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THE AVIFAUNA IN THE DIFFERENT LANDSCAPE COMPONENTS OF ARROYO SALADILLO, SOUTHERN SANTA FE PROVINCE, ARGENTINA

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ABSTRACT: In this study, we estimated and compared patterns of biodiversity of avifauna in the different landscape units that make up the middle basin of the Arroyo Saladillo, located in Santa Fe Province, Argentina. We found that species richness, abundance, and diversity were higher in the corridor than in the rest of the landscape units, with the simplified matrix showing the lowest values. The low-simplification matrix and patches showed similar values for the parameters analyzed. In addition, we analyzed avifauna abundance, richness, and diversity across different seasons and their relationship with the landscape units under study. We observed that richness, abundance, and diversity of wild birds were significantly higher during spring and summer compared to other seasons, with simplified matrix areas recording the lowest values for these indicators. Biological corridors and patches showed similar seasonal variability. The low-simplification matrix showed patterns of seasonal variability similar to those observed in patches. These results highlight the importance of biological corridors and relict areas with high diversity of woody plant species, which act as biodiversity islands. In addition, it is important to consider the role played by productive fields with a low degree of simplification as key habitats for the conservation of wild birds. We consider it essential to preserve this type of production in the region and to encourage the implementation of diversified production systems, since they play a fundamental role in the conservation of wildlife in the region.

KEYWORDS: *biodiversity, birds, landscape ecology, Pampas region*

Species diversity is a central topic in both community ecology and conservation biology (Villarreal et al. 2004). Its study has gained increasing relevance in recent years due to the modifications generated by human activities (Sala et al. 2000, Wilson et al. 2016).

In the Pampas region, agricultural expansion and population growth are key factors driving environmental transformation (Brown et al. 2006). Agricultural intensification has been mainly expressed through the expansion of double-cropping wheat–soybean systems, the widespread adoption of no-till farming, and the incorporation of transgenic cultivars (Aizen et al. 2009). These processes have drastically reduced natural environments and altered ecosystem structure and functioning, leading to fragmentation (Rimoldi & Chimento 2018). As a consequence, landscapes have become increasingly homogeneous, a condition identified as one of the main drivers of the decline of numerous vertebrate groups in temperate agroecosystems (Benton et al. 2003).

In this scenario, wildlife faces increasing threats due to habitat loss and fragmentation (IUCN 2008). The sensitivity of species to these alterations depends on their spatial requirements, diets, and behavioral responses to landscape change (Biasatti & Rimoldi 2022). Among the most affected groups, birds stand

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out for their ability to respond rapidly to environmental modifications at both regional and local scales, moving in response to resource variation or abandoning areas where resources are no longer available (Robinson et al. 2004, Guidetti 2020). However, these responses vary among species or assemblages, making birds valuable indicators for understanding ecosystem condition (Whelan et al. 2008, Wenny et al. 2011, Zufiaurre et al. 2016).

Beyond their role as bioindicators (BirdLife International 2022), birds perform key ecosystem functions with direct effects on human well-being, such as pollination (Murphy & Kelly 2001), regulation of invertebrate populations (Mols & Visser 2002), natural rodent control (Rimoldi & Curti 2021), and seed dispersal (Guidetti 2020).

At the landscape level, the distribution, abundance, and composition of bird communities are closely linked to land-use patterns, which determine habitat availability and quality (Allen & O'Connor 2000, Heikkinen et al. 2004, La Sorte 2006, Codesido & Busch 2010). Thus, environmental degradation can be assessed through changes in density, abundance, and distribution of populations across the different environments resulting from land-use patterns (Temple & Wiens 1989).

The impacts of intensive agriculture are not limited to habitat loss: the intensive use of pesticides and agrochemicals affects beneficial species, reducing biodiversity and weakening essential ecosystem services (Krüger 2013). However, certain well-managed agroecosystems can retain a considerable portion of their original biodiversity (Mermoz et al. 2016).

Both seasonal variation and anthropogenic land-use changes affect bird community dynamics. Seasonal changes in climate and food resource availability influence habitat use, causing fluctuations in richness, abundance, and composition (Codesido et al. 2004, López de Casenave et al. 2008, Evans et al. 2013). However, changes driven by rapid and extensive land-use transformation are often more pronounced, as they affect both species distribution and relative abundance across habitats, as well as the resources available to different functional groups (Zanette et al. 2000, Silva 2003).

In this context, the objective of this study was to compare bird assemblages among the different landscape components present in the middle basin of the Arroyo Saladillo (southern Santa Fe Province, Argentina). Specifically, we evaluated differences in richness, abundance, and diversity. Additionally, we assessed whether the observed spatial patterns (i.e., the hierarchy among landscape units) remain consistent across seasons, determining whether the unit with the highest and lowest diversity varies seasonally or remains constant.

MATERIALS AND METHODS

Study area

The Arroyo Saladillo basin is located between latitudes 32°55'S and 33°30'S and longitudes 60°35'W and 61°55'W (southern Santa Fe Province, Argentina), covering parts of the Rosario, San Lorenzo, Caseros, Constitución, and General López departments (Fig. 1). It spans approximately 3144 km², with elevation ranging from 115.5 m.a.s.l. to 18.5 m.a.s.l. The main channel flows in a W–SW to E–NE direction, draining into the Paraná River. The hydrographic network includes several permanent natural and artificial channels. The main watercourse is the Arroyo Saladillo, into which secondary channels such as Arroyo Candelaria, Sanford–Arequito Canal, Arroyo Pueblo Álvarez, Arroyo La Adela–La Esperanza, and Bombal Canal converge, among others. Mean annual precipitation is 1000 mm, distributed throughout the year with higher values between October and April. The middle basin is located between 33°30' and 33° S latitude and 61°30' and 61° W longitude.

In most of the upper and middle basin, soils are well drained, with moderate to moderately slow permeability, not prone to waterlogging and suitable for agriculture. In other sectors of the upper basin and in floodplains of watercourses, soils show imperfect drainage, leading to waterlogging problems (Mendez Zacarías & Zimmermann 2011).

Landscape units

In general terms, we distinguished three landscape components in the study area: the matrix, characterized by continuity, regularity, homogeneity, and, primarily, dominating the landscape due to its larger area relative to other components; patches, which are irregular polygonal or circular areas representing smaller, discrete habitat units within the matrix; and corridors, which are characterized by their key role in facilitating connectivity among all landscape units and by their elongated shape, in which one dimension (length) predominates over the other (width).

Based on this definition, we established four landscape units:

1) Highly simplified matrix (M1): characterized by annual double-cropping wheat/soybean, which has replaced former crop–livestock rotation systems. Transgenic glyphosate-resistant soybean predominates, favoring the adoption of no-till agriculture over more traditional practices.

2) Low-simplification matrix (M2): includes farms where multiple production systems coexist, generally agricultural–livestock systems, which may or may not incorporate agroecological practices. These areas show greater vegetation heterogeneity due to the presence of sown or natural pastures and sections with exotic or native trees maintained for shade and livestock functional purposes.

3) Patches (P): mainly composed of introduced tree species associated with former rural homesteads, such as *Eucalyptus* sp., *Melia azedarach*, and *Ligustrum* sp., although native species persist at low frequency, including Ceibo (*Erythrina crista-galli*), Ombú (*Phytolacca dioica*), Tala (*Celtis tala*), and White Algarrobo (*Prosopis alba*).

4) Corridor (C): defined by the Arroyo Saladillo channel as its main axis. Its extent depends on multiple environmental factors, particularly topography, which often limits agricultural activity (irregular relief such as undulations, depressions, and hills). As a result, it allows the persistence of natural or semi-natural habitats such as forests, shrublands, and grasslands.

Sampling

We established three sampling sites for each of the four landscape units (12 sites in total; Fig. 1). Sites were selected to represent all landscape units and to adequately cover the spatial extent of the middle basin of the Arroyo Saladillo. At each site, we established three 500 m transects separated by 100 m. Along each transect, we placed five fixed-radius count points (50 m), each lasting 15 min and separated by 100 m (Ralph et al. 1996). We recorded all birds detected within the radius, regardless of height. Birds in flight actively using the space (hunting, foraging, or moving between trees) were included.

Counts were conducted at each point twice per season over two consecutive years (2021–2022): once

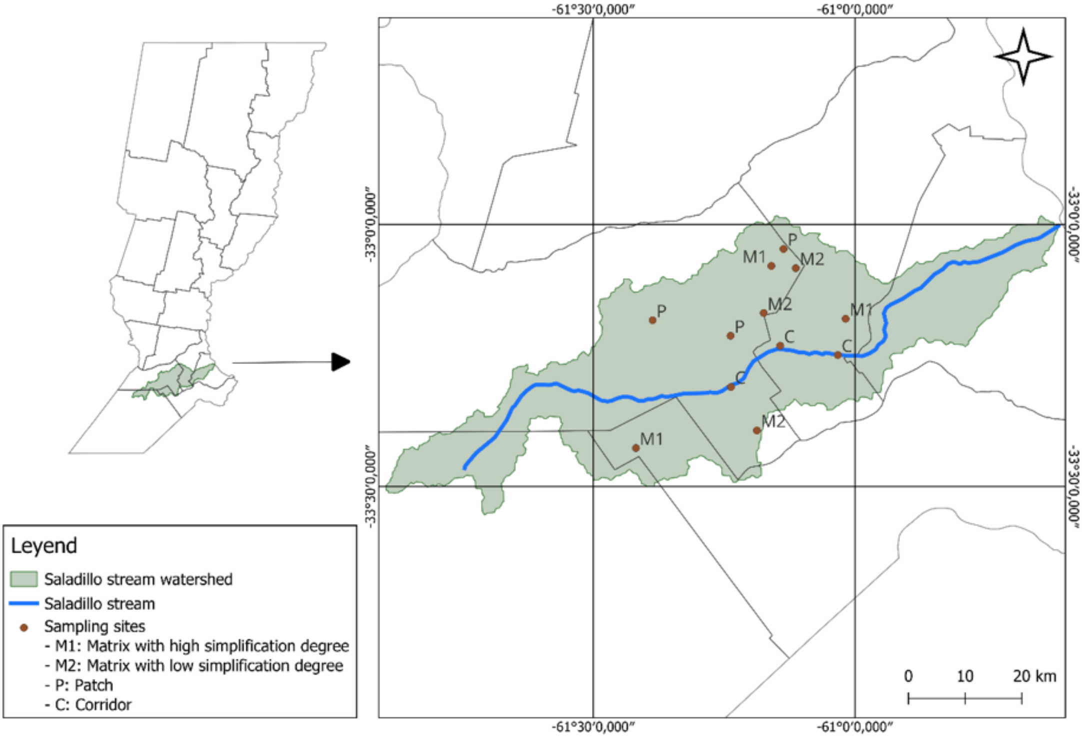

Figure 1. Delineation of the study area in the middle basin of the Arroyo Saladillo, southern Santa Fe Province, Argentina. Each point represents a sampling site. Legend: C (Corridor); M2 (Low-simplification matrix); M1 (Highly simplified matrix); P (Patch).

in the morning (starting 20 min after sunrise and up to 4 h after) and once in the afternoon (near sunset), following Villarreal et al. (2004). Counts were performed by two observers using binoculars.

Trophic guilds

We classified species into trophic guilds based on dietary information from *Birds of the World* (Billerman et al. 2025). Following Foncea et al. (2023), guilds were grouped into six categories according to the main dietary item: omnivores, granivores, nectarivores, herbivores, carnivores, and insectivores. The herbivore category includes both frugivores and folivores.

Statistical analyses

To characterize assemblages, we quantified total abundance (number of individuals recorded), species richness (number of species), and diversity using the Shannon–Wiener index (H'). This index simultaneously integrates richness and evenness (Moreno 2001, Magurran & McGill 2011) and was expressed as true diversity or effective number of species through the transformation D = exp(H') (Jost 2006).

We generated rarefaction curves (observed richness, S obs.) and non-parametric richness estimators (Chao 2, Jack 2, Bootstrap, and ICE) for each landscape unit, presented in five independent figures, each including the four corresponding curves per landscape unit (Magurran 1988, Colwell & Coddington 1994, Moreno 2001). Rarefaction curves were used to evaluate sampling effort and its adequacy for comparisons among landscape units.

To compare assemblage composition among landscape units, we used the Jaccard index together with cluster analysis, non-metric multidimensional scaling (NMDS), and PERMANOVA. The Jaccard index was calculated from a presence–absence matrix constructed for each landscape unit using the 'vegdist' function in the *vegan* 2.7-2 package in R version 4.5.2 (R Core Team 2025), specifying the 'jaccard' method and binary standardization. The resulting values were used to estimate pairwise similarity among landscape units and to perform hierarchical clustering using the UPGMA method (Unweighted Pair Group Method with Arithmetic Mean).

We implemented NMDS on a Bray–Curtis dissimilarity matrix derived from species abundance data. We used two dimensions and 999 permutations to assess solution stability, and we evaluated model fit using stress values. In addition, we applied PERMANOVA (with 999 permutations) on the same dissimilarity matrix, estimating the proportion of variance explained by landscape unit type (R^2) and its significance (p). These analyses were performed in R version 4.5.2 (R Core Team 2025). Ordination and community comparison analyses were conducted using the *vegan* 2.7-2 and *permute* 0.9-8 packages. Visualizations were produced with *ggplot2* 4.0.1 and data manipulation with *dplyr* 1.1.4.

To account for spatial dependence among observations from the same site, we complemented analyses with generalized linear mixed models (GLMMs) using the 'glmmTMB' function in R (R Core Team 2025). Site was included as a random factor (1 | site) to account for non-independence within spatial units. Fixed factors were landscape unit (C, P, M1, M2), season (winter, autumn, spring, summer), and year (2021, 2022), as well as two-way interactions 'landscape unit' with 'season', and 'lanscape unit' with 'year'.

For abundance, Poisson and negative binomial models showed convergence and fit issues, so we modeled the log-transformed variable (log(abundance + 1)) using a Gaussian distribution (family = gaussian), which satisfied model assumptions. For richness, we used a Poisson distribution (family = poisson), and for the Shannon index (H'), a Gaussian distribution.

Significance of fixed terms and interactions was assessed using the 'drop1()' function with chi-square tests. When interactions were significant, post hoc comparisons among landscape units within each season were performed using the *emmeans* package with Tukey adjustment.

Model adequacy was evaluated through residual simulations using the *DHARMa* package, with no relevant deviations from assumptions detected in any model.

We assessed trophic guild associations with landscape units using an indicator species analysis with the 'multipatt' function from the *indicspecies* package (v1.7.14). We used the IndVal.g statistic on a presence–absence matrix of guilds per landscape unit, with 999 permutations to assess significance ($\alpha = 0.05$).

RESULTS

We recorded a total of 25,302 birds (hereafter, records) belonging to 110 species, 39 families, and 17 orders. The best-represented order was Passeriformes, with 18 families and 62 species, accounting for 56.3% of the avifauna recorded in this study (Table 1).

Table 1. Bird species recorded in the middle basin of the Arroyo Saladillo, southern Santa Fe Province, Argentina, according to presence records at each sampling site. X indicates presence and 0 indicates absence.

Scientific name	**Common name**	**Location**			
		C	**P**	**M1**	**M2**
Family: Tinamidae					
Nothura maculosa	Spotted Nothura	X	X	X	X
Family: Anatidae					
Cygnus melancoryphus	Black-necked Swan	X	0	0	0
Callonetta leucophrys	Ringed Teal	X	0	0	0
Amazonetta brasiliensis	Brazilian Teal	X	0	X	0
Spatula versicolor	Silver Teal	X	0	0	0
Anas georgica	Yellow-billed Pintail	X	0	0	0
Anas flavirostris	Yellow-billed Teal	X	0	0	0
Family: Columbidae					
Columba livia	Rock Pigeon	X	X	X	X
Patagioenas picazuro	Picazuro Pigeon	X	X	X	X
Patagioenas maculosa	Spot-winged Pigeon	X	X	X	0
Zenaida auriculata	Eared Dove	X	X	X	X
Columbina picui	Picui Ground Dove	X	X	X	X
Family: Cuculidae					
Guira guira	Guira Cuckoo	X	X	X	X
Family: Ciconiidae					
Mycteria americana	Wood Stork	X	0	0	0
Ciconia maguari	Maguari Stork	X	0	0	0
Family: Rallidae					
Fulica rufifrons	Red-fronted Coot	X	0	0	0
Family: Threskiornithidae					
Plegadis chihi	White-faced Ibis	X	0	0	0
Family: Ardeidae					
Nycticorax nycticorax	Black-crowned Night Heron	X	0	0	0
Ardea cocoi	Cocoi Heron	X	0	0	0
Syrigma sibilatrix	Whistling Heron	X	X	X	X
Egretta thula	Snowy Egret	X	X	0	0
Butorides striata	Striated Heron	X	0	0	0
Ardea ibis	Western Cattle-Egret	X	0	0	0
Family: Phalacrocoracidae					
Nannopterum brasilianum	Neotropic Cormorant	X	0	0	0

Scientific name	**Common name**	**Location**			
		C	**P**	**M1**	**M2**
Family: Recurvirostridae					
Himantopus mexicanus	Black-necked Stilt	X	0	0	0
Family: Charadriidae					
Vanellus chilensis	Southern Lapwing	X	X	X	X
Family: Scolopacidae					
Tringa solitaria	Solitary Sandpiper	X	0	0	0
Tringa flavipes	Lesser Yellowlegs	X	0	0	0
Tringa melanoleuca	Greater Yellowlegs	X	0	0	0
Family: Tytonidae					
Tyto furcata	American Barn Owl	0	X	X	0
Family: Strigidae					
Athene cunicularia	Burrowing Owl	X	X	X	0
Megascops choliba	Tropical Screech-Owl	X	0	X	0
Family: Accipitridae					
Elanus leucurus	White-tailed Kite	X	X	X	0
Rupornis magnirostris	Roadside Hawk	X	X	X	X
Parabuteo unicinctus	Harris's Hawk	0	X	0	0
Family: Alcedinidae					
Chloroceryle amazona	Amazon Kingfisher	X	0	0	0
Chloroceryle americana	Green Kingfisher	X	0	0	0
Family: Picidae					
Colaptes melanochloros	Green-barred Woodpecker	X	X	X	0
Melanerpes candidus	White Woodpecker	0	X	0	0
Colaptes campestris	Campo Flicker	X	X	X	0
Family: Falconidae					
Caracara plancus	Crested Caracara	X	X	X	0
Daptrius chimango	Chimango Caracara	X	X	X	X
Falco sparverius	American Kestrel	X	X	X	X
Falco femoralis	Aplomado Falcon	X	X	X	0
Family: Psittacidae					
Myiopsitta monachus	Monk Parakeet	X	X	X	X
Family: Caprimulgidae					
Systellura longirostris	Band-winged Nightjar	0	X	0	0
Family: Trochilidae					
Hylocharis chrysura	Gilded Hummingbird	0	X	0	0
Chlorostilbon lucidus	Glittering-bellied Emerald	X	X	X	0

Scientific name	**Common name**	**Location**			
		C	**P**	**M1**	**M2**
Family: Thamnophilidae					
Taraba major	Great Antshrike	X	X	0	0
Family: Furnariidae					
Lepidocolaptes angustirostris	Narrow-billed Woodcreeper	0	X	0	0
Furnarius rufus	Rufous Hornero	X	X	X	X
Cinclodes fuscus	Buff-winged Cinclodes	X	0	0	0
Phacellodomus sibilatrix	Little Thornbird	X	X	0	0
Phacellodomus striaticollis	Freckle-breasted Thornbird	X	0	0	0
Anumbius annumbi	Firewood-gatherer	X	0	0	0
Schoeniophylax phryganophilus	Chotoy Spinetail	X	0	X	0
Synallaxis albescens	Pale-breasted Spinetail	0	0	X	0
Synallaxis frontalis	Sooty-fronted Spinetail	X	X	0	0
Family: Tyrannidae					
Serpophaga nigricans	Sooty Tyrannulet	X	X	0	0
Serpophaga subcristata	White-crested Tyrannulet	X	X	X	0
Serpophaga griseicapilla	Straneck's Tyrannulet	0	0	X	0
Elaenia parvirostris	Small-billed Elaenia	0	X	0	0
Pitangus sulphuratus	Great Kiskadee	X	X	X	X
Machetornis rixosa	Cattle Tyrant	X	X	X	0
Myiodynastes maculatus	Streaked Flycatcher	X	X	0	0
Tyrannus melancholicus	Tropical Kingbird	X	0	X	0
Tyrannus savana	Fork-tailed Flycatcher	X	X	X	0
Pyrocephalus rubinus	Vermilion Flycatcher	X	X	0	0
Lessonia rufa	Austral Negrito	X	0	X	0
Hymenops perspicillatus	Spectacled Tyrant	X	0	0	0
Knipolegus aterrimus	White-winged Black-Tyrant	0	X	X	0
Neoxolmis coronatus	Black-crowned Monjita	X	0	X	0
Xolmis irupero	White Monjita	X	0	0	0
Myiophobus fasciatus	Bran-colored Flycatcher	X	X	0	0
Myiarchus swainsoni	Swainson's Flycatcher	X	0	0	0
Family: Vireonidae					
Vireo chivi	Chivi Vireo	0	X	0	0
Family: Hirundinidae					
Tachycineta leucorrhoa	White-rumped Swallow	X	0	X	X
Progne tapera	Brown-chested Martin	X	X	X	0
Progne chalybea	Gray-breasted Martin	0	0	X	0

Scientific name	**Common name**	**Location**			
		C	**P**	**M1**	**M2**
Pygochelidon cyanoleuca	Blue-and-white Swallow	0	X	X	0
Family: Polioptilidae					
Polioptila dumicola	Masked Gnatcatcher	X	X	X	0
Family: Troglodytidae					
Troglodytes musculus	Southern House Wren	X	X	X	X
Family: Mimidae					
Mimus saturninus	Chalk-browed Mockingbird	X	X	X	X
Mimus triurus	White-banded Mockingbird	X	X	X	0
Family: Turdidae					
Turdus rufiventris	Rufous-bellied Thrush	X	X	X	0
Turdus amaurochalinus	Creamy-bellied Thrush	X	X	X	0
Family: Passeridae					
Passer domesticus	House Sparrow	X	X	X	X
Family: Motacillidae					
Anthus furcatus	Short-billed Pipit	X	0	0	0
Family: Fringillidae					
Spinus magellanicus	Hooded Siskin	X	X	X	0
Family: Passerellidae					
Ammodramus humeralis	Grassland Sparrow	0	0	X	X
Zonotrichia capensis	Rufous-collared Sparrow	X	X	X	X
Family: Icteridae					
Leistes superciliaris	White-browed Meadowlark	X	X	0	X
Molothrus rufoaxillaris	Screaming Cowbird	X	X	X	X
Molothrus bonariensis	Shiny Cowbird	X	X	X	X
Agelaioides badius	Grayish Baywing	X	X	X	X
Chrysomus ruficapillus	Chestnut-capped Blackbird	X	0	0	0
Family: Parulidae					
Geothlypis velata	Southern Yellowthroat	0	X	X	0
Setophaga pitiayumi	Tropical Parula	X	X	X	0
Family: Cardinalinae					
Piranga flava	Hepatic Tanager	0	X	0	0
Family: Thraupidae					
Embernagra platensis	Great Pampa-Finch	X	0	X	0
Saltatricula multicolor	Many-colored Chaco Finch	X	0	0	0
Coryphospingus cucullatus	Red-crested Finch	0	X	0	0
Rauenia bonariensis	Blue-and-yellow Tanager	0	X	X	0

Scientific name	Common name	Location			
		C	P	M1	M2
Sporophila caerulescens	Double-collared Seedeater	X	X	X	0
Microspingus melanoleucus	Black-capped Warbling Finch	X	X	0	0
Sicalis flaveola	Saffron Finch	X	X	X	X
Sicalis luteola	Grassland Yellow-Finch	X	X	X	X
Paroaria coronata	Red-crested Cardinal	X	X	X	0
Paroaria capitata	Yellow-billed Cardinal	X	0	0	0
Family: Sturnidae					
Sturnus vulgaris	Common Starling	X	X	X	X

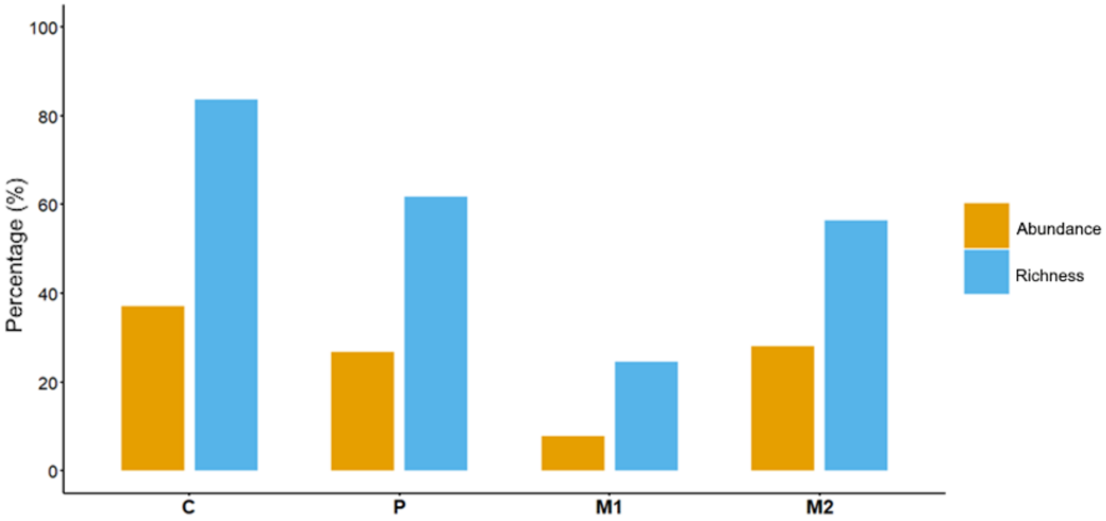

Figure 2. Percentage distribution of bird abundance and species richness among the habitats surveyed in the middle basin of the Arroyo Saladillo, southern Santa Fe Province, Argentina. Legend: C (Corridor); M2 (Low-simplification matrix); M1 (Highly simplified matrix); P (Patch).

Regarding trophic guilds, 52% of species belonged to the group of birds that feed primarily on invertebrates, followed by omnivores (14%), carnivores (11%), herbivores and granivores (9% each), and frugivores and nectarivores (2% each).

Comparison of bird assemblage structure among landscape units

In the corridor, we obtained 9386 records (37% of the total) and a richness of 92 species (83.6% of the recorded species). In the highly simplified matrix (M1), we obtained 1994 records (7.8%) and 27 species (24.5%). In the low-simplification matrix (M2), we obtained 7126 records (28.1%) and 62 species (56.3%). Finally, in the patches, we obtained 6798 records (26.8%) and 68 species (61.8%; Fig. 3).

Based on the behavior of richness estimators for each landscape unit, it seems unlikely that a higher number of species than those recorded would be obtained even with increased sampling effort, as species accumulation curves tended to stabilize (Fig. 4).

To facilitate the ecological interpretation of diversity values, we calculated true diversity (D = exp(H’)). The values obtained were the following: C = 55.780, P = 38.910, M1 = 15.880, and M2 = 28.820, indicating that the corridor harbors the highest effective number of species, while M1 maintains the lowest effective diversity.

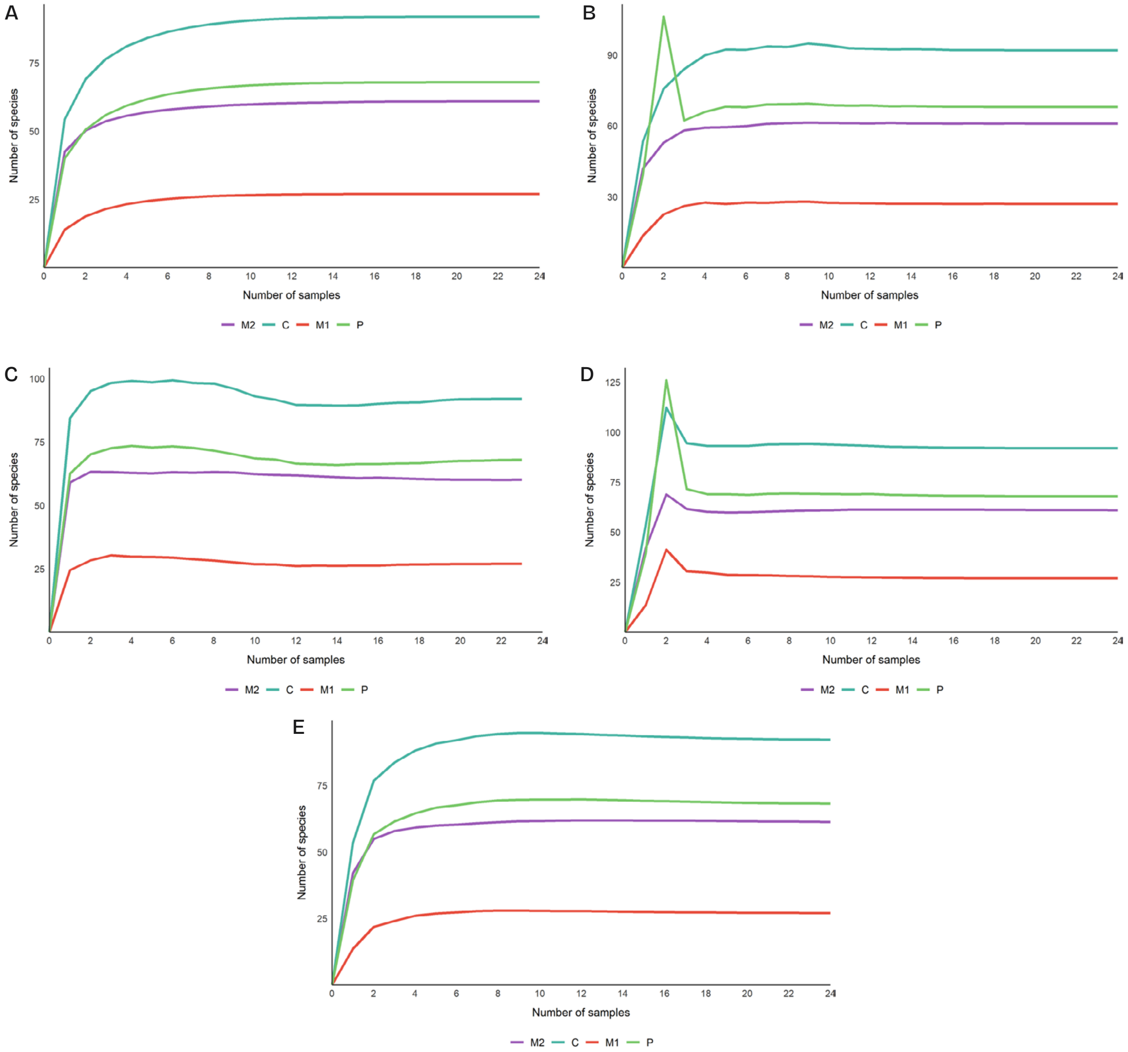

Figure 3. Species accumulation curves (S obs) and nonparametric species richness estimator curves for the four landscape units in the middle basin of the Arroyo Saladillo, southern Santa Fe Province, Argentina. (A) Observed richness (S obs), (B) ICE, (C) Chao 2, (D) Jack 2, and (E) Bootstrap. Each panel shows the curves for the four landscape units: corridor (C), patches (P), highly simplified matrix (M1), and low-simplification matrix (M2).

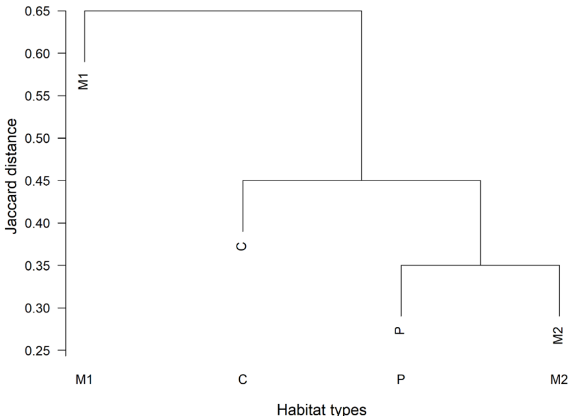

Figure 4. Hierarchical clustering dendrogram of bird species composition based on the Jaccard similarity index for each sampling site in the middle basin of the Arroyo Saladillo, southern Santa Fe Province, Argentina. Legend: C (Corridor); M2 (Low-simplification matrix); M1 (Highly simplified matrix); P (Patch).

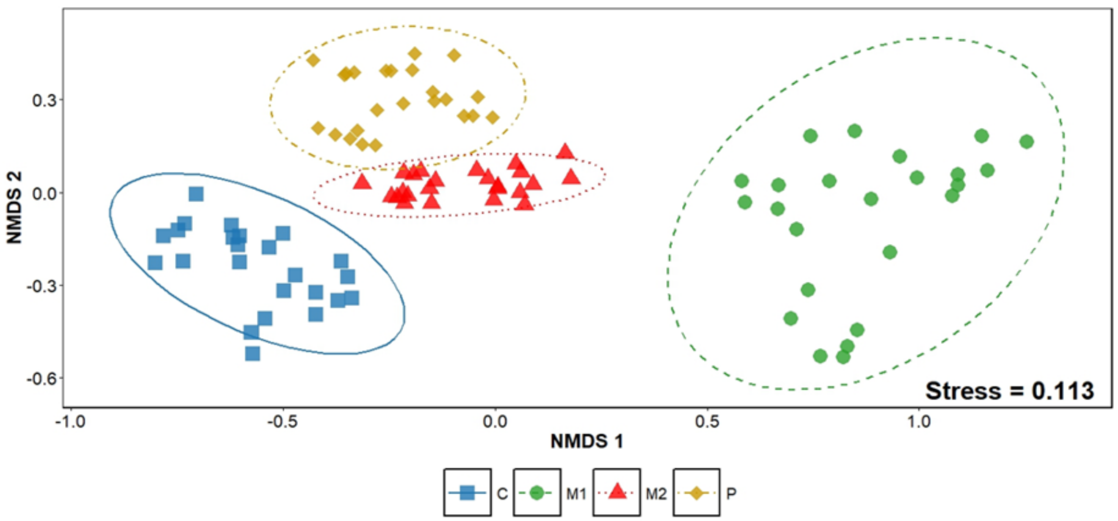

Figure 5. Non-metric multidimensional scaling (NMDS) ordination of bird species composition across four habitats in the middle basin of the Arroyo Saladillo, southern Santa Fe Province, Argentina. Legend: C (Corridor); M2 (Low-simplification matrix); M1 (Highly simplified matrix); P (Patch).

Comparison of species composition among landscape units

The Jaccard similarity coefficient showed low similarity in species composition between the highly simplified matrix (M1) and the other landscape units (corridor, patches, and low-simplification matrix), with values of J = 0.280, 0.360, and 0.430, respectively. The most similar landscape units were patches (P) and the low-simplification matrix (M2; J = 0.620), which also showed relatively high similarity with the corridor (0.510 and 0.520, respectively; Fig. 5).

These patterns are consistent with the NMDS, which showed a clear segregation among the four landscape units, indicating marked differences in species composition (Fig. 6). Sites clustered consistently in ordination space according to landscape unit, with the corridor showing the greatest differentiation from the highly simplified matrix (M1), while the low-simplification matrix (M2) and patches (P) showed more similar compositions. The PERMANOVA confirmed that landscape unit type explained a significant proportion of the observed variation ($R^2 = 0.545$, $p = 0.001$), indicating that each landscape unit harbors a distinct bird assemblage (Fig. 6).

Comparison of trophic guilds among landscape units

The distribution of trophic guilds varied among landscape units. In the corridor (C), patches (P), and the low-simplification matrix (M2), approximately half of the species were insectivorous. In contrast, in the highly simplified matrix (M1), this proportion decreased to 30%, where granivorous species predominated (37%). Omnivores reached their highest proportion in M2 (21%), with no major differences among the other units. Carnivores were most represented in C (12%), followed by P and M2 (9% each), while no species from this group were recorded in M1.

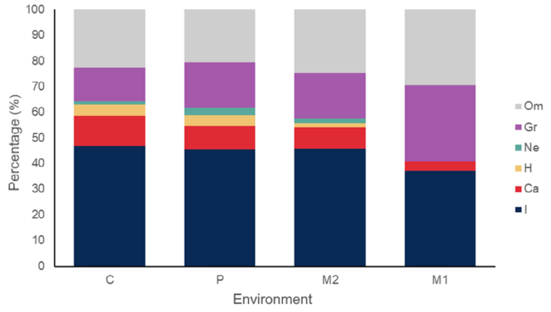

Figure 6. Percentage distribution of trophic guilds across the different habitats studied in the middle basin of the Arroyo Saladillo, southern Santa Fe Province, Argentina. Legend: Habitats: C (Corridor); M2 (Low-simplification matrix); M1 (Highly simplified matrix); P (Patch). Trophic guilds: Om (Omnivores); Gr (Granivores); Ne (Nectarivores); He (Herbivores); Ca (Carnivores); In (Insectivores).

The indicator species analysis ('multipatt') showed statistically significant associations of carnivorous, herbivorous, and nectarivorous guilds with specific landscape units ($p < 0.000$ in all cases). These three guilds were mainly associated with C, M2, and P and showed no association with M1. In contrast, omnivorous, granivorous, and insectivorous guilds did not show affinity for any particular unit, occurring broadly across all four landscape units.

Seasonal variation of bird assemblages among Landscape units

The GLMMs showed a significant interaction between landscape unit and season for all three analyzed variables (abundance: $\chi^2 = 92.410$, df = 9, $p < 0.001$; richness: $\chi^2 = 17.980$, df = 9, $p = 0.035$; diversity: $\chi^2 = 92.980$, df = 9, $p < 0.001$).

Post hoc Tukey comparisons revealed a consistent pattern across all seasons (Figs. 7, 8, 9): the corridor (C) showed the highest values, the highly simplified matrix (M1) the lowest, while patches (P) and the low-simplification matrix (M2) showed intermediate values with no significant differences between them in most seasons, particularly in spring (abundance and diversity: $p = 0.999$; richness: $p = 0.975$).

This pattern indicates that the hierarchy C > M2 = P > M1 is maintained throughout the year, although the magnitude of differences fluctuates seasonally.

The interaction between landscape unit and year was not significant for any of the variables ($p > 0.050$ in all cases), indicating that the observed patterns remained consistent between 2021 and 2022.

DISCUSSION

The analyses conducted in the present study highlight and reinforce not only the importance and role of patches and biological corridors in highly anthropized landscapes, but also the potential of diversified production systems to increase connectivity among ecosystem remnants of high conservation value. The results suggest that diversified production systems embedded within the dominant matrix as low-simplification areas (M2) provide a more complex and heterogeneous habitat for wildlife than conventional agricultural fields (M1), as they support greater bird richness and diversity, variables that are positively associated with habitat heterogeneity (Frutos et al. 2016). This structural diversity, at both the vertical and horizontal levels, provides a greater abundance and variety of microhabitats for birds, allowing them to select optimal sites to establish territories and complete their life cycles. In the present study, the low-simplification matrix (M2) tended to function similarly to patches (P) in terms of bird richness, abundance, and diversity, whereas the highly simplified matrix (M1) supported the most depauperate assemblages. Species recorded that may contribute to the control of rodent disease vectors associated with croplands include, for example, *Tyto furcata*, *Rupornis magnirostris*, and *Falco sparverius*. Biondi et al. (2005) described *Daptrius chimango* as a predator of several

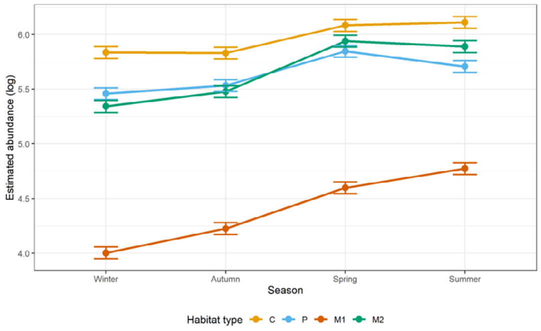

Figure 7. Estimated values from the generalized linear mixed model (GLMM) for bird abundance (log scale) across the four landscape units (C, P, M1, M2) throughout the seasons of the year in the middle basin of the Arroyo Saladillo, southern Santa Fe Province, Argentina. Error bars represent 95% confidence intervals. Legend: Sum (summer); Aut (autumn); Win (winter); Spr (spring); C (Corridor); M2 (Low-simplification matrix); M1 (Highly simplified matrix); P (Patch).

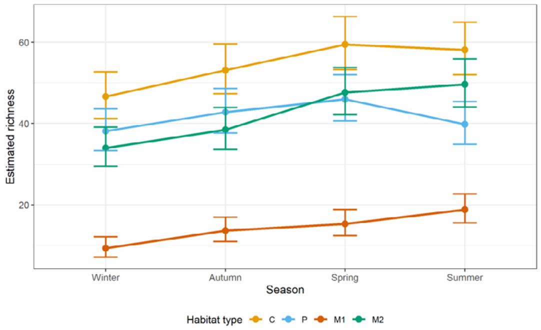

Figure 8. Estimated values from the generalized linear mixed model (GLMM) for species richness across the four landscape units (C, P, M1, M2) throughout the seasons of the year in the middle basin of the Arroyo Saladillo, southern Santa Fe Province, Argentina. Error bars represent 95% confidence intervals. Legend: Sum (summer); Aut (autumn); Win (winter); Spr (spring); C (Corridor); M2 (Low-simplification matrix); M1 (Highly simplified matrix); P (Patch).

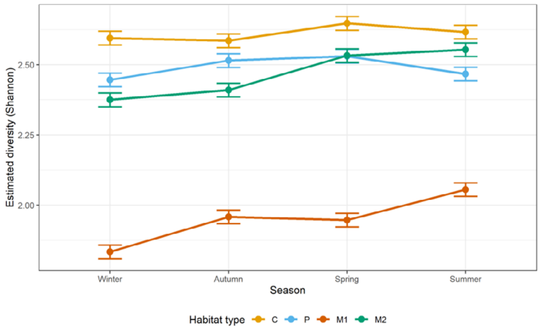

Figure 9. Estimated values from the generalized linear mixed model (GLMM) for the Shannon–Wiener diversity index across the four landscape units (C, P, M1, M2) throughout the seasons of the year in the middle basin of the Arroyo Saladillo, southern Santa Fe Province, Argentina. Error bars represent 95% confidence intervals. Legend: Sum (summer); Aut (autumn); Win (winter); Spr (spring); C (Corridor); M2 (Low-simplification matrix); M1 (Highly simplified matrix); P (Patch).

species of the family Scarabaeidae, which are known to damage a variety of crops. Likewise, some birds of prey play an important role in agroecosystems by contributing to the biological control of species that can affect crops, such as parakeets and doves (Sergio et al. 2008). However, some of these birds are scavengers and perform equally important ecological functions by removing organic remains, facilitating nutrient recycling, and reducing the proliferation of infectious sources that could promote zoonotic diseases (Morales-Reyes et al. 2015). Together, both groups contribute to the regulation and ecological balance of productive and natural environments.

The largest group of birds recorded belonged to the Passeriformes, which play an important role in controlling invertebrates that may be considered crop pests, as well as in consuming seeds, particularly those of grasses (Alessio et al. 2005, Goijman et al. 2020). Identifying key species that provide ecosystem services may be an appropriate starting point for developing conservation measures (Gorosabel et al. 2020). To achieve this, information that enables long-term population monitoring is essential, since it would allow assessment of how the ecosystem services provided by these species are affected.

The pattern observed for herbivores suggests greater selectivity in habitat use, possibly associated with specific requirements for plant resources available only in certain landscape units. In contrast, the homogeneous distribution of the remaining guilds suggests greater ecological plasticity and a higher capacity to exploit diverse trophic resources across the different habitat types evaluated.

These trends are reflected differently among landscape units, as is clearly evident in the agricultural environment (M1), where granivorous species account for a higher proportion of the assemblage, as reported by Verga et al. (2018) and Codesido et al. (2008). However, unlike Verga et al. (2018), who concluded that habitat fragmentation did not negatively affect the abundance of resources used by birds, our results show a reduction in the number of species in this environment as a consequence of habitat modification. As noted by Codesido et al. (2008), this type of simplification impoverishes the vegetation structure of croplands and their associated habitats, resulting in a decline in resource availability.

The low similarity in species composition between the highly simplified matrix (M1) and the other landscape units (C, P, and M2; J = 0.280, 0.360, and 0.430, respectively) may be associated with the high degree of habitat homogenization in this environment; the intensive use of agrochemicals, which reduces food availability (seeds and insects); and the lower presence of key structural elements such as trees and shrubs that many bird species use for nesting, perching, or foraging. This specialization of the agricultural landscape reduces the assemblage to a few generalist species, resulting in the loss of ecosystem services (Zaccagnini et al. 2011). In this regard, Codesido et al. (2013) reported that total bird abundance, as well as the abundance and richness of grassland specialists, were lower in cropland landscapes than in livestock and mixed-production landscapes. This occurs because crops, particularly under no-till farming and herbicide-tolerant soybean cultivation, simplify habitat structure and reduce roadside vegetation, and agricultural operations may reduce the nesting success of ground-nesting birds. The greater representation of generalist species in bird assemblages of Pampas agroecosystems suggests that agricultural activities that modify habitats often benefit these species, allowing them to become more common (Codesido et al. 2012). The same authors also pointed out that grassland specialist species are among the most vulnerable because of the destruction and fragmentation of their natural habitat by intensive agriculture. Similarly, Zufiaurre et al. (2016) reported that bird assemblages are impoverished in agricultural fields compared with livestock fields, attributing this difference to the greater structural homogeneity of croplands, which simplifies habitat and reduces the number of available niches, whereas livestock fields create greater structural variability and resource diversity through grazing. Annual cropland is therefore more detrimental to bird communities than cattle grazing in Pampas agroecosystems (Codesido et al. 2013). In our study, the highest similarity occurred between patches and the low-simplification matrix (P and M2; J = 0.620), suggesting that fields with lower levels of anthropogenic disturbance that retain natural elements can support part of the biodiversity typically associated with more conserved environments. Azpiroz & Blake (2009), in turn, suggested that planted pastures benefit several common species that do not reach high densities in croplands, but negatively affect birds restricted to native grasslands. Consequently, many Pampas bird species, particularly insectivores and granivores, can use both landscape units, whereas grassland specialists do not use planted pastures, making the conservation of natural remnants essential for their protection.

The patterns observed in the NMDS indicate that species composition differs consistently among landscape units, with clearly segregated communities. The marked separation of the corridor from the other units, together with the relative similarity between M2 and patches, suggests that the structural characteristics of each environment strongly influence the composition of its bird assemblages. Both approaches (the dendrogram based on the Jaccard coefficient and the NMDS ordination combined with PERMANOVA) evaluated community composition from complementary perspectives: the dendrogram reflects hierarchical similarity relationships, whereas the NMDS describes gradients in multivariate space, reinforcing the observed patterns. These results, supported by the PERMANOVA, reinforce the idea that each environment harbors a distinct bird community, probably associated with differences in vegetation cover, habitat heterogeneity, and resource availability.

In addition, M1 showed the greatest differences relative to the other landscape units in terms of richness, abundance, and diversity. This pattern can be explained by differences in land use, which generate variation in resource availability (Codesido et al. 2008). In particular, seasonal changes in diversity were more pronounced in M1, which is expected considering that the dominant crops in the region are planted in spring and harvested during summer–autumn, leaving fields with little vegetation cover throughout winter. In this regard, Leveau & Leveau (2004) noted that soybean monoculture is based on glyphosate-resistant cultivars and the intensive use of agrochemicals to eliminate weeds, leading to the impoverishment of vegetation structure and a consequent decline in bird abundance. According to Whitford (1997), interannual variation in bird diversity may also be associated with changes in precipitation regimes and with the transformations that vegetation undergoes throughout its phenological cycle.

In contrast, the M2 environment, with a lower degree of anthropogenic disturbance, showed higher values of richness, abundance, and diversity. This environment, characterized by greater ground cover and the presence of extensive livestock production, provides a more heterogeneous vegetation structure that promotes foraging opportunities on invertebrates and seeds (Codesido et al. 2008). Likewise, seasonal changes were less pronounced in this environment, which may be attributed to the effect of permanent pastures and livestock grazing, both of which introduce structural variability into the habitat. The results show that, across the four landscape units studied, bird richness and abundance were highest during spring and summer. These findings are consistent with those of Leveau & Leveau (2011), who attributed this pattern to the arrival of species that are austral migrants. In addition, it may be associated with the search for food and nesting sites, as this period coincides with the breeding season of most bird species.

The greatest seasonal changes were also recorded in M2, with marked declines from summer and spring to autumn. These results differ from those of Leveau et al. (2024), who proposed that greater diversity within landscape units leads to greater stability in bird diversity. Under this hypothesis, M1 would have been expected to exhibit the greatest seasonal variation. However, this discrepancy may be explained by the fact that landscape units such as M2 provide a greater abundance of resources during the breeding season, resulting in increased activity and the presence of species that arrive in search of food and nesting sites. This interpretation is consistent with Zufiaurre et al. (2016), who found that livestock fields consistently supported higher species richness than agricultural fields during spring and summer, whereas landscape units such as M1 consistently maintained low bird abundance and limited species turnover.

Our results indicate that bird diversity in the middle basin of the Arroyo Saladillo varies markedly among seasons, but above all according to land use and land cover in each landscape unit. Environments that retain greater vegetation diversity and experience lower levels of human disturbance, such as biological corridors, patches, and fields managed under more diversified production systems, support a greater abundance and variety of birds throughout the year. These findings highlight the importance of promoting management practices that integrate biodiversity conservation into productive landscapes. They also underscore the need to advance policies that recognize the value of vegetation patches and biological corridors as fundamental components of ecological balance in these highly transformed landscapes.

Regarding seasonal variation, the GLMMs showed that the hierarchy among landscape units remained consistent throughout the year: the corridor (C) exhibited the highest values of abundance, richness, and diversity in every season, whereas the highly simplified matrix (M1) consistently showed the lowest values, with no significant differences between patches (P) and the low-simplification matrix (M2) at any time of the year (post hoc comparisons, $p > 0.05$ in all cases). However, the magnitude of seasonal variation differed among landscape units: the decline in abundance from summer to autumn was more pronounced in C and M2 than in M1 and P (landscape unit × season interaction, $p < 0.001$), whereas the increase in diversity from winter to spring was greater in M2 and M1 than in C ($p = 0.012$). These findings differ partially from those reported by Zúñiga (2007), who found that spring was the season of highest diversity across all landscape units analyzed, suggesting that seasonal responses may vary according to land cover and land-use type.

Seasonal variation was also reflected in significant differences among most seasons, although summer and spring did not differ from one another. This pattern may be associated with the breeding and parental care period, as well as with seasonal changes in vegetation phenology that increase food availability for birds (Lorenzón et al. 2019, Leveau et al. 2024). Similarly, Codesido & Bilenca (2004) attributed higher bird diversity during these seasons to the greater abundance of invertebrates.

Regarding trophic guilds across the different landscape units, insectivorous birds were the best represented. These findings are consistent with those reported by Salas Correa & Mancera-Rodríguez (2018) and López-Muñoz et al. (2022), highlighting the importance of these trophic resources within the sampled landscape units.

In southern Santa Fe Province, Argentina, where grain and oilseed crops dominate the landscape and have led to a substantial reduction in natural habitats, changes in ecosystem structure and functioning, and, in most cases, habitat fragmentation (Rimoldi 2013), we found that bird assemblages tended to occur more frequently in the more stable landscape units, namely, the Arroyo Saladillo biological corridor, followed by patches and fields with a low degree of simplification. These findings support the proposal of Biasatti & Rimoldi (2022), who suggested implementing reverse fragmentation strategies in the region. This approach involves developing patches and biological corridors within the anthropogenic agroecosystem matrix to interrupt landscape homogeneity and promote biodiversity conservation in landscapes dominated by agricultural production.

Study limitations

The 100 m spacing between point counts is shorter than the 250 m generally recommended to ensure spatial independence in some sampling designs. This decision was dictated by the characteristics of the patch landscape unit (P), which consists of relatively small habitat areas where greater spacing would have compromised the representativeness of the sampled habitat.

Nevertheless, to account for the potential lack of independence among observations within each site, the analyses were complemented with generalized linear mixed models (GLMMs), including site as a random factor. The results were consistent with the initial analyses, suggesting that the observed patterns are robust despite this methodological limitation.

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