



Impacts of agricultural intensification on avian richness at multiple scales in Dry Chaco forests



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ABSTRACT

Agricultural expansion and intensification is driving rapid landscape modification in the South American Gran Chaco, affecting biodiversity at multiple spatial scales. Research on biodiversity change in modified landscapes has focused mainly on remnant habitat patches. However, the habitat quality of the matrix is increasingly recognized as a key element for planning conservation in agricultural landscapes. We employed a multi-model selection approach to test 13 hypotheses about the influence of spatial scales and structural attributes on the richness of bird assemblages and forest specialist species within matrix types at the Argentine Dry Chaco. We selected 27 cattle ranches where six structural attributes of vegetation operating at different spatial scales (plot, edge and landscape) varied independently across a matrix intensification gradient in the agricultural frontier. We found that structural attributes operating at the plot, edge and landscape scale have significant influence on overall richness, with plot-scale attributes being more important than edge and landscape-scale attributes in driving bird occurrence in the grazing matrix. Factors operating at the plot scale had the largest influence on the richness of forest specialist species in the matrix. These results suggest that planning for the long-term conservation of Dry Chaco forests avifauna should pay attention to the effects of local agricultural management. Where further cattle production intensification cannot be avoided, implementation of highly selective clearing methods can mitigate the degradation of habitat quality for birds. Where cattle production intensification has already occurred, native tree plantings on cleared areas can restore significant bird diversity.

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1. Introduction

The need for conservation planning in agricultural landscapes has never been greater. Today, more than two-thirds of the ice-free global terrestrial surface is used for agriculture (Ellis and Ramankutty, 2007). Most of the recent expansion and intensification of agriculture has occurred in subtropical and tropical regions of developing countries (Rudel et al., 2009). Notably, the expansion of soybean cropping and intensification of cattle ranching in the South American Gran Chaco has driven the highest rates of tropical forest loss of the 21st century globally (Hansen et al., 2013). These land-use changes modify biodiversity through processes at

multiple spatial scales, from landscape fragmentation and the formation of abrupt edges at the patch-matrix interface, to the degradation of vegetation within the matrix. Effective conservation planning in this threatened and understudied biome requires a better understanding of the relative importance of spatial scales in driving biodiversity patterns.

Modified landscapes are typically represented as mosaics of patches and corridors of native vegetation within a matrix dominated by human land-use, e.g. agriculture. As a result of this binary view, biodiversity in modified landscapes is usually measured within habitat patches and changes in biodiversity levels explained with regard to structural attributes operating at the patch scale (Fischer and Lindenmayer, 2007). However, patch-based studies may be providing an incomplete representation of biodiversity change in modified landscapes for two reasons. First, several matrix types were shown to retain biodiversity levels comparable to habitat patches (Perfecto and Vandermeer, 2010). Second, processes operating at spatial scales smaller (i.e. plot) and larger (i.e.

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landscape) than the habitat patch were shown to exert significant influence on biodiversity within patches (Cushman and McGarigal, 2004; Banks-Leite et al., 2013). We address these shortcomings by asking how structural attributes operating at multiple spatial scales influence bird species richness within matrix types found in agricultural frontier landscapes of the Argentine Dry Chaco.

Species responses to habitat modification vary according to their life history traits as these determine at what scale individuals perceive, select and use available conditions and resources. Knowledge about these differential responses is highly relevant for conservation planning for two reasons. First, changes in life history traits at the community level modify ecosystem functioning, which may have cascading effects on ecosystem services and human well-being (Díaz et al., 2011). Second, species with life history traits that confer habitat and/or diet specialization are usually those with greater sensitivity to habitat modification and therefore of higher conservation concern. In a scenario of shrinking Dry Chaco forests, the survival of forest specialist bird species largely depends on their ability to find suitable habitat in the agricultural matrix. Here we aim to answer whether the richness of forest specialist species within matrix types is affected differentially by structural attributes operating at different spatial scales, compared to the whole bird assemblage.

To answer these two questions, we will test hypotheses that explain species richness in matrix habitats by focusing on structural attributes operating either at the landscape scale (i.e. patches and the surrounding matrix), edge scale (i.e. patch-matrix interface) or plot scale (i.e. within the matrix). Among hypotheses focusing on landscape factors, the “dispersal” hypothesis proposes that species occurrence in the matrix is a function of the distance to fragments and the extent of suitable habitat in the landscape (i.e. proximity to and size of source populations, respectively, Tscharntke et al., 2012). In turn, Fahrig (2013) proposes an explanation independent of fragment size and isolation, in which species occurrence in the matrix depends on the extent of suitable habitat at the local and landscape scale (“habitat amount” hypothesis).

In another set of studies, the suitability of the matrix as bird habitat depends on the distance to a structurally complex vegetation edge (“edge effects” hypothesis) or just on how similar is the matrix and patch vegetation at the nearest edge (“edge contrast” hypothesis). The latter asserts that the more similar the vegetation is across the nearest edge, the more likely it will be to find forest specialist species in the matrix (Zurita et al., 2012). This effect occurs because species encounter suitable conditions to disperse, available resources and/or a favorable abiotic environment in the matrix (Driscoll et al., 2013). However, this effect is predicted to change with distance from the edge to the interior of the matrix as conditions, resources and the abiotic environment may become less suitable as species permeate into the matrix (“proximity to edge” hypotheses).

Finally, the intensity of disturbances caused by agricultural management at the plot scale is receiving increasing attention as a factor influencing species retention in the matrix (Kennedy et al., 2010). Managing the land for agriculture often involves the simplification of the structure of native vegetation to favor the growth of crops and pastures. Hence, agricultural management practices increase the intensity of disturbances (e.g. vegetation clearing, plant regrowth suppression) and affect the suitability of the matrix for native species. Here we found relatively high support for the “disturbance” hypothesis, indicating that processes operating within the matrix (i.e. plot scale) have a strong influence on bird species occurrence in matrix types of Dry Chaco agricultural frontier landscapes. This effect was more pronounced for forest specialist species, suggesting that planning for the long-term conservation of Dry Chaco forests avifauna should pay attention to the effects of local agricultural management.

2. Methods

2.1. Study site

The study area corresponds to the upper portion of the Bermejo–Pilcomayo Interfluve (Salta province, Argentina), a tract of dryland of ca. 2 Mha between the Pilcomayo and Bermejo rivers (Fig. 1). The Bermejo–Pilcomayo Interfluve is delimited to the west by the eastern foot of the Andes range (elevation 500–380 m, annual rainfall 1000–800 mm) and extends to the east over the Dry Chaco plains (elevation 380–240 m, annual rainfall 800–500 mm). It is covered by xerophytic semi-deciduous forests dominated by red quebracho (*Schinopsis quebracho-colorado*) and white quebracho (*Aspidosperma quebracho-blanco*) and to a lesser degree by palo blanco (*Calycophyllum multiflorum*) and palo amarillo (*Phyllostylon rhamnoides*) in humid areas, and by palo santo (*Bulnesia sarmientoi*) and *Prosopis* spp. in drier areas. Deforestation from 1977 to 2008 has produced more than 1.5 million ha of cleared areas in Salta province (26% of its area) and 116,200 ha in the Bermejo–Pilcomayo Interfluve (Paruelo et al., 2011). In the Argentine Chaco, annual deforestation rates for the period 2002–2008 ranged between 1.5 and 2.5%, surpassing Latin America (0.51%) and global deforestation rates (0.2%) (Seghezzo et al., 2011).

2.2. Matrix gradient and structural attributes

A matrix intensification gradient was identified in the study area comprising four types of cattle ranching systems of increasing land-use intensity: very-low (VLIS), low (LISS), intermediate (IISS) and high (HIPS). Twenty-seven cattle ranches were selected and six sampling points were located within the grazing matrix in each cattle ranch (see Section 2.3). Six structural attributes were assessed in each of the 162 sampling points (Fig. 2). Each attribute varied independently across the matrix intensification gradient due to differences among cattle production systems in: (i) type of vegetation clearing method used to increase forage productivity; (ii) location within the agricultural frontier, and (iii) size of grazing plots. Two of the structural attributes influenced habitat quality for birds at the plot scale (i.e. plot tree cover and plot vegetation complexity), two of them operated at the edge scale (i.e. distance to edge and edge vegetation complexity) and the remaining two captured landscape-scale effects (i.e. distance to forest and landscape forest cover). The definition and assessment of the six structural attributes was as follows:

- *Plot tree cover (PTC)*: land area covered by the arboreal strata in the grazing matrix, expressed as percentage of the sampling point area (0.2 ha). Tree cover at each sampling point was assessed via ocular estimation using a vertical tube. PTC was expressed as the quotient between zenith observations intercepted by the arboreal strata and total observations (25 per sampling point) multiplied by 100.
- *Plot vegetation complexity (PVC)*: number of vertical strata of vegetation at the grazing matrix. Six strata were identified (bare soil [BS], herbaceous [H], shrub [SH, 1–3 m], lower arboreal [LA, 3–5 m], middle arboreal [MA, 5–10 m] and higher arboreal [HA, >10 m]), and seven levels of plot complexity were defined based on combinations of vegetation strata (Table 1).
- *Edge vegetation complexity (EVC)*: number of vertical strata of vegetation at the edge of the nearest forest patch (definition of strata and complexity level as for PVC).
- *Distance to edge (DE)*: linear distance between the center of the grazing matrix (sampling point) and the nearest area where the vertical complexity of vegetation increases or decreases by 2 or

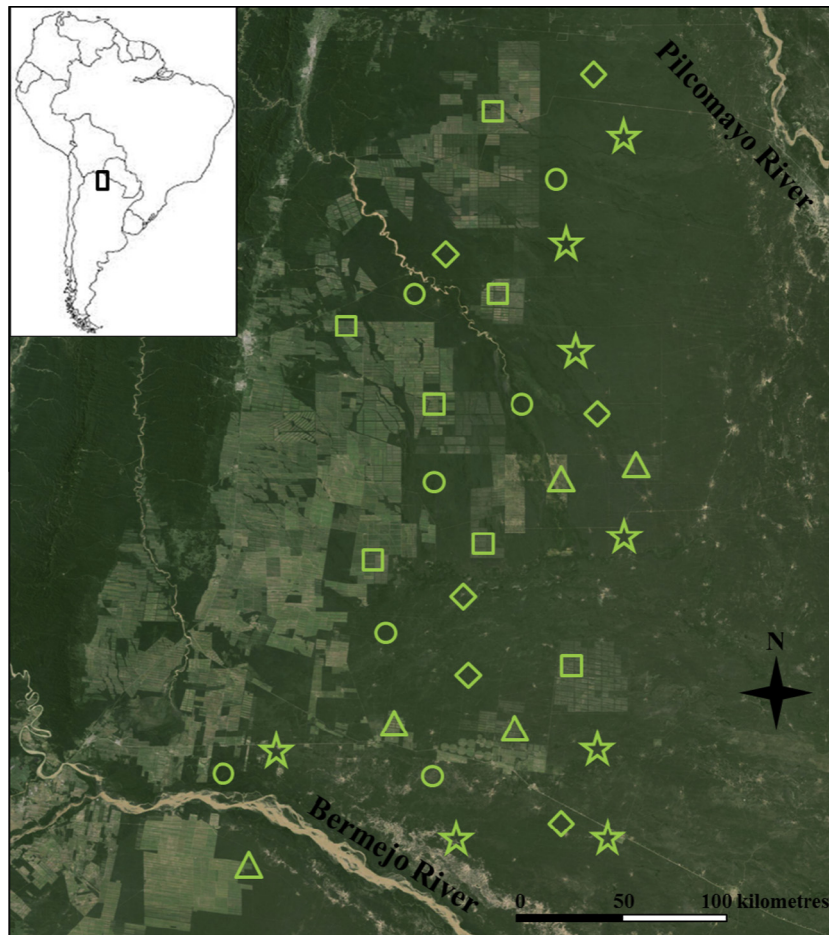


Fig. 1. Image of the Bermejo–Pilcomayo Interfluvium showing the distribution of the 33 sampling sites across the agricultural frontier (diamonds, forest fragments; stars, very low-intensity systems; circles, low-intensity systems; triangles, intermediate-intensity systems; squares, high-intensity systems). Image from 4/9/2013 downloaded from Google Earth. Inset: location of the Bermejo–Pilcomayo Interfluvium within South America.

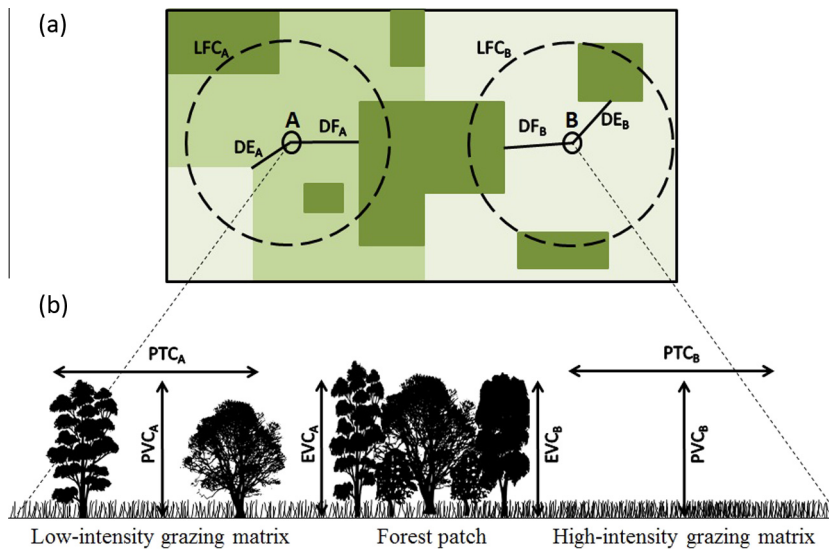


Fig. 2. Schematic representation of structural attributes measured at sampling points. (a) Aerial view of a typical landscape configuration at the study area, with forest patches (dark green) scattered along the grazing matrix. A and B are two sampling points (0.2 ha), one in a low-intensity grazing matrix (A) and other in a high-intensity grazing matrix (B). Note that distance to edge in point A is related to an area where vegetation complexity is lower, whereas in point B is related to an area where it is higher. (b) Cross sectional view of the vegetation between sampling points A and B. Meaning of abbreviations: PTC: plot tree cover; PVC: plot vegetation complexity; EVC: edge vegetation complexity; DE: distance to edge; DF: distance to forest; LFC: landscape forest cover. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
Ordinal categories used to describe vertical complexity of the vegetation.

Level of vegetation complexity	Combinations of vertical strata of vegetation ^a			
1	H	BS-SH		
2	H-SH	BS-LA		
3	H-LA	BS-MA		
4	H-MA	SH-LA	BS-HA	
5	H-HA	SH-MA	LA-MA	
6	H-MA-HA	SH-LA-MA	MA-HA	SH-LA-HA
7	LA-MA-HA	SH-LA-MA-HA		

^a Meaning of abbreviations for vegetation strata = BS: bare soil, H: pasture/herbaceous strata; SH: shrub strata; LA: lower arboreal strata; MA: middle arboreal strata; HA: higher arboreal strata.

more levels (Table 1). Distance to edge was measured in the field using a range meter.

- *Distance to forest (DF)*: linear distance between the center of the grazing matrix (sampling point) and the perimeter of the nearest forest patch. Forest patches were defined as fragments with trees taller than 3 m, tree cover greater than 50%, and an area larger than 100 ha. Forest patches were identified based on field observations and analysis of satellite images (Landsat TM form September 2009). Distance to forest was measured in ArcGIS (ESRI).
- *Landscape forest cover (LFC)*: land area covered by forests that fitted the above definition over a circular buffer area of 3000 m radius centered in the sampling point. LFC was expressed in a 5-point scale, with each point representing a quantile of percentage cover (e.g. 1 for 0–20%, 2 for 20–40% and so on). A 3000 m buffer area was used to measure LFC as recommended in previous studies (Mitchell et al., 2001; Deconchat et al., 2009).

In very-low intensity systems, PTC and PVC were high because native vegetation in the grazing matrix was not cleared (Table 2). These systems were located on pre-frontier areas with relatively small agricultural area (Fig. 1), and therefore had large LFC, comparatively low DF and similar PVC and EVC (low edge contrast). Cattle grazing at very low intensity over large areas created an extensive matrix of homogeneous vegetation and thus DE was very large.

In the grazing matrix of low-intensity systems, the forest understory was selectively cleared to stimulate the regeneration of native grasses, leaving a relatively high PTC and intermediate PVC and EVC (low edge contrast). DF and LFC were intermediate within the gradient as these systems were mostly located in expansion areas, i.e. where agriculture actively expands into native forests. Cattle grazed over relatively large grazing plots and therefore DE was large.

Table 2
Properties and attributes of matrix types along the matrix intensification gradient.

Properties and attributes of the matrix	Land-use intensity in the grazing matrix			
	Very-low	Low	Intermediate	High
Type of clearing	None	Selective	Selective	Total
Cattle yields (kg.ha ⁻¹ .year ⁻¹ ; range)	4–12	14–30	100–140	115–180
Frontier location	Pre-frontier	Expansion	Expansion	Consolidating
Management plot size (ha; range)	600 – 2200	200 – 700	80 – 260	100 – 330
Plot vegetation complexity (median)	6	5	4	1
Plot tree cover (%; mean ± SD)	81 ± 14.2	56 ± 22.5	37 ± 9.4	6 ± 5.4
Distance from center of grazing matrix to nearest edge (km; mean ± SD)	2.3 ± 0.7	0.7 ± 0.5	0.2 ± 0.2	0.5 ± 0.3
Edge vegetation complexity (median)	6	5	3	4
Distance from center of grazing matrix to perimeter of nearest forest patch (km; mean ± SD)	1.9 ± 1.1	2.3 ± 1.7	3 ± 2.1	4.4 ± 1.7
Landscape forest cover (quantile; median)	5	3	2	1

In intermediate-intensity systems, PTC and PVC were intermediate due to the selective removal of shrubs and trees to allow for the cultivation of high-yielding grasses beneath the tree canopy. Ranches developing this type of silvopastoral system were located mostly in expansion areas, where EVC, LFC and DF were intermediate. Relatively small grazing plots defined short DE in intermediate-intensity systems.

High-intensity systems consisted of intensively grazed pastures completely cleared of native woody vegetation, with very low PVC. These systems were located in areas undergoing the formation of large and continuous tracts of agricultural land (i.e. agricultural consolidation), and thus DF was large and LFC was low. Strips of degraded forests were usually left between pasture plots to act as windbreaks, so EVC was intermediate. DE was intermediate as pastures were cultivated over plots of intermediate size within the gradient.

2.3. Sampling strategy

We classified cattle ranches of the study area according to their type of cattle ranching system using cadastral data, field observations and satellite images. Then, one ranch of each type was randomly selected and each subsequent random choice was included in the sample if the closest ranch of the same type was at least 50 km apart (measured from the perimeter) to obtain a substantial coverage of the study area. The resulting sample consisted of seven high-intensity systems, five intermediate-intensity systems, seven low-intensity systems and eight very-low-intensity systems. We also sampled six forest patches within landholdings located close to selected ranches to assess the richness of forest specialist species in baseline habitats. Forest patches were larger than 100 ha and provided baseline data to ranches located at a distance of 5–50 km. We divided the matrix area of each cattle ranch and forest patch into a grid of 9 km² square cells and a sampling point was established in the center of six randomly selected cells. In this way, we avoided double counting of birds and potential correlations among sampling points as inter-point distance was at least 3000 m, which is larger than the daily dispersal range of most bird species. Between May and August 2010, we surveyed 162 sampling points once for structural attributes and bird species richness, and an additional 36 sampling points in forest patches for bird species richness only.

2.4. Bird sampling

We established a 25 m radius count point in each of the 198 sampling sites, where we counted birds once during the non-reproductive season (May–August 2010). We detected birds by sight or sound and recorded all individuals staying in, entering, or leaving the site over 20 min. We counted birds when bird activity was greatest, either 3 h after dawn or 3 h before dusk. Counts

were balanced within each type of production system for dawn and dusk sampling. We minimized imperfect detection of birds in two ways. First, we used fixed-radius point counts instead of, for example, open-radius point counts or transect counts to control for differences in detection range among sampling sites with different vegetation structure (Martin and McIntyre, 2007). Second, a single observer (M.E.M.) undertook all bird counts, which reduced detection bias associated with differences in observer performance.

2.5. Multi-model data analysis

We employed an information-theoretic approach to consider uncertainty in the choice of explanatory models. We first created a model set consisting of 13 alternative hypotheses (Table 3). Among these, there was the full model containing all predictor variables and six models representing the following hypothesis: (i) disturbance hypothesis containing factors operating at the plot scale (PTC and PVC), (ii) edge effects hypothesis containing factors exerting their influence at the edge (EVC and DE), (iii) dispersal hypothesis containing factors operating at the landscape scale (DF and LFE), (iv) edge contrast hypothesis combining plot and edge vegetation complexity, (v) habitat amount hypothesis combining forest cover at the local and landscape scale, and (vi) local effects hypothesis combining factors operating at the plot and edge scale. Finally, we also examined six models containing only one of the six predictor variables each.

We classified bird species as forest specialist (i.e. species preferring forest as their primary habitat), habitat generalist (i.e. species occurring in forest and non-forest habitats) and open habitat (i.e. species preferring grasslands and open shrubland as primary habitat). We used the overall richness and the richness of forest specialist species as response variables. We carried out multiple regression analyses on data from the 162 sampling points located in the different types of grazing matrix. We plotted all pairs of predictor and response variables (12 pairs) to explore the type of function (linear, binomial quadratic, binomial cubic) that best described their relationship. We calculated goodness of fit indices and the Akaike Information Criterion corrected for small sample sizes (AICc) for the 13 candidate models on each of the two response variables via regression analyses (26 tests) using the appropriate model basis for each case (linear or non-linear).

After that, we ranked the models according to their respective AICc values from smallest to largest and compared model

probabilities by calculating the difference in AICc between the first-ranked model and following ones (ΔAICc). All models within 2 AICc units from the first-ranked model were considered part of the best model subset. When ΔAICc for the second-ranked model was higher than 2, the first-ranked model was regarded as the best single model. Models with ΔAICc larger than 12 were interpreted as implausible models (Burnham and Anderson, 2002). The ratio between the weight of evidence carried by the best model(s) and subsequent ones indicate their degree of support (Lukacs et al., 2007).

Finally, we estimated the effects of individual predictors following the procedure described by Burnham and Anderson (2002), which consists of: (i) weighting coefficients by multiplying model coefficients and model weight, and (ii) averaging weighted model coefficients across models included in the best subset. We considered coefficients not included in a model as having a value of 0, hence, multi-model averaged coefficients shrank towards 0 and the extent of the shrinkage depended on the cumulated weight of the models without the variable (Lavoue and Droz, 2009). In addition, the explanatory power of individual factors was assessed considering the number of times an individual factor is present within the best model subset (Stephens et al., 2007). In the case of one single best model, effects were estimated from coefficients of the first-ranked model.

3. Results

3.1. Bird species richness

We recorded 119 bird species: 97 in forest fragments, 79 in very-low-intensity systems, 78 in low-intensity systems, 63 in intermediate-intensity systems, and 42 in high-intensity systems. In all types of production systems, observed richness represents more than 80% of estimated true species richness using a common estimator (i.e. Chao1). Although species richness per ranch may have been underestimated, the total species inventory of each type of production system is relatively complete.

We observed a high number and proportion of forest specialist species in production systems where land-use intensity was minimal (in forest fragments: 54 species, 56% of species observed were forest specialists), very low intensity systems (VLIS: 38 species, 49%) and low intensity systems (LISS: 33 species, 43%) (Fig. 3). In silvopastoral systems of intermediate intensity (IISS), we detected 20 forest specialist species (31%). In contrast, habitat generalist species (23 species, 45%) and species affiliated with open habitats

Table 3
Description of hypotheses tested using the multi-model selection approach.

Hypothesis	Predictor variables ^a						Meaning
	PTC	PVC	EVC	DE	DF	LFC	
Full model	1	1	1	1	1	1	Factors operating at the plot, edge and landscape determine bird species richness
Local effects	1	1	1	1	0	0	Only factors operating at the plot and edge determine bird species richness
Plot cover	1	0	0	0	0	0	Tree cover at the plot scale determines bird species richness
Habitat amount	1	0	0	0	0	1	Forest cover at the sampling point and landscape scale determines bird species richness
Disturbance	1	1	0	0	0	0	Land-use management factors operating at the plot determine bird species richness
Plot complexity	0	1	0	0	0	0	Vegetation complexity at the plot determine bird species richness
Edge contrast	0	1	1	0	0	0	Difference in vegetation structure between plot and edge determine bird species richness
Landscape cover	0	0	0	0	0	1	Forest extent at the landscape scale determines bird species richness
Dispersal	0	0	0	0	1	1	Only factors operating at the landscape scale determine bird species richness
Proximity to edge	0	0	0	1	0	0	Distance to edge determines bird species richness
Edge effects	0	0	1	1	0	0	Edge complexity and distance to edge determine bird species richness
Proximity to forest	0	0	0	0	1	0	Distance to forest determines bird species richness
Edge complexity	0	0	1	0	0	0	Vegetation complexity at the edge determines bird species richness

^a Meaning of abbreviations for predictor variables: PTC: plot tree cover; PVC: plot vegetation complexity; EVC: edge vegetation complexity; DE: distance to edge; DF: distance to forest; LFC: landscape forest cover.

(18 species, 43%) dominated avian communities on high-intensity pasture systems (HIPS).

3.2. Factors affecting richness of all species

Correlation between all pairs of the six habitat attributes was relatively low ($r < 0.5$), corroborating that structural attributes varied independently across the matrix intensity gradient. The full model containing all predictor variables explained 44% of the variance in richness of overall species. It could be regarded as the best single model because it had the lowest AICc, and Δ AICc between this and other candidate models was relatively high (4.61) (Table 4). This model was ≈ 10 times more likely to be the best fitting model than the second-ranked model (Local effects; evidence ratio = 10.03), indicating moderate support for the full model. The first (Full model) and second (Local effects) models represent the majority of evidence (99%). The remaining models can be considered implausible as their Δ AICc was larger than 12.

Regression coefficients for all predictor variables were statistically significant ($p < 0.05$; Table 5). The largest effects were those of plot vegetation complexity (standardized $\beta = 0.861$, $p < 0.001$) and plot tree cover (standardized $\beta = 0.749$, $p < 0.001$). As expected,

overall richness increased with increasing vertical complexity of the vegetation at the grazing plot, and to a lesser extent at the edge. An increase of four units in plot vegetation complexity led to a gain of five species in the avian assemblage if all other variables are held constant. Also, overall richness increased with increasing tree cover at the plot. An increase of 16% in tree cover led to a gain of one bird species if all other variables are held constant. Finally, overall richness responded positively to distance to edge and negatively to distance to forest, with an increase of 512 m in distance to edge and a decrease of 2.14 km in distance to forest associated with a gain of one bird species, all other variables being constant.

3.3. Factors affecting richness of forest specialist species

When predicting richness of forest specialist species, several options appeared as likely candidates to be the best model (i.e. Δ AICc < 3 ; Table 6). The subset of the four best-ranking models (i.e. local effects, full model, disturbance and habitat amount hypotheses) provided $\approx 99\%$ of the evidence obtained within the whole set of models tested. Any of the models in the best subset were ≈ 260 times more likely than any of the others tested to be the best-fitting model, indicating a strong support for them. Explanatory power in the subset of best models was good, with 58% to 61% of the variance explained for the richness of forest specialist species.

The model containing all structural attributes and the local effects model were the first and second best models and captured 36% and 35% of the evidence within the model subset, respectively. The third and fourth-ranked models represented the disturbance and habitat amount hypotheses and captured 17% and 10% of the evidence, respectively. Structural attributes operating at the plot scale were present in the three best-ranked models, of which plot tree cover was also present in the fourth-best model, i.e. habitat amount hypothesis. Structural attributes operating at the edge scale were present in the first and second-best models, while landscape forest extent was present in the second and fourth-best models within the best subset. Estimated effects were consistent with these results, as plot-scale factors have a significantly greater influence than edge and landscape-scale factors on the richness of forest specialist birds in matrix habitats.

Regression coefficients of plot tree cover, plot vegetation complexity and distance to edge were statistically significant ($p < 0.05$), while landscape forest cover was only marginally significant ($p < 0.1$) (Table 5). Richness of forest specialist species

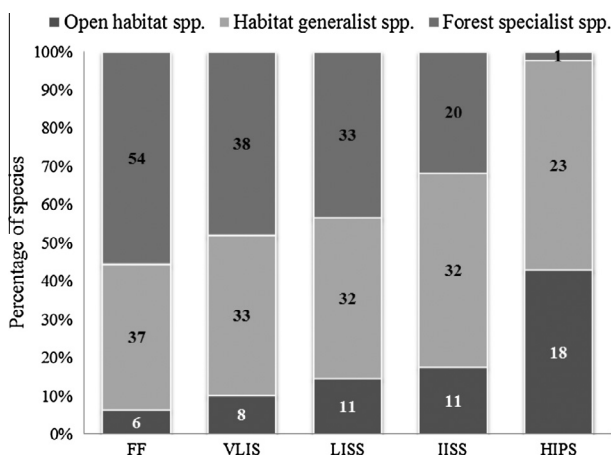


Fig. 3. Number and proportion of species within habitat preference groups detected in forest fragments (FF) and the four types of cattle production systems: very-low-intensity systems (VLIS), low-intensity silvopastoral systems (LISS), intermediate-intensity silvopastoral systems (IISS), and high-intensity pasture systems (HIPS).

Table 4

Summary statistics of the multi-model selection approach with overall richness as the response variable.

Hypothesis	Predictor variables ^a						R^2	Residual sum of squares	AICc	Δ AICc	Akaike weights
	PTC	PVC	EVC	DE	DF	LFC					
<i>All species</i>											
Full model	1	1	1	1	1	1	0.439	752.08	266.17	0	0.9071
Local effects	1	1	1	1	0	0	0.407	794.82	270.79	4.61	0.0904
Plot cover	1	0	0	0	0	0	0.349	872.44	279.59	13.41	0.0011
Habitat amount	1	0	0	0	0	1	0.354	865.95	280.47	14.29	0.0007
Disturbance	1	1	0	0	0	0	0.352	868.44	280.94	14.76	0.0005
Plot complexity	0	1	0	0	0	0	0.321	910.80	286.60	20.42	<0.0001
Edge contrast	0	1	1	0	0	0	0.311	924.44	291.13	24.95	<0.0001
Landscape cover	0	0	0	0	0	1	0.293	948.16	293.15	26.98	<0.0001
Dispersal	0	0	0	0	1	1	0.172	1109.92	320.93	54.75	<0.0001
Proximity to edge	0	0	0	1	0	0	0.082	1230.51	335.64	69.467	<0.0001
Edge effects	0	0	1	1	0	0	0.083	1230.14	337.69	71.52	<0.0001
Proximity to forest	0	0	0	0	1	0	0.054	1269.19	340.68	74.51	<0.0001
Edge complexity	0	0	1	0	0	0	0.015	1320.79	347.18	81.01	<0.0001

^a Meaning of abbreviations for predictor variables: PTC: plot tree cover; PVC: plot vegetation complexity; EVC: edge vegetation complexity; DE: distance to edge; DF: distance to forest; LFC: landscape forest cover.

Table 5

Single-model (all species) and multi-model averaged (forest specialist species) coefficients.

Predictor variable	Estimated effects (Standardized β coefficients) ^a	
	All bird species ^b	Forest-specialist bird species ^c
Plot tree cover	0.749 [*]	0.370 [†]
Plot vegetation complexity	0.861 [*]	0.314 [†]
Edge vegetation complexity	0.260 [†]	0.056
Distance to edge	0.304 [*]	0.089 [†]
Distance to forest	-0.239 [‡]	0.034
Landscape forest cover	0.215 [*]	0.123 [*]

^a Meaning of symbols for significance levels: * $p < 0.1$, † $p < 0.05$, ‡ $p < 0.01$, § $p < 0.001$.

^b Coefficients derived from the best single model.

^c Coefficients averaged from the subset of best models.

responded positively to increases in tree cover and vegetation complexity at the plot scale, with one forest species expected to be added to the assemblage for every 32% increase in tree cover and for every two units of vegetation complexity, if all other variables are held constant. In turn, the number of forest specialist species increased with increasing distance to edge, with an increase of 2 km in distance to edge leading to a gain of one forest specialist species.

4. Discussion

Ecological research is providing increasing evidence of the important role of some types of matrix in favouring biodiversity retention in agricultural landscapes, moving away from the general conception of agricultural matrices as inhospitable environments and population sinks (Prugh et al., 2008). However, most studies still focus on the effects of the matrix in mediating the persistence of species within habitat patches, implicitly considering that the only role for an agricultural matrix is to serve as a conduit for inter-patch migration and not as habitat in its own. Here we present one of the few empirical studies evaluating the factors influencing the habitat quality of several types of agricultural matrices. The evaluation is based on several structural attributes operating at different spatial scales and varying independently across a matrix intensification gradient comprising multiple land-use systems.

Birds are key players in the functioning of forest ecosystems, contributing to the supply of multiple services such as seed

dispersal, biological control, pollination and the regeneration of native plant species (Whelan et al., 2008). In the Argentine Chaco, forest clearing for pasture expansion and cattle grazing intensification modifies structural attributes of matrix vegetation at multiple scales (Mastrangelo and Gavin, 2012). Our results indicated that the occurrence of bird species in the grazing matrix was affected by structural changes occurring at the local scale (i.e. plot and edge), and to a lesser extent at the landscape scale. This suggests that Chaco bird species are particularly sensitive to local management factors driving the intensification of the grazing matrix, such as the choice of methods to clear forests (e.g. total vs. selective) and increase forage productivity (grass cultivation vs. regeneration).

Structural changes occurring at the local scale had a greater influence on forest specialist species compared to the whole avian assemblage. The variation in species richness of forest specialists was best explained by four models containing two key structural attributes operating at the plot scale: tree cover and vegetation complexity. Clough et al. (2009) also found a prominent influence of local factors in driving bird richness in Indonesian cacao agroforests, with 35% of the variation explained by a model containing tree species richness and number of tall trees as predictor variables. Our best model subset explained a comparatively higher proportion (between 58% and 61%) of the variation in the richness of forest specialist birds. This suggests that the disturbances introduced by local management on plot vegetation structure strongly influences the habitat quality of the matrix for forest specialist species.

The greater plausibility of hypotheses ascribing a larger influence to structural attributes operating within the grazing matrix is in agreement with several studies in tropical and subtropical agricultural landscapes. High tree cover and vegetation complexity in the matrix has been consistently associated with higher avian richness in the Costa Rican countryside (e.g. Hughes et al., 2002), Australian grazing lands (e.g. Manning et al., 2006) and Southeast Asian agroforests (e.g. Clough et al., 2009). For example, the reduction of shade trees in cacao agroforests from 80% to 40% is associated with the loss of most forest specialist bird species in the matrix (Steffan-Dewenter et al., 2007). Here, an increase in plot vegetation complexity from intermediate to high-intensity systems via native tree plantings can produce a gain of five forest specialist species in the matrix. Native tree plantings can also maintain or even increase cattle yields through the ecosystem services provided by trees in the grazing matrix (e.g. fertilization of pastures, shadow for cattle) (Murqueitio et al., 2011).

The potential role of native tree plantings in restoring bird diversity in the grazing matrix highlights the notion that

Table 6

Summary statistics of the multi-model selection approach with richness of forest-affiliated species as the response variable.

Hypothesis	Predictor variables ^a						R ²	Residual sum of squares	AICc	Δ AICc	Akaike weights
	PTC	PVC	EVC	DE	DF	LFC					
<i>Forest specialist species</i>											
Local effects	1	1	1	1	0	0	0.597	438.37	173.79	0	0.3639
Full model	1	1	1	1	1	1	0.607	426.95	173.89	0.09	0.3471
Disturbance	1	1	0	0	0	0	0.583	453.96	175.20	1.41	0.1797
Habitat amount	1	0	0	0	0	1	0.580	456.91	176.26	2.46	0.1059
Landscape cover	0	0	0	0	0	1	0.551	488.06	184.91	11.11	0.0014
Plot cover	1	0	0	0	0	0	0.546	493.17	186.60	12.81	0.0006
Dispersal	0	0	0	0	1	1	0.552	486.94	186.64	12.84	0.0005
Edge contrast	0	1	1	0	0	0	0.55	489.73	187.57	13.77	0.0003
Plot complexity	0	1	0	0	0	0	0.542	498.36	188.31	14.51	0.0002
Edge effects	0	0	1	1	0	0	0.318	741.11	255.10	81.30	<0.0001
Edge complexity	0	0	1	0	0	0	0.279	783.61	262.08	88.29	<0.0001
Proximity to edge	0	0	0	1	0	0	0.145	929.42	289.90	116.10	<0.0001
Proximity to forest	0	0	0	0	1	0	0.136	939.14	291.600	117.80	<0.0001

^a Meaning of abbreviations for predictor variables: PTC: plot tree cover; PVC: plot vegetation complexity; EVC: edge vegetation complexity; DE: distance to edge; DF: distance to forest; LFC: landscape forest cover.

management disturbances can be used to enhance native avifauna. Planners and managers can benefit from the strong influence of agricultural management by promoting and/or implementing the type of disturbance regimes that are known to increase bird diversity. For example, many decades of cattle grazing have reduced the structural complexity of native vegetation around domestic areas of low-intensity systems. However, [Macchi and Grau \(2012\)](#) found that the abundance of most Chaco bird guilds is high in such areas, potentially in response to the availability of additional resources (water and food sources) and the maintenance of tall trees. Similarly, [Mastrangelo and Gavin \(2012\)](#) found that silvopastoral systems maintaining tree cover above 30% provide habitat for 60–70% of the number of Chaco bird species found in nearby forest patches. This means that management disturbances in low and intermediate-intensity systems can be used to favor biodiversity retention in the grazing matrix, without needing to take land out of production.

We found hypotheses ascribing importance to processes operating at the landscape scale (e.g. “dispersal” hypothesis) and to a lesser extent to edge effects to be implausible explanations of bird occurrence in the matrix. This result supports the conclusions of a meta-analysis of 89 studies of terrestrial fauna on six continents, which found that structural attributes indicating the degree of isolation relative to source populations at the landscape scale were poor predictors of occupancy for many species in fragmented landscapes ([Prugh et al., 2008](#)). Moreover, the meta-analysis showed that local characteristics of the matrix had a strong influence on occupancy patterns across many taxa, as found here for birds. In turn, the implausibility of explanations related to edge effects can be expected when considering the regional context. The presence of abrupt edges has been a common feature in Chaco landscapes as these originally consisted of a mosaic of forests, savannah and scrubland ([Morello et al., 2005](#)). As a result, some Chaco bird species may have evolved preference for, or tolerance to, forest edges.

Overall, our findings indicate that processes that modify the structural attributes of the vegetation within the grazing matrix have a prominent role in driving the distribution of bird species in agricultural frontier landscapes of the Dry Chaco. These results have important implications for planning interventions aimed at conserving Chaco avifauna and the ecosystem services it supports. Where a significant proportion of native avifauna has already adapted to novel disturbance regimes, low-intensity systems should be maintained as these favor the occurrence of bird species in the agricultural matrix. Moreover, functional roles played by birds in this type of matrix can contribute to the stable supply of ecosystem services relevant to local ranchers. Where further cattle production intensification cannot be avoided, selective methods of forest clearing can be promoted to produce a silvopastoral matrix that provides habitat continuity for most bird species and reduces edge contrast, while significantly increasing cattle yields ([Table 2](#)). Finally, where cattle production intensification has already occurred, planting of native trees on cleared areas can encourage the restoration of significant bird diversity. Native tree planting can also increase economic returns by increasing pasture productivity in the long-term. Overall, attention to local-level land-use management and ecological restoration strategies are likely to have lasting effects on avifaunal diversity.

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