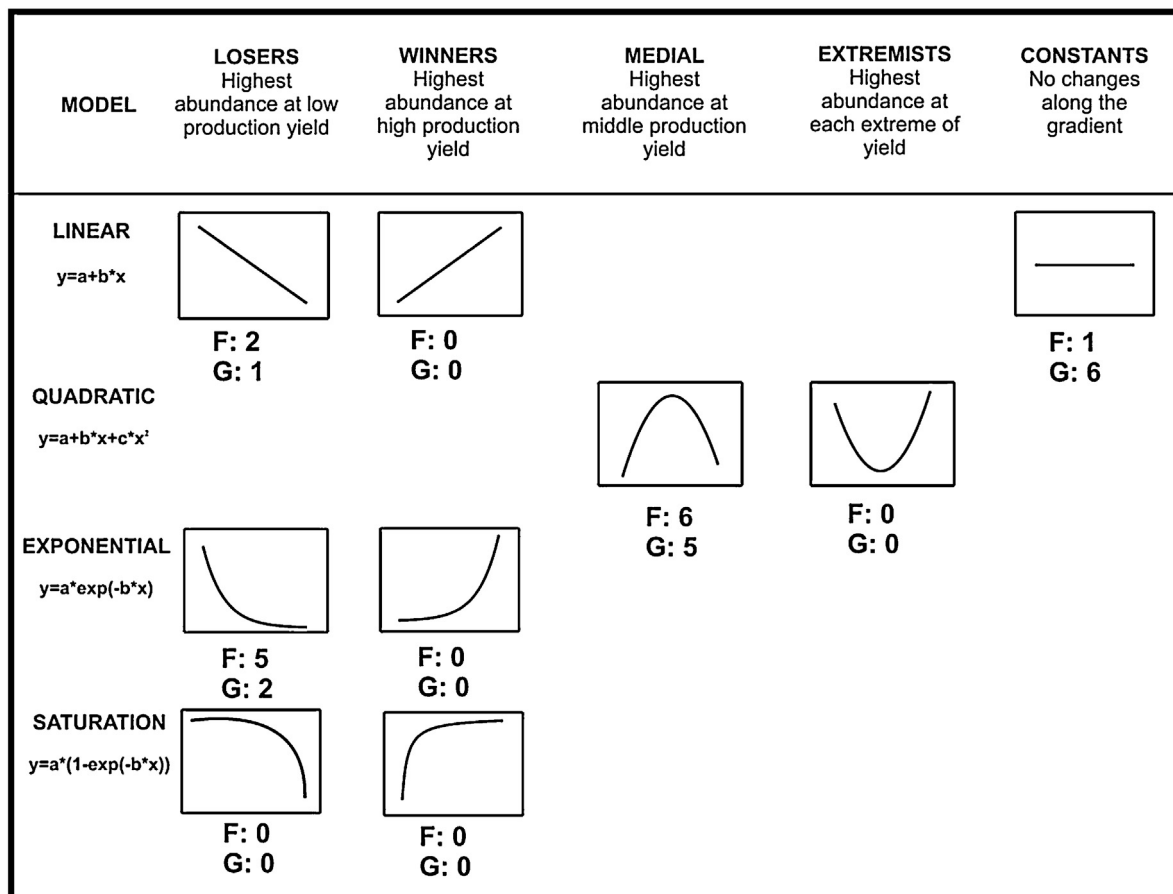


Fig. 2. Diagram of bird's guilds responses along the productive gradients. Considering the type of response in the columns: Losers, Winners, Medial, Extremist, and Constant; and the describing models in the fills: Linear, Quadratic, Exponential, and Saturation. The letters F (Forest) and G (Grasslands) below each graph indicates the numbers of guilds that were described by that curve for each gradient.

Supplementary Fig. S2 associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agee.2013.04.011>.

In order to describe how birds guilds vary along the production gradients (Objective 3) we classified the response of each guild in five categories: Losers (frequency decreases along the production gradient), Middle distance trend (frequency peaks at intermediate distances, taking comparatively lower values at both extremes of the gradient), Winners (frequency increase along the gradient), Extremists (frequency is higher in the extreme that at intermediate levels of production), and Constant (no changes on frequency along the gradient). Each of these categories could be described by more than one possible function (Fig. 2): constant (no distance effect), linear, exponential and saturation (positive for Winners and negative for Losers), and quadratic (positive reflects Middle distance trend, negative reflect Extremists trend). Models were fitted to data in the R Development Core Team (2010) using maximum likelihood estimator package *bbmle* (<http://lib.stat.cmu.edu/R/CRAN/web/packages/bbmle/>) to adjust the functions. For the probabilistic component of the model we used the Poisson distribution for count data of guilds frequency (Bolker, 2008). To select the best fitting function for each variable we used the corrected Akaike Information Criterion (AICc), comparing the differences of the AICc values ($\Delta AICc$) between the models with the lower AICc, where $AICc_{mim}$ is the AICc value for the best-fitting model. Values of $\Delta AICc > 2$ are considered plausible to model selection (Burnham and Anderson, 2002).

3. Results

3.1. Meat productivity in different land uses

In an order of increasing meat productivity, the different land use types were: *puestos* extensive livestock, natural grasslands, silvopastures, implanted pastures and soybean agriculture (Fig. 3). Silvopastures represented an increase of c. $50 \text{ kg ha}^{-1} \text{ year}^{-1}$ from natural grasslands and c. $100 \text{ kg ha}^{-1} \text{ yr}^{-1}$ from *puestos*; and another increase of c. $50 \text{ kg ha}^{-1} \text{ yr}^{-1}$ occurred in the transition from silvopastures to implanted pastures. The last transition, from implanted pastures to soybean crops (assuming is used to feed pork) was much steeper (c. $200 \text{ c. } 50 \text{ kg ha}^{-1} \text{ yr}^{-1}$). Given the high variability in the yields reported for implanted pastures, the highest yields of this land use were equivalent to the average soybean yields. The meat productivity based on soybean depends on the animal species considered. If instead of pork, soybean is used for cattle feed meat production ends up with values quite similar to the implanted pastures productivity ($222 \text{ kg ha}^{-1} \text{ yr}^{-1}$); whereas if is used for chicken feeds is much more efficient ($1113 \text{ kg ha}^{-1} \text{ yr}^{-1}$, Fig. S1 Supporting information).

The GLM simpler model considering meat production as the dependent variable and land uses as a factor did not present homogeneity of variance, thus we included the heteroscedasticity into the model, which resulted in a model significantly better according to the Likelihood ratio test ($p < 0.01$). Land uses explained half of the variation of the meat production data ($r^2 = 0.51$, $F = 234.9$, $AIC = 2106$, $-\text{LogLik} = -1043$). The model that included precipitations data as a covariable, to account for environmental effects, was not significantly better based on the Likelihood ratio test ($p = 0.19$). With the exception of silvopastures and grasslands, all the other categories differed significantly according to the LSD test ($p < 0.05$, Fig. 3).

3.2. Land use gradients based on birds composition

We considered a total of 165 bird's species within the six land use/cover categories of the study area. The two-dimension NMDS ordination based on species composition had a total stress of 15.7 (less than 20 is considerable acceptable). Axes one and two of the NMDS ordination explained 23 and 45% of the variation of birds species frequency respectively ($p = 0.02$ in both cases; Fig. 4a and b).

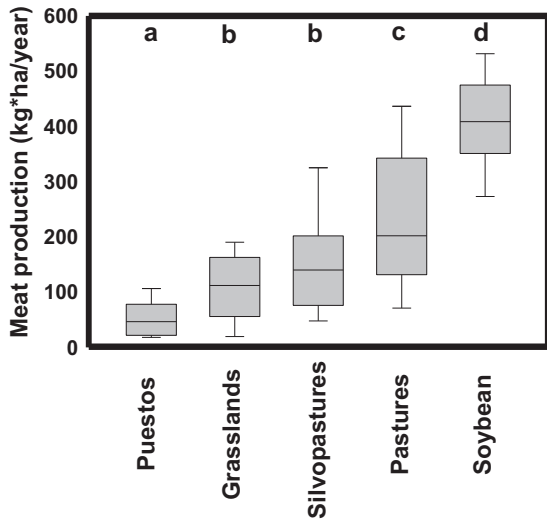


Fig. 3. Boxplot of estimated meat production for the main land uses of the dry Chaco. Mean values are marked inside the boxplots, errors bars indicates the 90th and 10th percentiles. Letters indicates homogenous groups based on LSD test.

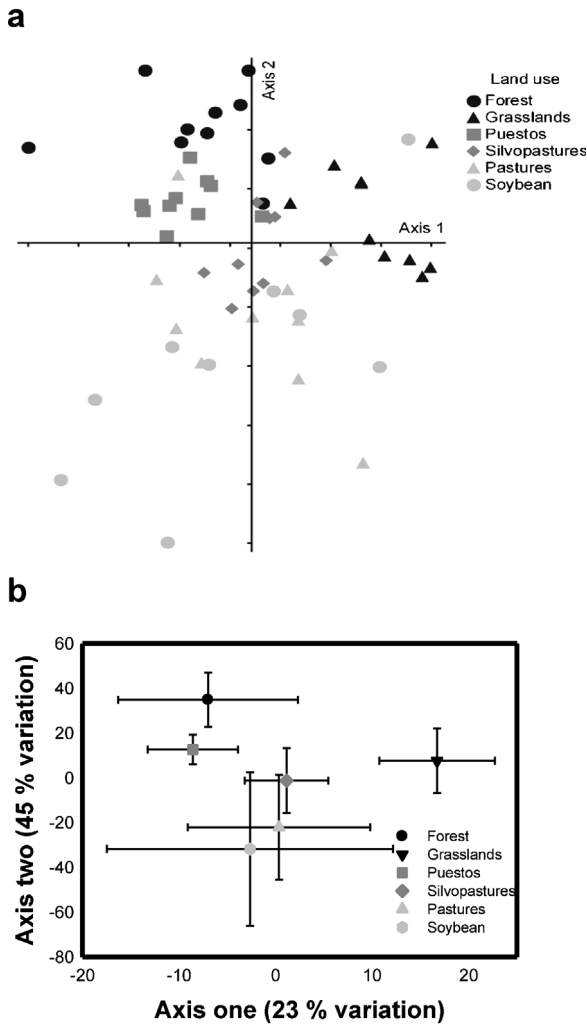


Fig. 4. NMDS ordination based on bird's relative frequency indicating the relationship between land uses (a) centroids of all the considered sites (b) each centroid represent the mean value of all the centroids of each land use, bars indicates the standard deviation of the scores for each axes.

Forest and Grasslands sites differed significantly in axis 1 scores (Mann *U* Whitney, $z = -3.74$, $p < 0.01$). The average scores of the different land uses on axis 2 were negatively and strongly correlated with productivity ($r = -0.86$, $r^2 = 0.74$, $p = 0.03$, Fig. 4). Based on these patterns, we can define two main land use intensification gradients, respectively starting from protected forest and natural grasslands: (1) the “Forest gradient”: natural forest, extensive livestock (*puestos*), silvopastures, implanted pastures and soybean crops; and (2) the “grasslands gradient”: natural grasslands, silvopastures, implanted pastures and soybean crops. In this scheme, NMDS axis two can be interpreted as a gradient of land use intensification, with natural land cover categories in the positive values (in turn separated in their origin between grasslands and forests by axis 1) and intensive production systems in the negative values.

Environmental variables were correlated with the NMDS axes, but with r^2 values much lower than land use productivity. The scores of axis one of the NMDS were correlated to the latitude ($r = -0.34$, $p < 0.01$) and to the annual precipitations ($r = 0.29$, $p = 0.02$). The scores of axis two were not significantly correlated with the environmental variables.

3.3. Community and guilds response along different productive gradients

Avian diversity differed significantly between land uses: species richness (Kruskall–Wallis $H = 18.78$, $p < 0.01$) and Shannon's diversity (Kruskall–Wallis $H = 19.45$, $p < 0.01$). Both metrics showed the same pattern. Forest, *puestos*, silvopastures and pastures presented the highest richness and diversity values, followed by native grasslands. Soybean was the land use with the lowest richness and diversity, with values approximately 40% lower than protected forests (Table 1).

In all the analyses in relation to the productivity gradient there was a decreasing trend in the three variables analyzed (richness, density and similarity), but the shape of the trend differed (Fig. 5). Along the forest gradient the slope of species richness was almost constant along the forest–*puestos*–silvopastures portion, and decreased abruptly to pastures and soybean. Along the grassland gradient, the richness increased from grasslands to silvopastures (on average 0.2 species per ton of meat), decayed to pastures (on average -1.13 species per ton of meat), and continued decreasing to soybean (Fig. 5a and d). Species richness and diversity in the soybean fields (the less diverse land cover) was about forty percent lower than in protected forests and 30% lower than natural grasslands. Bird's density decayed monotonically along the forest gradient while in the grasslands gradient, total individuals number peaked in silvopastures, then decayed to pastures (still having more individuals than in grasslands), and sharply decayed to soybean (Fig. 5b and e). Similarity to both protected forests and natural grasslands decreased exponentially; implying relatively low similarity between the two baseline natural land covers (protected forests and natural grasslands) and the less productive managed land covers (Fig. 5c and f). Rank abundance curves showed a higher dominance of a few species on open land uses (grasslands, pastures, and soybean) when compared to woody land categories (Fig. S2, Supporting information).

At the guild level, the response along the forest gradient was diverse. The Medial trend characterized Arboreal granivores ($\Delta AICc = 14.5$), Carnivores ($\Delta AICc = 10.9$), Long flight insect hunters ($\Delta AICc = 4.1$), Scavengers ($\Delta AICc = 1.0$), Terrestrial granivores ($\Delta AICc = 7.5$), and Terrestrial and Foliage granivores insectivores ($\Delta AICc = 3.6$). Seven guilds responded as Losers along the gradient; five of them described by an exponential model: Arboreal omnivores ($\Delta AICc = 1.2$), Bark insectivores ($\Delta AICc = 1.4$), Foliage insectivores ($\Delta AICc = 1.2$), Nectarivores ($\Delta AICc = 16.9$), and Terrestrial omnivores ($\Delta AICc = 0.4$); and two as linear Losers: Short flight insect hunters ($\Delta AICc = 5.1$) and Terrestrial insectivores ($\Delta AICc = 3.6$). The guild composed by aquatic species presented no major changes along the forest gradient (Fig. 2; Table S3, Supporting information).

Supplementary Table S3 associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agee.2013.04.011>.

Along the grasslands gradient we found five guilds responding as Medial trend: Aquatic ($\Delta AICc = 4.5$), Arboreal granivores ($\Delta AICc = 5.6$), Arboreal omnivores ($\Delta AICc = 6.9$), Bark insectivores ($\Delta AICc = 2.1$), and Carnivores ($\Delta AICc = 0.5$). Three guilds responded as Losers, two of them being best described by an exponential model: Foliage insectivores ($\Delta AICc = 0.4$) and Terrestrial and foliage insectivores granivores ($\Delta AICc = 0.2$); the other Losers guild, Short flight insect hunters ($\Delta AICc = 0.8$), was best described by a linear model: six guilds presented no response along the gradient, fitting best to a constant model: Long flight insect hunters ($\Delta AICc = 0.8$), Nectarivores ($\Delta AICc = 1.1$), Scavengers ($\Delta AICc = 0.4$), Terrestrial granivores ($\Delta AICc = 2.0$), Terrestrial insectivores ($\Delta AICc = 0.6$), and Terrestrial omnivores ($\Delta AICc = 2.0$) (Fig. 2; Table S3, Supporting information).

We found similar a number of Medials guilds in the forest gradient (6) than in the grassland gradient (5), coinciding in two cases: Arboreal granivores and Carnivores. Two guilds behaved as Losers in both gradients: Foliage insectivores and Short flight insect hunters. Six guilds showed no major changes along the grasslands gradients, compared to only one guild in the forest gradient; and we found no Winner guilds along the forest and grasslands gradients.

4. Discussion

The need to increase global food production and at the same time preserve biodiversity and ecosystem services has promoted

Table 1

Mean values of bird community richness, Shannon's diversity, total individuals frequency, and percentage of similarity to forest and grasslands based on Bray–Curtis dissimilarity index.

	Richness (S)	Shannon (H)	Individuals	% Similitude to forest	% Similitude to grasslands
Forest	37.4	3.379	515.35	100	39
Grasslands	29.4	3.136	353.10	39	100
Puestos	38.3	3.404	490.05	73	46
Silvopastures	38.8	3.443	462.55	56	56
Pastures	33.8	3.268	410.85	39	47
Soybean	21.4	2.687	223.89	31	37

research aiming to simultaneously assess this trade-off in different regions of the world (Tscharrntke et al., 2012). These studies have focused on forested ecosystems and assumed a relatively simple gradient from one baseline “natural” habitat type (typically mature forest) to an intensive productive system of the region (e.g. Aratrakorn et al., 2006; Phalam et al., 2011; Dorrough et al., 2007; Clough et al., 2011). Research aiming to balance production and conservation is much needed in tropical and subtropical dry forest ecosystems, which are among the most threatened biomes (Hoekstra et al., 2005; Grau et al., 2008; Portillo-Quintero and Sánchez-Azofeifa, 2010) because of past and current agriculture expansion (Clark et al., 2010; Aide et al., 2012). However, this biome is often characterized by at least two structurally different land cover types (forests and grasslands) which differ both in their potential for meat production (the typical goal of land use in this biome) and in their habitat quality for wildlife. The Gran Chaco is a typical example of this biome with forest covering most of the region but grasslands also being an important component of present-day (Cardozo et al., 2011, Tálamo et al., 2012) and, more so, of pre-European landscapes (Morello and Saravia Toledo, 1959). Our study described avian community differences between forest and grasslands (Fig. 4), as well as their relationship with other land uses; providing basis for evaluating the production/conservation trade-offs along the main land use gradients.

Land uses differ by a factor of eight on their average per-hectare meat productivity (research Objective 1; Fig. 3). Avian communities can be ordered along two main land use intensity gradients from protected forests and from native grasslands, to intensive land uses (Fig. 4). The percent of variance in avian composition explained by land uses (75% of the most important NMDS axis) was much higher than that of geographical environmental variables (c. 11.5% of the second most important axis, research Objective 2), despite the fact that we covered a considerable range of latitude (around 400 km) and rainfall variation (300 mm of annual rainfall). Along the forest gradient we found minor effects of both the latitude and

precipitation (research question 2). The abundance of most birds guilds decayed exponentially or linearly along the “forest gradient”, which would suggest a LSP land use strategy could be more appropriate; while along the “grassland gradient” guilds abundance peaked at intermediate levels of production or remain constant (without major changes), potentially favoring a LSH approach. In both cases, however, similarity to natural reference decayed exponentially (research question 3), suggesting that some components of biodiversity are only well protected in relatively intact environments, which would be more easily maintained in a LSP land use strategy. The heterogeneity captured by the two gradients combine the effects of land use intensification with the background differences between woody and open habitats; which clearly resulted in significant differences in habitat quality for bird communities.

Soybean crops are the most productive system. When soybean is computed as meat production using its most common use (pork feed), it doubles the yield of the most productive livestock systems and multiplies by a factor of eight the meat yield of the extensive *puestos* livestock systems that dominate the region. Per-hectare yields are a key variable to define land use spatial optimization, and our results coincide with Grau et al. (2008) in emphasizing that soybean may play a key role to meet targets of agriculture production with a comparatively low area (i.e. favoring a LSP strategy). It is also the less diverse land cover type in terms of birds composition, with approximately half the species richness of those of extensive livestock systems, and a similar degree of dissimilarity to baseline natural land covers. To further assess the trade-offs involved in a conservation strategy including intensive agriculture, research should assess other impacts of soybean and other crops in the area (e.g. maize, beans, sorghum), such as fertilizers and pesticides contamination (e.g. Fearnside, 2001). The main drivers of deforestation in the Chaco has been related to global factors (technological development and international prices, Grau et al., 2005), nevertheless unsuitable areas for agriculture (due to soils or climate) could further favor a land sparing strategy because the cost

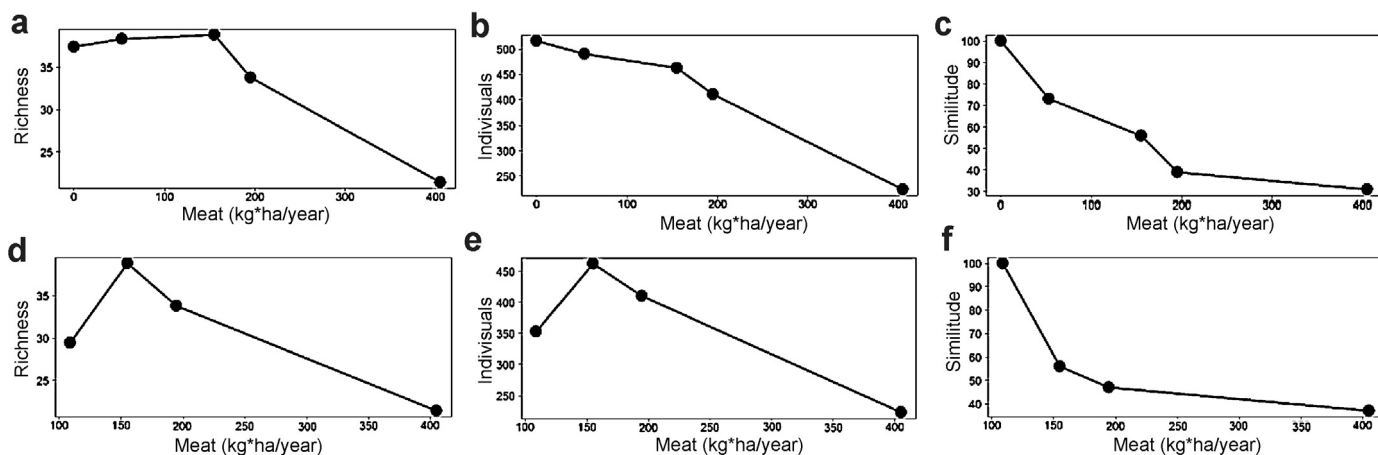


Fig. 5. Descriptors of bird's community parameters along meat productive gradients of forest (upper row) and grassland (lower row). Richness (a, d), individuals frequency (b, e) and similarity (c, f).

of conserving marginal areas not suitable for agriculture would be lower; being those land more easily destined to conservation. The only case where this synergistic response between environmental heterogeneity and birds conservation would not apply, is if the suboptimal areas to agriculture were also not preferred by birds communities (specially forest communities). To test that idea a comparison between forest quality and heterogeneity and birds communities would be necessary. In summary, our results suggest that for the forest gradient (which would be representative of the larger area of the dry Chaco) land sparing appear to be the best suited strategy to conserve bird's communities. This synergistic response between environmental heterogeneity and bird's conservation could not occur if the marginal areas to agriculture were also suboptimal to forest bird's communities. The advantages of a LSP strategy are partially resulting from the high efficiency of pork to convert soybean into meat. This is representative of the current real use of soybean, and it may even be considered an underestimation since part of the soybean production is also used for chicken feed, which is between two and three times more efficient than pork. In contrast, if soybean were used to feed cattle, the lower conversion efficiency may imply that a LSH strategy could be comparatively more valuable to preserve biodiversity at certain production targets (Fig. S1, Supporting information).

Avian diversity of silvopastures and implanted pastured were analyzed by [Mastrangelo and Gavin \(2012\)](#), who based on the relatively high species diversity in silvopastures with intermediate levels of production, concluded that this type of LSH system was the optimal strategy when only livestock systems (i.e. excluding soybean) were considered. Consistently, we also found relatively high diversity in silvopastures, providing habitat for some forest and open habitat species. However along the "forest gradient" we found only 56% of similarity between silvopastures and protected forests, and many avian guilds (Arboreal omnivores, Bark insectivores, Nectarivores, Foliage insectivores and Terrestrial omnivores) decreased exponentially along this gradient, showing low abundance in the silvopastures systems. In consequence, both species and functional guilds with low abundance at intermediate levels of production would benefit from a LSP strategy. Others guilds, such as Terrestrial foliage granivores, omnivores (composed mostly by *Emberizidae* species characterized by seed consumption), Terrestrial granivores (pigeons and doves), Carnivores and Scavengers, were very common in pastures and silvopastures; being potentially favored by a LSH strategy. Since it is likely that silvopastures systems will expand in the region in the coming decades, further research to investigate its consequences for biodiversity is a main priority ([Fumagalli, 2003](#); [Rossi, 2010](#); [Kuntz et al., 2012](#)). Along the same lines, the high variation in yield within the most productive livestock systems reflects a diversity of management practices at the local scale that should be further explored in relation to biodiversity conservation.

Protected forests and the *puestos* system of extensive livestock management showed 73% of avian composition similarity (Fig. 5). This is very important since most of the area of the dry Chaco is occupied by *puestos*. The relatively high similarity in terms of avifauna could be associated with various causes: the long history of use of Chaco closely associated with the installation, development and decay of the *puestos* systems ([Morello and Saravia Toledo, 1959](#); [Bucher and Huszar, 1999](#)); the effect of the *puestos* on vegetation is degradative and progressive so the changes in forest structure and physiognomy are gradual, except for abrupt changes within the 250–500 m around the *puestos*, were many avian guilds increases their abundances in response to water and food availability ([Macchi and Grau, 2012](#)); many protected areas have some cows and goats, or had histories of human use prior to its creation. Some avian guilds decreased in abundance between protected forest and the *puestos*: Arboreal omnivores (median size birds many of them being

fruit consumers at some level); Bark insectivores (woodpeckers and woodcreepers), Foliage insectivores (small size species of middle strata), Nectarivores (hummingbirds), and Terrestrial omnivores (big size species frequently hunted by the *puestos* holders; Table S2, Supporting information). Silvopastures and the *puestos* fall into the yellow zone of the national forest law; which allows productive practices while keeping some forest cover. While the *puestos* are closer to forest in terms of avian diversity and patterns of similarity, silvopastures were approximately three times more productive, suggesting a conflict for land optimization in the yellow zone of the national categorization.

[Green et al. \(2005\)](#) related the shape of the response of species density with the conservation strategies that would maximize the production/conservation trade-offs. Along the productive gradients, species whose density decays abruptly along the gradient requires of unaltered habitat (exponential Losers species), would be favored by the land sparing strategies; while species that could maintain their abundance at intermediate (saturation Losers and Medial species) levels of the gradients will support the land sharing perspective. In this study, at the guild level, we found both types of response, being the proportion of this response different along the two considered gradients. In the case of the forest gradient the most common guild response (7/14) were exponential and linear Losers, which would favor LSP. In contrast, along the grassland gradient most guilds responded as Medials, thus potentially favoring LSH. However many of the Medials guilds in the grasslands gradient differ in species composition with respect to natural grasslands; indicating the differences between conserving species or groups by their richness and density, or conserving habitat-specific species as those found in natural grasslands. Spatially explicit models will be needed to integrate these results; but in order to do so; we need to acknowledge the spatial complexity of the Chaco landscape, which was in part addressed in objective 2. In addition, evaluating the response of other types of organisms and ecosystems services could be helpful to fully assess the impacts of these highly productive systems.

Many authors hypothesized that the dry Chaco original physiognomy was a mosaic of woodlands and open savannas, which experienced substantial woody encroachment as a consequence of overgrazing during the past century (e.g. [Morello and Saravia Toledo, 1959](#); [Bucher and Huszar, 1999](#); [Adámoli et al., 1990](#)). Grasslands may have arisen either by responding to ancient river courses that changed soil characteristics or due to human intensive fire management related to hunting ([Tálamo et al., 2012](#)). Our results did support the importance of native grasslands as a habitat for a distinct avifauna, but we found little similarity between bird's assemblages of natural grasslands and implanted pastures. Based on birds composition (Axis 2, Fig. 3), natural grasslands seems to hold a unique composition of birds species that separate them from other land uses, indicating its high conservation value. Both the national territorial ordination law and global policies such as REDD+ are forest-oriented conservation initiatives. Our results emphasize that they are clearly neglecting the high conservation value of natural grasslands jeopardizing their future even inside protected areas, where fire-exclusion practices are leading to woody encroachment.

From a land planning perspective intensive uses such as soybean and implanted pastures compete in the green zone of the national territorial ordination. Considering that both systems are quite different in terms of avian composition to forest and natural grasslands; and that soybean doubles the yielding of implanted pastures; soybean would be a more efficient use in the production/conservation balance. However, the high variability in planted pastures yields indicates that specific management of these systems may also contribute to meeting production targets. Based on yields patterns and avian diversity silvopastures systems are

a better option than implanted pastures, however these two systems does not compete in the space due to de national ordination plan. Silvopastures do compete with the *puestos* systems in the low intensity manage zone; while silvopastures outweigh the *puestos* in terms of yields, their impact on forest avian diversity is severe.

The response of biodiversity to LULC varies among taxonomic groups, being generally described by monotonic decay or decay after a unimodal response land use intensity gradients (Butsic et al., 2012). Our results coincided with both of these trends depending of the considered gradient. Along the forest gradient bird's richness remained high in the tree covered land uses (forest/*puestos*/silvopastures), and then decayed a little trough pastures and sharply to soybean (Fig. 5). The total of number of individuals registered decreased monotonically along the forest gradient, showing overall larger birds density in unaltered habitats. The comparisons of these results based on compositional similarity response to forests, were described by an exponential curve (Fig. 5c); involving significant compositional changes along these gradients, and potentially favoring LSP. Along the grasslands gradient we found an unimodal response of the richness and density of birds (Fig. 5d, e). Pastures and soybean fields were characterized by many generalist species, commonly associated with human-disturbed conditions (e.g. cowbirds and doves). Avian composition of natural grasslands was very different from silvopastures, pastures and soybean (Fig. 5f); which would also potentially favor a LSP scheme in which natural grasslands and their particular biota are specifically protected. The effects of livestock on natural grasslands and their fauna are poorly understood for the dry Chaco. Grasslands were characterized by combination of typical open habitat bird species (e.g. *Aimophila strigiceps*, *Melanopareia maxilliani*, *Saltatricula multicolor*) and species that also occur in forest (e.g. *Asthenes baeri*, *Crypturellus tataupa*, *Thamnophilus caerulescens*, *Poospiza melanoleuca*, *Poliophtila dumicola*, *Stigmatura budytoides*). Instead, pastures presented a species composition more similar to crops, with many common species such as *Zenaida auriculata*, *Myiopsitta monachus*, *Columbina picui*, *Patagioenas maculosa*, *Pitangus sulphuratus*, *Molothrus bonariensis*, *Caraca plancus*, *Coragyps atratus*, *Vanellus chilensis*, *Thraupis bonariensis*, and *Machetornis rixosa*. In part, this pattern could be explained by landscape configuration: while natural grasslands are relatively small and frequently surrounded by forest; planted pastures and soybean fields tend to occur in close proximity and in extensively deforested patches (field observations).

In the evaluation of guild patterns, along the forest gradient most Losers guilds presented an abrupt decay, indicating their dependency on undisturbed forest. This includes Bark insectivores and Foliage insectivore which could require of well structured forest, with trees and shrubs holding for food resources (Lopez de Casenave et al., 1998; Macchi and Grau, 2012). Terrestrial omnivores subject to hunting (Tinamidae, Cariamidae and Craciidae) were also dependent of forest. Consistently with previous studies, Long flight insect hunters were associated to more open habitats (Lopez de Casenave et al., 1998; Macchi and Grau, 2012), and were more common in pastures than in soybean fields, possibly related to resource declines resulting from the application of herbicides and pesticides (Fearnside, 2001). Carnivores and Scavengers species clearly prefer open habitats were they find better access to animal preys; silvopastures, where they combine visibility, resources availability, and perches appear as the ideal habitat (field observations). Terrestrial foliage granivores omnivores composed mostly by Emberizidea species (characterized by seed consumption) were very common in pastures and silvopastures. We found a similar pattern in Terrestrial granivores (pigeons and doves), which include several of the most abundant species of the region, causing several problems as agriculture pests and disease vectors (Bruggers et al., 1998). In the case of the grassland gradient several guilds

have no discernible trend along the open habitat gradient, while other guilds were more abundant in managed pastures (Table S2, Supporting information).

This study provides empirical evidence of the effects of the main land use gradients on avian diversity of dry Chaco. The large increase in yields represented by soybean crops, and decays in many guilds densities in intermediate productive systems, resulting in low similarity with mature forests; suggests that a LSP strategy, including intensive agriculture and well-protected forests and native grasslands could best balance nature conservation and food production; particularly in the case of forest species. The high biodiversity associated to native grasslands indicate that forest-centered conservation strategies are insufficient, and land use planning should specifically include grasslands as conservation targets. National territorial ordination laws, different land use preferences among different social actors, and differences between woody and grasslands habitats imply social and biophysical constraints that are not captured by the single-gradient forest-oriented conservation paradigms and the current LSP-LSH dichotomy. To optimize land use considering these constraints, we need spatially explicit models than can be fed with the biodiversity and agriculture production data produced in this study.

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