

LONG-TERM ASSOCIATION OF *TYRANNUS SAVANA* AND *STURNELLA SUPERCILIARIS* DENSITY WITH LAND COVER AND CLIMATIC VARIABLES IN AGROECOSYSTEMS OF ARGENTINA

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ABSTRACT.— Agricultural expansion and intensification resulted in important changes in the agricultural landscape of the Pampas region, Argentina. We used linear mixed models to analyze the relationship between environmental variables associated to land use/cover, productivity and climate and changes in densities of two bird species, the Fork-tailed Flycatcher (*Tyrannus savana*) and the White-browed Blackbird (*Sturnella superciliaris*). The study area in central Argentina was divided in three agroproductive sub-regions: (1) predominantly agricultural, (2) mixed agricultural–rangeland and (3) mixed agricultural–forested rangeland. Bird populations were sampled annually during 2003–2011 using point-transects along secondary roads (48 transects). Mean estimated density for Fork-tailed Flycatcher was 0.132 ind/ha, increased in the agricultural sub-region and was associated with decreasing forest cover and increasing fallow and weedy fields cover. Mean density of the White-browed Blackbird was 0.045 ind/ha, decreased in the agricultural–rangeland sub-region and increased in landscapes with more perennial pastures, fallow and weedy fields and annual pastures, avoiding sites with more forest cover. Productivity and climatic variables only showed a strong association with White-browed Blackbird density. Our results suggest that land use/cover, productivity and climatic factors are important variables when planning strategies to conserve bird population at a regional level in agroecosystems of Argentina.

KEY WORDS: *Argentina, biological monitoring, bird population trends, density, EVI, land use, rainfall, temperature.*

RESUMEN. ASOCIACIÓN A LARGO PLAZO DE LA DENSIDAD DE *TYRANNUS SAVANA* Y *STURNELLA SUPERCILIARIS* CON VARIABLES DE COBERTURA DE LA TIERRA Y CLIMÁTICAS EN AGROECOSISTEMAS DE ARGENTINA.— La expansión e intensificación agrícolas resultaron en importantes cambios en el paisaje agrícola de la Región Pampeana Argentina. Se utilizaron modelos lineales generalizados mixtos para analizar la relación entre la densidad de dos especies de aves, la Tijereta (*Tyrannus savana*) y el Pecho Colorado (*Sturnella superciliaris*), y variables ambientales asociadas a la cobertura, los usos de la tierra, la productividad vegetal y las condiciones climáticas. El área de estudio en la región central de Argentina se dividió en tres subregiones: (1) predominantemente agrícola, (2) agrícola–ganadera y (3) agrícola–ganadera bajo bosque nativo. Las aves fueron muestreadas anualmente durante 2003–2011 en 48 transectas de puntos localizadas en caminos secundarios. La densidad promedio de la Tijereta fue de 0.132 ind/ha, se incrementó significativamente en la subregión agrícola, y estuvo asociada a la disminución en la cobertura de bosque y al incremento en la proporción de cobertura de rastrojo y campo en descanso. La densidad del Pecho Colorado fue de 0.045 ind/ha, decreció en la subregión agrícola–ganadera y se incrementó en paisajes con mayor proporción de pasturas perennes, cobertura de rastrojo, campos en descanso y pasturas anuales, evitando sitios con mayor cobertura de bosque. La productividad y las variables climáticas solamente mostraron una asociación fuerte con la densidad del Pecho Colorado. Nuestros resultados sugieren que la cobertura de usos de la tierra, la productividad y los factores climáticos son importantes al planificar estrategias de conservación de aves a escala regional en los agroecosistemas de Argentina.

PALABRAS CLAVE: *Argentina, densidad, EVI, monitoreo biológico, precipitaciones, temperatura, tendencia poblacional de aves, uso de la tierra.*

The simplification of agricultural landscapes, associated with habitat loss and agricultural intensification, has been shown to reduce the availability of resources for many bird species with specific requirements (Benton et al. 2003, Vickery et al. 2009, Guerrero et al. 2012) and, consequently, the abundance of these species (Chamberlain et al. 2000, Donald et al. 2006). The decreases on bird abundance are related to local changes in vegetation cover, structure and diversity (Heikkinen et al. 2004, Filloy and Bellocq 2007). Simplification of agricultural landscapes also produces changes in temporal population dynamics of bird species (Boulinier et al. 1998, 2001).

Species may respond differently to land use and climatic factors (Firbank et al. 2008, Karsh and MacIver 2009, Concepción and Díaz 2010). Some species may be negatively affected, eliciting negative population trends, and some others may be positively affected, with resulting increases in their population abundance (Holt 2003, Both and te Marvelde 2007, Angert 2009, Both et al. 2010). However, some other species may not be affected and maintain their abundance relatively stable, at least in the short term (Siriwardena et al. 1998, Fewster et al. 2000), because they may have been able to exploit alternative food supplies or search for food over a wide area for a period of time (Chamberlain et al. 2000). In any case, bird responses are thought to be determined by life-history characteristics such as regional abundance or the tolerance range to environmental factors (climatic, topographic or biological factors; Brown and Lomolino 1998, Newbold et al. 2013, Bradshaw et al. 2014, Bregman et al. 2014). Consequently, an important challenge for biodiversity conservation is to determine species responses to annual variations in land use and climatic conditions, in order to improve assessments of impacts and risks and thus develop appropriate mitigation strategies. Interannual variations in climate is another factor known to influence reproduction and survival of songbirds (Newton 1998). In particular, temperature and precipitation can influence directly bird survival and breeding success via inclement weather and indirectly through its effects on food abundance (Newton 1998, Morrison and Bolger 2002, Wilson et al. 2011).

During the last half-century (1950–2000), the increasing worldwide demand for food,

important key technological advances in the agricultural sector, and high national and international competitiveness, have triggered agricultural expansion and intensification in regions of Argentina such as the Pampas, Espinal and Chaco (Viglizzo et al. 2004, Grau et al. 2005, Zak et al. 2008, Gasparri and Grau 2009). In these regions, native cover types (grasslands and forests) have been extensively replaced by annual crops (Viglizzo et al. 1997, Paruelo et al. 2005, Baldi and Paruelo 2008). Additionally, the excessive and extensive use of agrochemicals, soil degradation and habitat loss and fragmentation, have strongly degraded remaining original vegetation (Zaccagnini and Calamari 2001, Paruelo et al. 2005, Boletta et al. 2006, Baldi and Paruelo 2008, Codesido et al. 2008, Oesterheld 2008, Gasparri and Grau 2009). Consequently, habitat quality for resident biota has been affected, influencing the abundance and persistence of birds on those regions (Fernández et al. 2003, Filloy and Bellocq 2007, Codesido et al. 2008, Cerezo et al. 2011, Gavier-Pizarro et al. 2012, Macchi et al. 2013).

Given that incorporation of new lands to agricultural production on those regions is expected to continue in the following decades (Zak et al. 2008, Baldi and Paruelo 2008, Nori et al. 2012), potentially affecting habitat quantity and quality for avian populations, it is important to determine bird population status and to evaluate the influence of environmental factors on bird populations at a regional level for developing management and conservation strategies for birds and their habitats. A previous study conducted in central Argentina showed that relationships between bird densities and land use types depended on bird feeding guild, with insectivorous birds relying either in annual crop area or non-plowed fields, and granivorous birds having a weak relationship with land use (Gavier-Pizarro et al. 2012). However, the study only evaluated these relationships using data from 2007–2009, trading space for time through a gradient of land use/cover transformation from totally transformed areas to those dominated by natural vegetation, but did not evaluate temporal trends. Variations in environmental factors in agroecosystems (e.g., diminished food supplies as a result of climatic events, less suitable nesting habitat as a result of land use change) and their influence on bird popula-

tion assessed during short-term periods would not reflect a potential time lag induced by the life history of species, which can be observed in long-term studies (Chamberlain et al. 2000, Bennet et al. 2006, Cueto et al. 2008).

In this study, we explored bird-habitat relationships for two common insectivorous bird species from the Neotropics (Stotz et al. 1996), the Fork-tailed Flycatcher (*Tyrannus savana*) and the White-browed Blackbird (*Sturnella superciliaris*), during the austral breeding season (Fraga 2016, Mobley and Garcia 2016). The Fork-tailed Flycatcher is an austral migrant species member of the South American Temperate–Tropical migratory system (SATT; Joseph 1997, Jahn et al. 2013). It inhabits open habitats, preferring savannas and pastures with scattered trees and bushes where this species builds nests (Mobley and Garcia 2016). White-browed Blackbird is a resident species distributed along central-east South America, where it prefers lush wet meadows and humid grasslands, nowadays particularly common in agricultural fields or pastures with wheat, oat, alfalfa and others (Fraga 2016). This species nest on the ground within grasslands, pastures or crops (Fraga 2016). The study extended for nine years, from 2003–2011. The

consideration of a longer time span compared to the previous study (three years in Gavier-Pizarro et al. 2012) allowed us to evaluate bird population trends and spatial patterns of bird-habitat relationships over time, within specific sub-regions. This more comprehensive analysis would allow us to corroborate or refute short-term bird-habitat relationships found in Gavier-Pizarro et al. (2012). Knowledge of population trajectory and status of the Fork-tailed Flycatcher and the White-browed Blackbird and their associations with environmental factors at a regional scale on a long-term span also could be useful to support conservation initiatives for these species.

METHODS

Study area

The study area comprised 128 200 km² of the Pampas and Espinal ecoregions (Cabrera 1976) in central Argentina (Fig. 1). Temperatures in the area vary between 13 °C (annual mean minimum) and 23 °C (annual mean maximum) (Soriano et al. 1991), and mean annual precipitation is about 1000 mm (Brescia et al. 1998, Messina et al. 1999). A portion of the area corresponds to the Espinal ecoregion, which

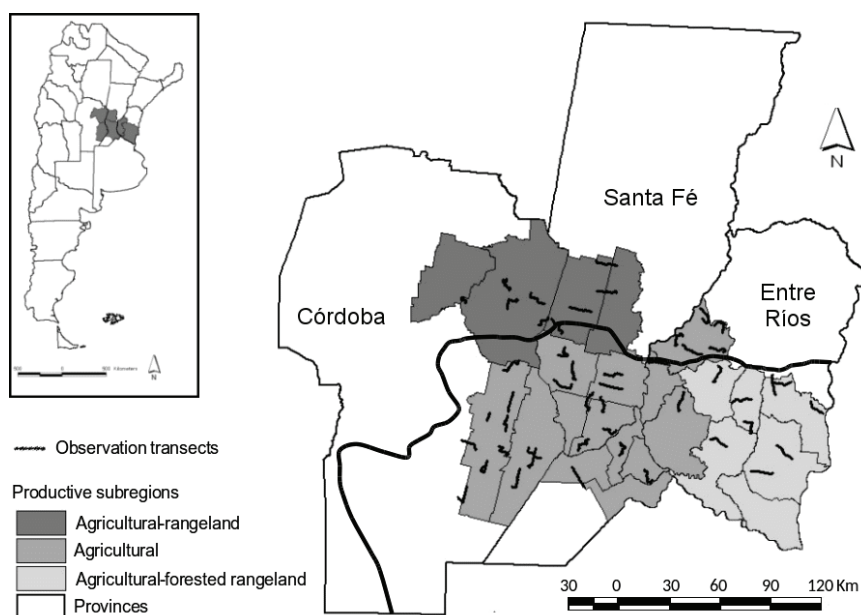


Figure 1. Map of the study area showing the productive sub-regions and location of sampling transects along secondary and tertiary roads in agroecosystems of central Argentina. The black line separates Espinal (north) and Pampa (south) ecoregions (adapted from Matteucci 2012a).

extends from the center of Santa Fe Province to northeastern Córdoba and northern Entre Ríos provinces (Fig. 1). The Espinal is characterized by remnants of xerophytic forest dominated by species such as *Prosopis* spp., *Acacia* spp., *Celtis ehrenbergiana* and *Geoffroea decorticans*, immersed in an agricultural matrix (Lewis et al. 2009, Matteucci 2012a). Another portion of the area corresponds to the Pampas ecoregion, which extends from southern Santa Fe Province to southeastern Córdoba and southern Entre Ríos provinces (Fig. 1). The Pampas were originally characterized by grasslands dominated by *Stipa* spp., *Bromus* spp. and *Poa* spp. (Cabrera 1971, Matteucci 2012b). However, grasslands have been modified and in many cases replaced by agricultural and cattle production activities (Matteucci 2012b). Agricultural crops cover the largest percentage of the area, including soybean, wheat, corn, sunflower and sorghum, in order of importance.

Sampling design

The area was stratified into three sub-regions, based on the predominant production activity: (1) agriculture (agricultural sub-region), (2) mixed agriculture and cattle-ranching activities (agricultural-rangeland), and (3) mixed agriculture and cattle-ranching activities with forest understories incorporated into cattle rangelands (agricultural-forested rangeland). This stratification was made based on the 1993 national agricultural and livestock survey, in which the central region of Argentina was divided into zones according to dominant productive activities (INDEC 1995). Additionally, we placed a grid with a cell size of 30 × 30 km over the complete study area using a Geographical Information System. In each sub-region, we selected grid cells using a systematic design (one of every two) with a random start (Canavelli et al. 2003, 2004). On each cell, we randomly selected a secondary or tertiary road as a survey route for bird observation.

Each survey route (48 in total) contained 30 points, separated by a distance of 1 km. On each point, the abundance of bird species was recorded during 3 min using distance sampling methods (Bibby et al. 2000, Buckland et al. 2001). Routes were sampled once a year (January) during 2003–2011, and between 06:00–11:00 or 15:00–20:00 h, by two experi-

enced observers previously trained in the field sampling protocol. January was selected for field sampling due to biological reasons, including breeding season and presence of migratory species, potential greater risks of birds to agrochemical exposure and, finally, for logistic reasons (extended observation period due to sunlight hours). Further sampling details can be found in Canavelli et al. (2003) and Zaccagnini et al. (2010).

Estimation of bird density

Density for each species was estimated using the software Distance (version 5.0; Buckland et al. 2001, Thomas et al. 2002). We first conducted exploratory analyses to detect and correct the presence of clustering, evasive movements and extreme values (Buckland et al. 2001, Thomas et al. 2002). We then truncated and eliminated data for both species beyond 250 m of each observation (90% of detections were made within this distance). Additionally, we manually defined seven distance classes (0–30, 30–50, 50–75, 75–100, 100–150, 150–200 and 200–250 m) to improve data organization and model adjustment to data.

Species density was estimated using a combination of three models (uniform, half-normal and hazard rate), and two adjustment terms (cosine and polynomial). Model fit was evaluated using q-q plots, Kolmogorov-Smirnov and Cramer-von Mises tests, as well as visual analysis of the detection probability function. The most parsimonious models were selected using the Akaike Information Criterion (*AIC*; Akaike 1974, Buckland et al. 2001, Burnham and Anderson 2002). The *AIC* selection considers the fit as well as the complexity of the model, and allows comparison of several models simultaneously (Johnson and Omland 2004). The *AIC* values reflect the amount of “information” lost when a model is used to approximate conceptual reality; thus, the model with the lowest *AIC* value is selected as the best model (Burnham and Anderson 1998).

The half-normal model with a cosine adjustment was selected for both species based on its consistently lower *AIC* value. For each species, we estimated the detection probability function globally (i.e., combining all years) and bird density for each route and year by stratifying per year and post-stratifying per route,

Table 1. Description of predictive variables included in statistical models of bird-habitat relationship for the Fork-tailed Flycatcher (*Tyrannus savana*) and the White-browed Blackbird (*Sturnella superciliaris*) in agroecosystems of central Argentina.

Variable	Definition
Year	Year of sample
Pper	Proportional cover of perennial pastures
PC1	Component 1 of PCA, representing a gradient of annual crops cover (+) vs. forests and fallow and weedy fields cover (-)
PC2	Component 2 of PCA, representing a gradient of plowed fields cover and annual pastures cover (+)
PC3	Component 3 of PCA, representing a gradient of plowed fields cover (+) vs. annual pastures cover (-)
PC4	Component 4 of PCA, representing a gradient of fallow fields cover (-) vs. forests cover (+)
EVI	Enhanced Vegetation Index
MinTemp	Annual minimum temperature
MaxTemp	Annual maximum temperature
Rain	Mean monthly rainfall for the four previous months to the sampling period (September-January)

with conventional distance sampling procedures (Buckland et al. 2001).

Environmental variables

Many studies have postulated that intensification of agriculture through land use changes or climatic factors may have contributed to farmland bird decline (Chamberlain et al. 2000, Benton et al. 2003, Lemoine et al. 2007, Cueto et al. 2008, Niven et al. 2009). Although it is known that these factors have an impact on birds, it is unclear which is currently most important for the Fork-tailed Flycatcher and the White-browed Blackbird at regional and sub-regional scales. Climatic variables used in models were temperature (annual mean minimum and maximum) and rainfall (four-month average; see below) (Table 1). Temperature and rainfall were calculated for each route, taken from the nearest meteorological station of the National Institute of Agricultural Technology (INTA). Given that the bird breeding season in central Argentina extends from September to January, we averaged monthly rainfall over this four-month period for each year, with the assumption that species abundance in January will be influenced by rainfall in the four previous months to the sampling period (first days of January). This relationship could be based on the food availability for bird species, given that phenology of plants and insects observed in January can be associated with rainfall occurred in previous months (De Juana and García 2005). It also could be related to bird's breeding performance, because cli-

matic conditions can influence the metabolism of bird females and also directly affect egg and chick survival (Barkowska et al. 2003, Dunn 2004).

Some bird species depend on particular environmental conditions along land use/cover gradients and primary productivity could have an influence (Fischer et al. 2006, Schrag et al. 2009). Primary productivity, a measure of the energy entering an ecosystem, was measured using the Enhanced Vegetation Index (EVI; Table 1). We selected this index instead of NDVI (Normalized Difference Vegetation Index), due to EVI is more responsive to canopy structural variations, including leaf area index, canopy type, plant physiognomy, and canopy architecture (Gao et al. 2000, Huete et al. 2002). EVI was developed to optimize the vegetation signal, improving sensitivity in high biomass regions and, therefore, improving vegetation monitoring through a decoupling of the canopy background signal and climatic influences (Matsushita et al. 2007, Jiang et al. 2008). For each route per year, we extracted EVI values from a MODIS satellite image (mid-January) with a 250 m resolution (EOS-Terra images/MODIS, mid-January of each year). An EVI value was estimated for each 250 × 250 m pixels centered on the midpoint location of each route. Then, EVI values were rescaled by dividing the values by 10000, assuming value in a 0–1 range. Low value areas indicate scarce or no vegetation while high value areas indicate vigorous vegetation.

Land use/cover variables were obtained from the field, based on the proportional cover of land use classes visually estimated in a 200 m radius circle around each sampling point. The land use classes (each representing a variable) were: annual crops (corn, soybean, sunflower and sorghum-summer crops), annual pastures (millet, oats), perennial pastures (alfalfa, clover), plowed fields (i.e., bare soil), fallow and weedy fields, and forests (native, introduced, or mixed). To have a unique value of proportional cover for each class at the route level, we averaged the proportion of each cover class on each point over all the observations points in a route. Variables of vegetation cover were highly correlated ($r \geq 0.7$, except for perennial pastures cover), making difficult the interpretation of relationships between individual variables and bird abundance. Therefore, we used Principal Components Analysis (PCA; McCune et al. 2002) to obtain independent measures of land use/cover variables (Table 1). PCA is a multivariate ordination technique which represents a data set containing many variables (in this case, vegetation cover variables) with a smaller number of composite or latent variables (the components or axes of the PCA; Graham 2003, Dormann et al. 2013). These axes are orthogonal (i.e., they are completely uncorrelated), and represent the strongest covariation patterns among the variables in the original data set (McCune et al. 2002). The first four PCA components represented 49, 19, 16 and 15% of the total variance in the original data matrix and were at least moderately correlated ($r \geq 0.4$) with at least one land cover variable (Table 2). Given the value and sign of correlations of the first component (PC1) with the original variables, this axis represented a gradient from sites with low annual crops cover and high forests and fallow and weedy fields cover to sites with high annual crops cover and low forests and fallow and weedy fields cover. The second component (PC2) represented a gradient of covariation between plowed fields and annual pastures (i.e., a gradient of sites with low to high values of both variables). The third component (PC3) represented a gradient of sites with high values of plowed fields cover and low values of annual pastures cover and sites with low values of plowed fields cover and high values of annual pastures cover. Finally, the fourth component (PC4) represented a

Table 2. Results of a Principal Components Analysis of land use/cover variables recorded on sampling transects along secondary and tertiary roads in agroecosystems of central Argentina. Correlations between components and variables are shown.

	PC1	PC2	PC3	PC4
Variables				
Annual crops	0.96	0.15	0.04	0.00
Annual pastures	-0.50	0.61	-0.60	-0.10
Plowed fields	-0.47	0.61	0.64	-0.02
Fallow and weedy fields	-0.73	-0.23	-0.01	0.63
Forests	-0.71	-0.39	0.07	-0.57
% explained variance	49	19	16	15

gradient of sites with low forests cover and high cover of fallow and weedy fields to sites with high forests cover and low proportional cover of fallow and weedy fields. In order to evaluate the potential effects of multicollinearity, we calculated Spearman correlation coefficients between all candidate variables. Spearman correlations were generally low ($r_s \leq 0.30$), and thus we assumed that our results were not significantly affected by multicollinearity.

Species density-environment models

Because of the nested structure of the data (points within routes, routes within sampling periods, sampling periods within observers), we used linear mixed modelling to analyse the relationship between the estimated density for each bird species and annual environmental variables (Pinheiro and Bates 2000). In all models, bird density was the dependent variable. The fixed effects (i.e., independent or predictive variables) were the year (to test for a temporal trend) and the environmental variables describing climatic, primary productivity and land use/cover variation (Table 1). All predictive variables were standardized to vary between 0 and 1, to be able to compare model coefficients directly. Random effects were observer, route and sampling period (morning or evening). Also, sub-region was used as a random effect for models that used the complete, regional data set. Bird density data was log-transformed to meet the statistical assumption of a normal error distribution. In general,

Table 3. Comparison of the structure of statistical models of bird-habitat relationship for the Fork-tailed Flycatcher (*Tyrannus savana*) and the White-browed Blackbird (*Sturnella superciliaris*) in agroecosystems of central Argentina. AIC values for each model structure in the complete study region (CSR) and in the agricultural-rangeland (AR), agricultural-forested rangeland (AFR) and agricultural (A) productive sub-regions are shown. NC: non-convergence.

Model structures	Fork-tailed Flycatcher				White-browed Blackbird			
	CSR	AR	AFR	A	CSR	AR	AFR	A
Standard multiple regression model	339.91	117.49	109.00	78.98	495.48	60.74	139.61	340.00
With random effects	320.70	120.92	110.32	56.04	454.62	63.72	139.78	319.83
With several random effects and heterogeneous variances	NC	122.42	NC	58.05	441.04	64.20	NC	NC
With one random effect and heterogeneous variances	307.07	120.68	93.98	58.05	492.60	59.49	NC	340.37
With spatial autocorrelation	331.65	115.90	110.96	48.92	481.02	61.94	140.26	328.09

model errors did not meet the variance homogeneity assumption, and we re-fitted models with a heterogeneous variance structure between years (Pinheiro and Bates 2000). Finally, because of the spatial nature of our sampling scheme, we also fitted models with a spatial autocorrelation error structure. Because of the aforementioned features associated to our data set, we fitted models with four different structures, for each species and sub-region, and for the complete study region (all sub-regions combined): (1) without ran-

dom effects, assuming homogeneity of variances and independence between errors (standard multiple regression model); (2) with random effects and heterogeneity of variances between years; (3) with random effects and homogeneity of variances between years; and (4) without random effects and assuming homogeneity of variances, but with a temporal and spatial autocorrelation structure, to test for lack of independence between errors (Table 3). We used AIC values to select among these different model structures; the used

Table 4. Initial 15 models of bird-habitat relationship for the Fork-tailed Flycatcher (*Tyrannus savana*) and the White-browed Blackbird (*Sturnella superciliaris*) in agroecosystems of central Argentina fitted to data. Predictive variables included in models are described in table 1.

Model type	Predictive variables in model
Full model (all predictive variables)	Year+Pper+PC1+PC2+PC3+PC4+EVI+MinTemp+MaxTemp+Rain
Trend + land use + climate	Year+Pper+PC1+PC2+PC3+PC4+MinTemp+MaxTemp+Rain
Land use + EVI + climate	Pper+PC1+PC2+PC3+PC4+EVI+MinTemp+MaxTemp+Rain
Land use + climate	Pper+PC1+PC2+PC3+PC4+MinTemp+MaxTemp+Rain
Trend + land use + EVI	Year+Pper+PC1+PC2+PC3+PC4+EVI
Trend + EVI + climate	Year+EVI+MinTemp+MaxTemp+Rain
Trend + land use	Year+Pper+PC1+PC2+PC3+PC4
Land use + EVI	Pper+PC1+PC2+PC3+PC4+EVI
Land use	Pper+PC1+PC2+PC3+PC4
Trend + climate	Year+MinTemp+MaxTemp+Rain
EVI + climate	EVI+MinTemp+MaxTemp+Rain
Climate	MinTemp+MaxTemp+Rain
Trend + EVI	Year+EVI
Trend	Year
EVI	EVI

model structure was the one with the lowest AIC value (Table 3). All analyses were conducted in R software with the *nlme* (Pinheiro et al. 2013) and *lattice* (Sarkar 2008) packages.

Once the optimal model structure was found, best-fitting models were selected using a combination of traditional hypothesis testing and Kulback-Leibler Information methods, particularly AIC values and Akaike weights (w_i) (Burnham and Anderson 1998, 2001, Anderson et al. 2000). For each bird species, we initially fitted a set of 15 models with different combinations of year (i.e., linear temporal trend), land use/cover, EVI, and climatic variables (Table 4). We used this exploratory approach, rather than a more restricted set of *a priori* models (Burnham and Anderson 1998, 2002), because we had no prior information on the explanatory power of our variables in combination. Then, for each model, we examined the P -values for each predictive variable in the set, selected variables with $P \leq 0.20$, and re-fitted the model using only those variables. The number of fitted models for each species varied between 22 for Fork-tailed Flycatcher in the agricultural-rangeland sub-region and 24 for White-browed Blackbird in agricultural-forested rangeland sub-region. Finally, we used AIC and w_i values to choose the best-fitting models from the final set of fitted models (Table 5). When differences between AIC values were small (≤ 2 units), w_i values were used as indicators of the strength of evidence for each model. The w_i is interpreted as the approximate probability that model i is the best model in the set of models being considered (Anderson et al. 2000).

We used multi-model inference or model averaging (Burnham and Anderson 2002) to compare the effect size of individual predictive variables. Model averaging consists in obtaining an averaged coefficient value from several models, weighted by each model's w_i (Burnham and Anderson 1998). We obtained an averaged coefficient for each predictive variable from the set of models with a sum of $w_i \geq 0.95$ (i.e., the confidence model set). The number of models in confidence sets was much smaller than the complete set of models for each bird species, varying between two models for Fork-tailed Flycatcher in the complete study region and the agricultural-rangeland sub-region and six models for the White-browed Blackbird in the agricultural-

Table 5. Confidence set of models of bird-habitat relationship for the Fork-tailed Flycatcher (*Tyrannus savana*) and the White-browed Blackbird (*Sturnella superciliaris*) in agroecosystems of central Argentina. AIC and w_i values for each model in the complete study region (CSR) and in the agricultural-rangeland (AR), agricultural-forested rangeland (AFR) and agricultural (A) productive sub-regions are shown. Predictive variables included in models are described in table 1.

Model	AIC	w_i
Fork-tailed Flycatcher (CSR)		
Pper+PC4	285.2	0.94
Pper+PC4+MaxTemp	290.7	0.06
White-browed Blackbird (CSR)		
Pper+PC1+PC2+PC3+PC4+EVI	504.1	0.82
Pper+PC1+PC2+PC3+PC4+EVI+MaxTemp+Rain	507.9	0.12
Year+Pper+PC1+PC2+PC3+PC4+EVI	509.7	0.05
Fork-tailed Flycatcher (AR)		
PC1+PC4	100.1	0.63
EVI	101.3	0.34
White-browed Blackbird (AR)		
Pper+PC4+EVI	62.7	0.87
Pper+PC3+PC4+EVI	67.7	0.07
EVI	68.1	0.06
Fork-tailed Flycatcher (AFR)		
PC2+PC4+EVI	91.1	0.41
EVI	91.8	0.29
PC3+PC4	92.0	0.26
White-browed Blackbird (AFR)		
Year	101.1	0.45
Year+EVI	102.1	0.27
PC1+PC2+PC4+MaxTemp	104.8	0.07
Year+PC1+PC2+PC4	105.0	0.06
Pper+PC1+PC2+PC4+EVI	105.7	0.04
Fork-tailed Flycatcher (A)		
Pper+PC1+PC4	27.9	0.30
MinTemp	28.0	0.29
EVI	28.9	0.18
Year	29.5	0.14
Pper+PC1+PC4+EVI	31.3	0.06
White-browed Blackbird (A)		
Pper+PC1+PC2+PC4+MinTemp+MaxTemp+Rain	342.4	0.55
Pper+PC1+PC2+PC4+EVI+MinTemp+MaxTemp+Rain	343.2	0.38
Pper+PC2+PC4+EVI	349.0	0.02

forested rangeland sub-region. Overall mean (\pm SD) number of models in confidence sets was 4.4 ± 2.4 .

Table 6. Mean (\pm SE) values of the regression coefficient (β), 95% confidence intervals and associated statistics for land use cover variables recorded on sampling transects along secondary and tertiary roads in agroecosystems of central Argentina that showed a significant temporal trend.

	β	95% CI	R^2	P
Complete study region				
Annual crops	-0.23 ± 0.04	[-0.33, -0.14]	0.77	0.002
Perennial pastures	-0.04 ± 0.01	[-0.07, -0.01]	0.55	0.022
Agricultural-rangeland				
Annual crops	-0.20 ± 0.04	[-0.30, -0.10]	0.77	0.002
Agricultural-forested rangeland				
Fallow and weedy fields	-0.13 ± 0.04	[-0.22, -0.04]	0.61	0.013
Agricultural				
Annual crops	-0.31 ± 0.05	[-0.42, -0.19]	0.85	<0.001
Perennial pastures	-0.03 ± 0.01	[-0.05, -0.01]	0.70	0.005
Fallow and weedy fields	0.13 ± 0.05	[0.00, 0.25]	0.46	0.040

RESULTS

Trends in population density

Fork-tailed Flycatcher mean (\pm SE) density was approximately three times higher than the density of the White-browed Blackbird (0.132 ± 0.01 and 0.045 ± 0.01 individuals/ha, respectively; Fig. 2). Population density of the Fork-tailed Flycatcher showed statistically significant changes only in the agricultural sub-region, where it increased, while the density of the White-browed Blackbird significantly

decreased only in the agricultural-rangeland sub-region (Fig. 2). However, both trends were probably influenced by outlier values, such as the unusually high density of the Fork-tailed Flycatcher in 2008 and White-browed Blackbird in 2003 (Fig. 2).

Annual changes in environmental variables

Vegetation productivity and climatic variables did not show statistically significant annual changes in the analysed period either on the complete study region or the sub-

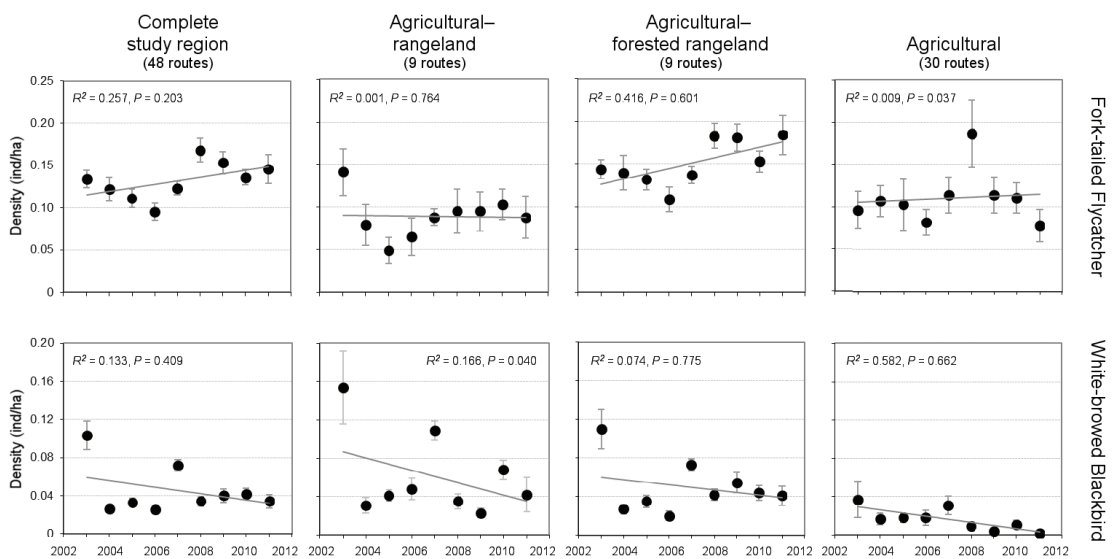


Figure 2. Variation in density (individuals/ha) of the Fork-tailed Flycatcher (*Tyrannus savana*) and the White-browed Blackbird (*Sturnella superciliaris*) in agroecosystems of central Argentina during 2003–2011. Mean (\pm SE) values for each species in the complete study region and in the agricultural-rangeland, agricultural-forested rangeland and agricultural productive sub-regions are shown.

regions. However, land use variables showed temporal trends on some cases (Table 6). Annual crops showed a negative trend in the complete study region and in the agricultural and agricultural-rangeland sub-regions. Additionally, perennial pastures showed a negative trend in the complete study region and in the agricultural sub-region. Finally, fallow and weedy fields presented a negative trend in the agricultural-forested rangeland sub-region but a positive trend in the agricultural sub-region (Table 6).

Bird density and environmental variables

Bird density was related to environmental variables to different degrees, depending on the species and sub-regions. The density of the Fork-tailed Flycatcher increased in landscapes characterized by decreasing forest

cover and increasing fallow and weedy fields in the complete study region and in all sub-regions (positive relationship to PC4; Figs. 3A–D). Additionally, the density decreased with increasing plowed fields cover and decreasing annual pastures, but only in the agricultural-forested rangeland sub-region (negative association to PC3; Fig. 3C). In the agricultural-rangeland sub-region, although the Fork-tailed Flycatcher increased in landscapes with high proportion of annual crops cover and decreased in sites with low fallow and weedy fields and forest cover (positive association with PC1; Fig. 3B), it was still strongly associated to the fourth component, and this association was higher than its association to PC1. Thus, its negative association to PC1 (and thus to its usually preferred cover types, low fallow and weedy fields) was probably asso-

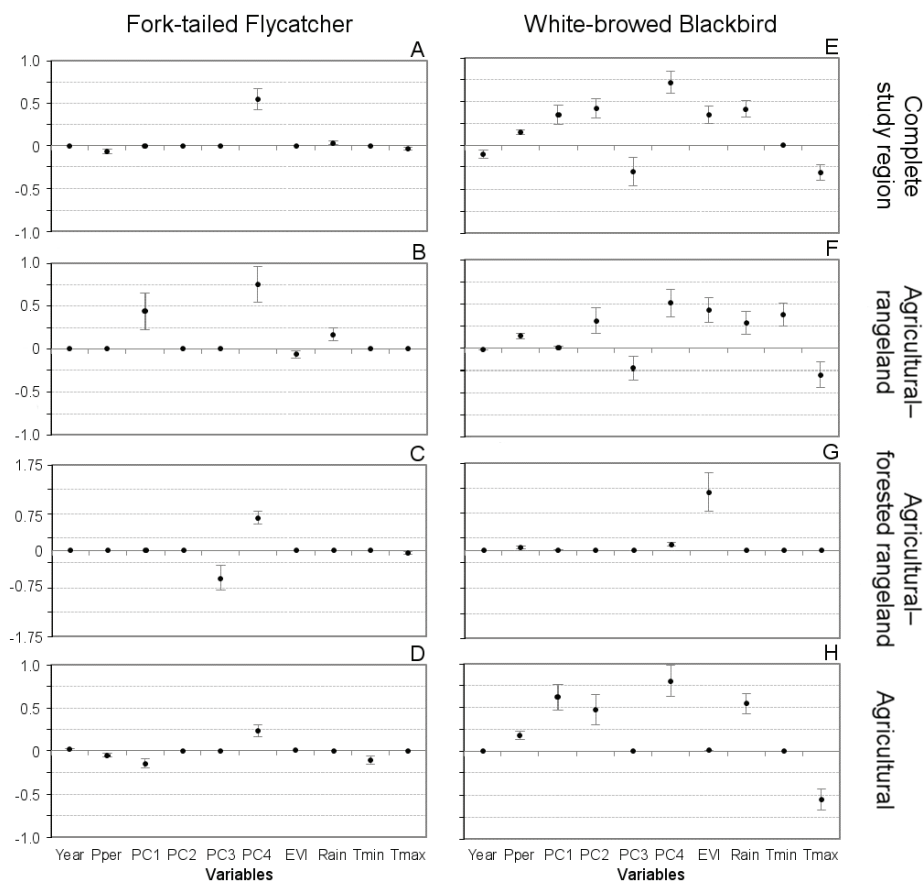


Figure 3. Mean (\pm SE) values of coefficients (adjusted by Akaike weights) for all predictive variables included in statistical models of bird-habitat relationship for the Fork-tailed Flycatcher (*Tyrannus savana*) and the White-browed Blackbird (*Sturnella superciliaris*) in agroecosystems of central Argentina. Values for the complete study region and for the agricultural-rangeland, agricultural-forested rangeland and agricultural productive sub-regions are shown. Predictive variables are described in table 1.

ciated to its avoidance of forest which, on PC1, was associated to fallow and weedy fields. In the agricultural sub-region, however, its relationship to PC1 was inverted to that shown in the agricultural–rangeland sub-region. Perhaps in the agricultural region, the amount of fallow and weedy fields is higher or forest cover is much lower, thus making these landscapes more attractive. Climatic variables were weakly associated: the density of the Fork-tailed Flycatcher showed a positive relationship with rainfall in the agricultural–rangeland sub-region (Fig. 3B) and was also weakly and negatively related to annual minimum temperature in the agricultural sub-region (Fig. 3D).

The density of the White-browed Blackbird increased with decreasing fallow and weedy fields and forest cover and increasing annual crops cover (positive association to increases in PC1) in the complete study region (Fig. 3E) and in the agricultural sub-region (Fig. 3H). Additionally, it increased in landscapes with high proportion of annual pastures and plowed fields (positive associations to PC2), and increased in landscapes with low proportion of forest cover and high cover of fallow and weedy fields (positive associations to PC4) in the complete study region (Fig. 3E) and in the agricultural–rangeland (Fig. 3F) and the agricultural (Fig. 3H) sub-regions. Its density was also positively associated with perennial pastures, both in the complete region and in all sub-regions (Figs. 3E–H). Furthermore, White-browed Blackbird decreased with increasing plowed fields and decreasing annual pastures cover (negative relationship to PC3) in the complete study region (Fig. 3E) and in the agricultural–rangeland sub-region (Fig. 3F). In contrast to the density of the Fork-tailed Flycatcher, climatic variables and vegetation productivity were more strongly associated with the density of the White-browed Blackbird. It showed a positive relationship with rainfall and EVI but decreased with annual maximum temperature in the complete study region (Fig. 3E) and in most of the sub-regions. In sharp contrast to its more complex response in the agricultural–rangeland and agricultural sub-regions, where it responded to multiple environmental variables, this species only responded to EVI in the agricultural–forested rangeland sub-region (Fig. 3G).

DISCUSSION

Land use/cover and productivity were the main factors explaining the long-term population changes of the Fork-tailed Flycatcher and the White-browed Blackbird in agroecosystems of central Argentina. These results strengthen the weak relationships found in the previous short-term study (Gavier-Pizarro et al. 2012), highlighting the importance of monitoring long-term population trends (Magurran et al. 2010).

Different bird responses to landscape changes may be related to degrees of specialization to landscape elements (Andr en et al. 1997). In our study, both species responded mainly to evolving land use change and, to a lesser degree, to climatic variables. The lower relation of Fork-tailed Flycatcher density with climatic variables could be due to the lack of significant variations on these variables on the study area included on the wide distribution range of this species (Fraga 2016). Goijman et al. (2015) found high occupancy rates of the Fork-tailed Flycatcher in east central Argentina. White-browed Blackbird was associated with variation in temperature and rainfall (at the regional level and in two sub-regions: agricultural–rangeland and agricultural), showing an association with more rainy and cooler areas. Recent studies in Europe and North America have shown that bird declines are strongly associated to temperature and rainfall (Newton 1998, Morrison and Bolger 2002, Dugger et al. 2004, Szep et al. 2006, Studds and Marra 2007, 2011, Wilson et al. 2011). In particular, species with a low thermal maximum showed the sharpest declines (Jiguet et al. 2010). In this study, climatic variables did not show a temporal trend or significant differences between sub-regions. Additionally, we did not find a relation between variations in density of the White-browed Blackbird with more rainy periods (e.g., in 2005 and 2010), which likely reflect a time lag in the functional response of birds. However, the density of the White-browed Blackbird thrived in wet and temperate habitats, in coincidence with the reported preference of this species for lush wet meadows and humid grasslands (Fraga 2016).

Temporal changes in bird densities in agricultural landscapes have been related to temporal land cover changes in Europe and North

America (Chamberlain et al. 2000, Donald et al. 2001, Murphy 2003, Reif et al. 2008, Gaston 2010). In Argentina, previous studies also have shown changes in bird abundance in relation to land use and cover types (Fillooy and Bellocq 2007, Gavier-Pizarro et al. 2012, Weyland et al. 2014). A general pattern observed in this study was a gradient from landscapes with scarce forest cover but with more fallow and weedy fields sustaining more Fork-tailed Flycatcher densities, although statistically significant only in the agricultural sub-region, to landscapes with more perennial pastures and annual crops and less fallow and weedy fields and forest cover where the White-browed Blackbird was most abundant.

The density of the Fork-tailed Flycatcher was positively associated to increasing fallow and weedy fields cover and decreasing forest cover. Although this species is reported as a habitat generalist (Mobley and Garcia 2016), in this study it was strongly associated to higher fallow fields cover, which on average occupies a small proportion of studied landscapes. Contrary to this general pattern, in the agricultural-rangeland sub-region this species was positively associated to the first component (this axis went from landscapes dominated by fallow and weedy fields and forest cover, to landscapes dominated by annual crops). Thus, this relationship contradicts its usual association to fallow and weedy fields cover. We believe that in this sub-region the species is mainly avoiding forest cover, even though these ends of the component are also represented by fallow and weedy fields cover. In addition, in this sub-region its response to the fourth component, although explaining only approximately 30% of the variation of the first one, was more strongly associated. Thus, considering both components 1 and 4, the species tends to avoid landscapes with forest cover.

In a shorter time span, Gavier-Pizarro et al. (2012) found a positive relationship between the Fork-tailed Flycatcher and non-plowed fields, indicating a preference for semi-natural habitats, and Fillooy and Bellocq (2007) found a negative association with increasing percentage of arable farmland. Additionally, this species prefers nesting in open savannas over closed forest habitats in the Brazilian Cerrado (Marini et al. 2009). Feichtinger and Veech (2013), in a study with Scissor-tailed

Flycatcher (*Tyrannus forficatus*), found a positive association with open land cover types (such as grassland, pasture-hayfield and cropland) and a negative association with forest and scrubland cover. Thus, the maintenance of fallow fields cover in landscapes with low forest cover is probably important for the conservation of birds associated to grassland and savannas. In contrast to the White-browed Blackbird, the general lack of response of Fork-tailed Flycatcher density to climatic factors could be explained by their ecological requirements, which were not influenced by small yearly or spatial variations in the study region.

The White-browed Blackbird, a bird species preferring pastures, agricultural lands and grassland habitats (Narosky and Yzurieta 1987, Stotz et al. 1996, Camperi et al. 2004, Azpiroz et al. 2012, Fraga 2016), showed a relatively consistent response to landscape changes in the agricultural-rangeland and the agricultural sub-regions, increasing in landscapes with more perennial pastures, fallow and weedy fields and annual pastures, and avoiding sites with more forest cover. Its abundance has also been negatively related to increasing native forest in another study conducted in the central part of Argentina for the 2003–2006 period (Schrage et al. 2009). These results probably reflect the species' reported ability to use a variety of open habitats (Narosky and Yzurieta 1987, Stotz et al. 1996, Camperi et al. 2004, Fraga 2016) as well as its plasticity to changing environments, allowing them to survive in landscapes dominated by open, non-woody habitats and to tolerate the intensive agriculture that typifies the study region. Goijman et al. (2015) found high variability in occupancy estimation over time of the White-browed Blackbird, but it appears to be declining.

Given the high relationship of these two bird species on semi-natural open (non-woody) habitats, such as fallow and weedy fields and annual pastures, we can infer that the conservation of both species would depend on the conservation of these habitat types. Additionally, these remnants of natural or semi-natural habitats would help to maintain a relatively high proportion of avian diversity. Finally, as the studied species have a relatively wide tolerance to habitat variation, further studies would have to be dedicated to grassland-

dependent species as well as to variables related to the whole bird community, in order to establish more precise and systematic base-lines for bird management and conservation at regional scales.

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