ORIGINAL ARTICLE

Diversity and dominance in bird assemblages across habitats in the Ñeembucú wetlands complex

Fátima Ortiz[1] | Patricia Salinas[1] | Medes Mendoza[1] | Griselda Zárate[1] |
Fátima Piris da Motta[1] | Alberto Esquivel[2] | Karina Núñez[1] | Fernando Silla[3]

[1]Escuela de Biología, Facultad de Ciencias Exactas y Naturales (FACEN), Universidad Nacional de Asunción, San Lorenzo, Paraguay

[2]Wildlife Paraguay, Benito Juárez, Luque, Paraguay

[3]Área de Ecología, Facultad de Biología, Universidad de Salamanca, Salamanca, Spain

Correspondence
Fernando Silla, Área de Ecología, Facultad de Biología, Campus Unamuno s/n, Universidad de Salamanca, Salamanca, Spain.
Email: fsilla@usal.es

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Abstract

Understanding how diversity responds to habitat heterogeneity in a landscape is a central issue for implementing effective conservation plans. In this study, we analyzed how the composition and abundance of neotropical bird assemblages vary among habitats in the Ñeembucú Wetlands Complex, the largest wetland system in Paraguay. Bird surveys were conducted during 1 year within dominant habitats in the landscape: riparian forests, natural grasslands, savannas, and anthropized sites. The Ñeembucú Wetlands Complex showed a high bird richness (209 species) that contrasted with a pattern of dominance by a small set of 16 species that comprised half of the abundance. This set of oligarchic species consists of generalist species that exploited a wide variety of habitats and were well adapted to human disturbance, contributing to an important overlap in the composition of assemblages. However, despite this overall similarity, there is still significant differentiation in bird assemblages, especially between habitats with the most contrasting vegetation physiognomy. Riparian forests and savannas showed higher diversity values than the more structurally homogeneous grasslands. Also, all natural habitats showed, in general, higher diversity values than anthropized sites. Oligarchic species had higher importance in anthropized environments, which also had the most uneven distribution of abundance between species, indicating the dominance by a smaller number of species and the loss of ecological diversity as farmland and urban development increase.

Abstract in Spanish is available with online material.

KEYWORDS
anthropogenic impact, avian assemblages, beta diversity, habitat heterogeneity, neotropical wetlands, oligarchic species, Paraguay

1 | INTRODUCTION

Understanding how habitat heterogeneity enhances biological diversity is a central issue for implementing and improving effective conservation (Anderle et al., 2022), especially in nonprotected areas where anthropogenic land use leads to habitat loss and fragmentation (Guadagnin & Maltchik, 2007; Morante-Filho et al., 2015) and the erosion of beta diversity (β-diversity; Karp et al., 2012, 2018). β-diversity

can be defined as the variation in community composition among a set of sites within a given spatial or temporal extent (Anderson et al., 2011; Whittaker, 1960). However, β-diversity depends on the degree of habitat specialization and the relation between the abundance of specialist versus generalist species in heterogeneous landscapes. For example, if specialist species, those adapted to narrow environmental conditions or limited food resources, are locally abundant in their preferred habitats (like forest-specialist species), an increase in landscape heterogeneity by land-use changes may also increase β-diversity in the tropics (Newbold et al., 2016). Alternatively, generalist species have, by definition, broad environmental tolerances, and, if they are dominant in abundance in the landscape, the resulting habitat conversion may favor the same species and homogenize communities (Karp et al., 2018). Patterns of generalist and abundant species in tree communities have given rise to the emerging concept of "hyperdominance" in the study of diversity and functioning of tropical ecosystems (Fauset et al., 2015; Ter Steege et al., 2013). This concept originates from the seminal work by Pitman et al. (2001), who reported a consistent pattern of dominance by a relatively small but abundant set of plant species, called "oligarchs." Since then, evidence has accumulated reinforcing the existence of a general pattern of oligarchic dominance in tropical forests (Arellano et al., 2016; Morera-Beita et al., 2019; Svenning et al., 2004). However, whereas the term "oligarchs" refers to highly abundant and frequent species at the landscape-regional level, "hyperdominant" refers to larger geographic scales such as the Amazon basin.

Birds are one of the most diverse groups of vertebrates and, owing to the multiple ways in which they can be directly and indirectly observed, are excellent for studying patterns in diversity and community organization (Karp et al., 2012; Montaño-Centellas et al., 2021; Pellissier et al., 2018). Birds also play key roles in many ecological processes, such as pollination, seed dispersal, the regulation of invertebrate populations, and scavenging (Sekercioglu et al., 2016; Pigot et al., 2020). Moreover, in some geographical areas, such as the tropics, there is a high diversity of bird species, which has been explained, in part, by higher net primary productivity allowing for increased niche packing (Pellissier et al., 2018; Pigot et al., 2016). Thus, because of the important impact that habitats have on bird ecology and conservation, numerous studies have set out to analyze how the characteristics of habitats, such as vegetation complexity and composition, and abiotic factors, mainly temperature and humidity, can influence the structure and the composition of bird assemblages, and how environmental heterogeneity in the landscape contributes to alpha and beta diversity (Azpiroz & Blake, 2009; Anderle et al., 2022; de Deus et al., 2020; Guadagnin & Maltchik, 2007; Karp et al., 2012, 2018; MacGregor-Fors & Schondube, 2011; Morante-Filho et al., 2015; Maya-Elizarrarás & Schondube, 2015).

In contrast, few comparable data sets are available that analyze the abundance and distribution of tropical bird communities, especially at scales relevant to questions of species dominance (Blake & Loiselle, 2009), which limits our understanding of factors influencing bird community structure. In tropical forests, bird assemblages dominated by a small set of species have been described (Anderson & Naka, 2011; Blake, 2007; Blake & Loiselle, 2009; Naka, 2004; Robinson et al., 2000). However, it is not clear whether these patterns of abundance are the result of the local dominance of a small group of species or true oligarchic species (sensu Pitman et al., 2013). Dominance by locally abundant species can arise via two nonexclusive processes: (1) by species highly adapted to the biotic and abiotic components of their environment (niche hypothesis); and (2) by neutral processes (sensu Hubbell, 2001), where individuals of all species can thrive equally well and are competitively equal, but with limited propagule dispersal that spatially structures community composition (Tuomisto & Ruokolainen, 2006). Conversely, oligarchic species, in the strict sense, are abundant and frequent species that have broader environmental tolerances than less common species, although not necessarily indifferent to environmental heterogeneity, showing higher abundances in the most favorable habitats (Morera-Beita et al., 2019; Pitman et al., 2013).

To analyze how the composition and abundance distribution of neotropical bird assemblages vary among habitats throughout a landscape, we focused our attention on the Ñeembucú Wetlands Complex, the largest wetland system in Paraguay. The Ñeembucú Wetlands Complex is located within the Paraguay-Paraná-La Plata river system, which has the 9th largest water discharge into oceans and the 5th largest drainage area of rivers worldwide (Junk, 2013; Milliman & Meade, 1983). It comprises an extensive area of clustered shallow lakes, flooded savannahs, grasslands, and forested patches, and is one of the least explored regions in Paraguay (Mereles et al., 2005). Until recently, most of the Ñeembucú Wetlands Complex has existed in an almost pristine state due to a low human population density. However, from 2006 to 2021 there has been an increasing trend toward the loss of forest and vegetated wetlands due to agricultural and urban development, with extensive cattle ranching and agriculture (rice, wheat, and soy) being the main economic activities in the area (O'Leary, 2022). Consequently, for this work, we established two hypotheses. The first hypothesis stated that all the habitats of the Ñeembucú Wetlands Complex would show a consistent pattern of dominance by a relatively small set of oligarchic bird species (sensu Pitman et al., 2013). In a second hypothesis, and complementary to this pattern, we also expected that the oligarchic species would have greater weight in the total abundance in anthropized habitats. By contrast, the locally dominant species (nonoligarchs) would be more important in natural habitats since the composition and abundance of bird assemblages would vary relative to the dominant habitat types of the Ñeembucú complex (riparian forests, natural grasslands, palm savannas, and anthropized habitats). Specifically, we expected anthropized habitats to have the lowest values for the different components of alpha diversity and more impoverished assemblages than those of natural habitats.

2 | METHODS

2.1 | Study area

The study areas are located in the Humid Chaco ecoregion, in the Ñeembucú Department (southern Paraguay, Figure 1), and belong to the Ñeembucú Wetlands Complex. The regional climate is tropical humid with a marked seasonality: the mean annual precipitation averages 1400–1500 mm (Fogel, 2000) but with a dry season in winter. The average temperatures are around 16–17°C in winter (May–August) and 25–26°C in the warmer season (December–March). The altitude of the study area ranges between 50 and 124 m above sea level (a.s.l.).

Four dominant habitat types were considered in the landscape: riparian forests, natural grasslands, savannas, and anthropized habitats. Riparian forests are directly or indirectly associated with water, as they are subject to periodic flooding during the summer; they can be found along the edges of rivers, streams, and lakes or forming forest islands surrounded by wetlands and floodplains (de Egea et al., 2012; Vogt & Mereles, 2005). Primary forest patches have a main canopy that is up to 25 m high, dominated by *Enterolobium contortisiliquun*, *Syagrus romanzoffiana*, *Aspidosperma quebracho-blanco*, *Libidibia paraguariensis*, *Microlobius foetidus*, and *Guazuma ulmifolia*. Savannas are also subject to periodic flooding and are found on soils with high clay and salt content. The dominant species is the palm *Copernicia alba*, with a sparse or absent shrub layer,
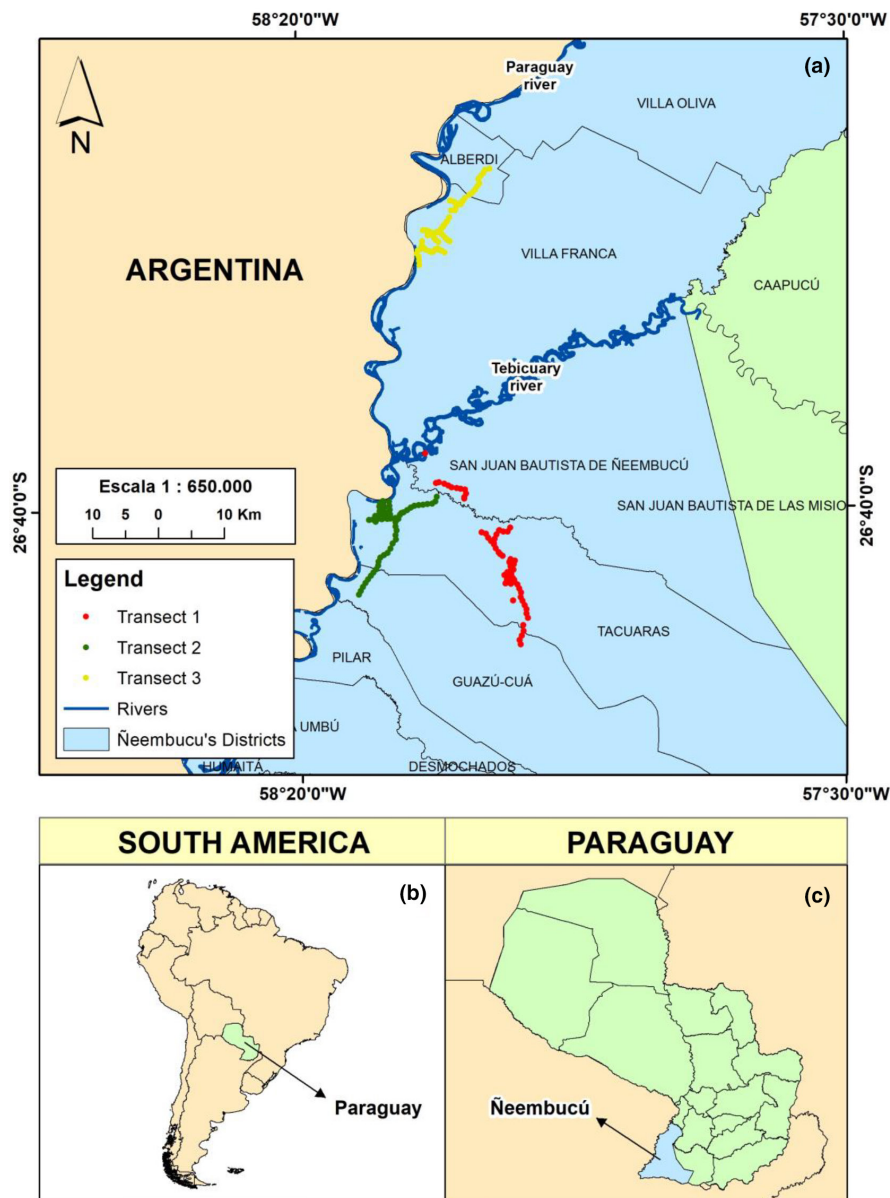
FIGURE 1 (a) Locations of the count points along the three transects in the Ñeembucú Wetland Complex; (b) Location of Paraguay in South America; (c) Location of Ñeembucú Department in Paraguay.

and an herbaceous cover dominated by *Hyptis lappacea*, *Pluchea sagittalis*, and *Chromolaena christiaeana* (de Egea et al., 2012; Vogt & Mereles, 2005). In the paleobasins of the Paraná River, where soils are sandy, the landscape is dominated by grasslands of *Andropogon* spp., *Coleataenia prionitis*, *Elionurus muticus*, *Sorghastrum pellitum*, and *Schizachyrium* spp., and sometimes with the presence of scattered woody species such as *Cecropia pachystachya* and *E. contortisiliquum* (de Egea et al., 2012; Vogt & Mereles, 2005). The selected anthropized count points included modified sites with a clear human influence that were mainly located on ranches and the periphery of small townships and villages. They generally comprised individual houses with yards, barns, orchards, small pastures, and unpaved roads (Figure S1).

2.2 | Field sampling and data collection

In the terrestrial habitats identified in the study area, bird surveys were carried out during 158 point counts between October 2020 and July 2021. Forty-three points were selected in riparian forests, 30 in natural grasslands, 50 in *Copernicia* savannas, and 35 in anthropized sites. The number of points per habitat was based on their importance within the landscape, but not directly proportional due to accessibility constraints and security issues. The sampling points were distributed along three transects in the districts of Alberdi, Guazú-Cuá, San Juan Bautista, and Tacuarás Villa Franca (Figure 1) and were separated by a minimum distance of 500–600m to avoid counting the same individuals twice (Esquivel & Peris, 2008). Although it was initially planned to sample each point count three times, for security reasons 41% of the points (11 of 43 points in riparian forest, 14 of 30 in natural grasslands, 23 of 50 in savannas and 17 of 35 in anthropized sites) could only be sampled twice; the rest were sampled three times. At each point count, all birds seen or heard within a radius of 50m from the center of each site within 5min of arriving at the sample point were counted (Ralph et al., 1996). Bird sampling began at dawn, from 6:00 to 10:00a.m., and during the afternoon, from 4:00 to 7:00p.m. Of the total of 408 inventories, 143 were carried out in the dry season (May–September), and 265 in the wet season (October–April). Adverse weather conditions (heavy rains) were avoided, and all bird sampling was carried out by the same person (Fátima Ortíz).

Oligarchic species were defined in terms of abundance and frequency, being the dominant species that contributed to 50% of all individuals detected during all point counts conducted (Ter Steege et al., 2013) and being present in more than half of the habitats (≥3 habitats). Local dominants were defined as the species that comprised 50% of all individuals detected in one habitat type but excluding the oligarchic species. Species that were neither oligarchic nor locally dominant could range from frequent but low abundance species to very rare species (species recorded with a single individual). In addition, species were classified as waterbirds (WB), wetland dependent (W), and non-wetland dependent (N-W) following Lorenzón et al. (2019).

2.3 | Data analysis

Hill numbers (Hill, 1973) were calculated as estimators of the alpha diversity of bird assemblages in each habitat type using the R package *iNEXT* (Chao et al., 2014; Hsieh et al., 2022). We calculated species richness ($q = 0$), Shannon's exponential of diversity ($q = 1$), where species are weighted by their frequencies, and Simpson diversity ($q = 2$), the inverse of Simpson concentration, which increases the weight of more common species at the expense of rare species. Rarefaction/extrapolation curves were estimated for each q order and habitat, and extrapolations were made to the twice the number of individuals sampled per habitat. Confidence intervals (CI) at 95% were estimated to determine whether there were significant differences among habitat types-overlapping confidence intervals implied there were no significant differences (Hsieh et al., 2022). Sample coverage was used as an estimator of the reliability of comparisons of the rarefaction/extrapolation curves (Chao & Jost, 2012).

Differences in the proportion of oligarchic species among habitats were assessed through a linear model using the *lm* function of the *vegan* package (Oksanen et al., 2022). For this, a model incorporating habitat type as fixed term (M_{hab}) was compared with a null model set by removing the fixed term (M_{null}) using the Akaike Information Criterion corrected for small sample size (AICc, Anderson & Burnham, 2002), and habitat type was considered significant when $\Delta AICc M_{hab}-M_{null}$ was ≥2.0 units (Anderson & Burnham, 2002). Post hoc comparisons between habitat types were performed using the *emmeans* function of the *emmeans* package (Lenth, 2024). Normality and homoscedasticity of the linear model were checked with the Shapiro–Wilk and Breusch-Pagan tests, respectively.

To explore differences in the composition of bird assemblages among habitats, we performed a nonmetric multidimensional scaling (NMDS) using Bray-Curtis as a measure of dissimilarity. Since the number of visits to each sampling point was not the same, we standardized the data so the value for any variable (species) for each sampling point was expressed relative to the maximum value for that sampling point in the whole data matrix (Quinn et al., 2002). To obtain a convergent solution and an interpretable graphical configuration consistent with the distances of the dissimilarity matrix (stress value <0.2; Quinn & Keough, 2002), we set the number of dimensions (k) to 5 and performed 1000 iterations using the *metaMDS* function of the vegan package (Oksanen et al., 2022). NMDS analyses were performed for the entire dataset and for the dry (May–September) and wet (October–April) seasons. To test for differences in bird composition among habitats, we performed a permutational multivariate analysis of variance or PERMANOVA (Anderson et al., 2001), a nonparametric method for partitioning distance matrices using the permutation test with pseudo-F ratios and thus calculating p-values. Significant differences among all habitats were tested using 1000 permutations, Bray–Curtis dissimilarity and PERMANOVA were calculated through the *vegdist* and *adonis* functions of the vegan package (Oksanen et al., 2022), while significant differences between habitat pairs were tested using the *pairwise. adonis* function of the *pairwiseAdonis* package (Martinez Arbizu, 2020). In addition,

a similarity percentage analysis, SIMPER, was performed using the *simper* function of the vegan package (Oksanen et al., 2022) to decompose the Bray–Curtis dissimilarity and estimate the percentage contribution of each species to the overall mean dissimilarity (Clarke, 1993).

In addition, beta diversity between habitat pairs was calculated. Considering bird abundances, beta diversity was divided into two components: balance and abundance gradient (Baselga, 2017). Balanced (β.BAL) variation in abundance occurs when individuals of some species in one habitat are replaced by the same number of individuals of different species in another habitat, and an abundance gradient (β.GRA) is where some individuals are lost from one habitat to the other but without loss of species (Baselga et al., 2017). When using abundance data, the balance and abundance gradient components are analogous to the turnover and nestedness components of incidence-based dissimilarity (Baselga, 2010, 2017), respectively. Partitions of beta diversity were calculated using the Bray-Curtis distance with the *betapart* package (Baselga et al., 2023).

3 | RESULTS

We found a total of 209 bird species, 182 genera, 54 families, and 26 orders from a record of 7362 individuals (2419 in savannas, 2015 in riparian forests, 1749 in anthropized sites and 1179 in grasslands), with Passeriformes being the order with the highest number of species (101). Twenty-one of the bird species were migratory. According to IUCN (2023), three species were listed as being Near Threatened (NT): *Rhea americana*, *Amazona aestiva*, and *Sporophila ruficollis* and, based on the MADES list of protected species (2019), the endangered species *Ara chloropterus* and the threatened *Accipiter bicolor*

species were also detected. The number of species per habitat ranged from 115 (natural grasslands) to 157 (palm savannas), with 34.9% of the 209 species being detected in the four habitats. Sample coverage was extremely high and similar among the habitat types (98.5–99.3) which allowed robust comparisons of diversity estimates between habitat types. Palm savannas showed greater richness than grasslands and anthropized habitats (order $q = 0$, Figure 2), while forested sites presented intermediate values. Concerning Shannon diversity, riparian forests and palm savannas presented the largest and most similar values, while anthropized habitats presented the lowest diversity (order $q = 1$, Figure 2). Finally, riparian forests had the largest Simpson diversity indicating that this habitat, although it had fewer species and a similar Shannon index than savannas, had a higher evenness among the common species (and that the high number of species in savannas is related to the presence of rare species). And once again, anthropized habitats presented the lowest Simpson diversity, with palm savannas and grasslands showing intermediate values (order $q = 2$, Figure 2).

Considering the entire landscape, 16 species (7.7% of all species) were classified as oligarchic species, representing 51.0% of all individuals, with all species being detected in all four habitat types. Of the 16 species, 14 were considered N-W species, one was a wetland species (*Progne tapera*), and one was a waterbird (*Aramides ypecaha*). In all four habitats, a subset of these oligarchic species accounted for between 41.2% and 47.8% of the local abundance (Figure 3, Table 1), with the anthropized habitat having the highest percentage (47.8%), and the riparian forests showing the lowest percentage (41.2%) of local abundance accounted for by oligarchic species. Local dominant species (not classified as regional oligarchic species) made up 2.5% to 9.1% of the abundance detected in all habitat types, with the riparian forests being the habitat with the most local dominant species
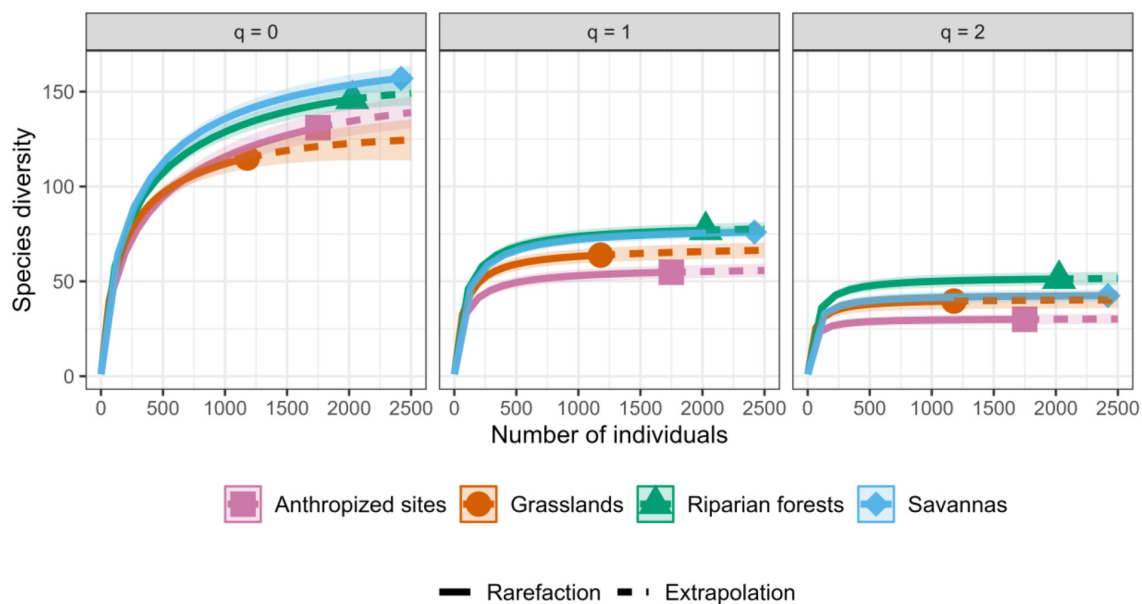
FIGURE 2 Rarefaction (solid line segment) and extrapolation (dotted line segments) curves based on sample size with 95% confidence intervals (shaded areas) for the four separate habitat types, in order of diversity: $Q = 0$ (species richness), $q = 1$ (Shannon's diversity) and $q = 2$ (Simpson's diversity). The solid squares/dots/triangles represent the reference samples.
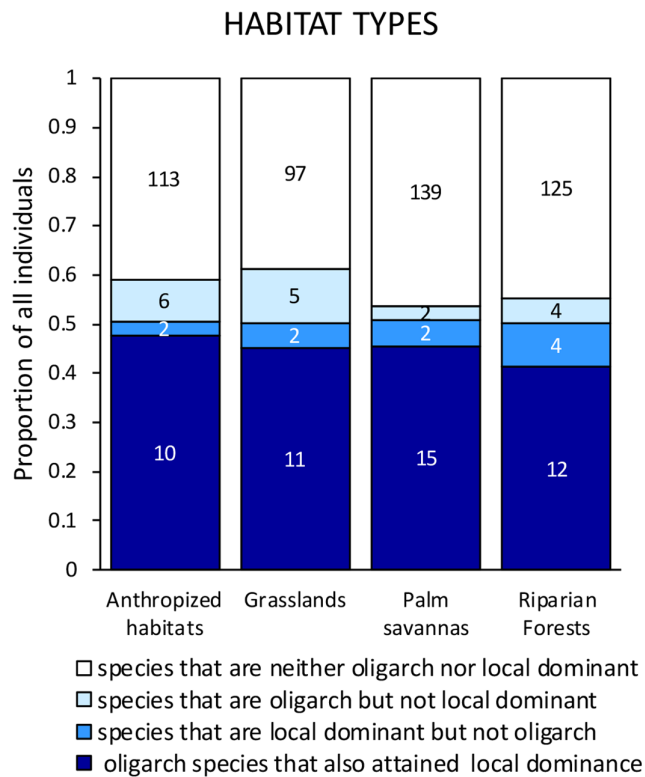
HABITAT TYPES

FIGURE 3 Proportions of abundance by habitat type belonging to species that are oligarchs, local dominant, or none of these. Integers show the number of species in each compartment. Local dominants (oligarch or not) are species that contributed to the accumulated 50 percent of individuals found in that habitat. Oligarchs are species that contributed to the cumulative 50% of individuals in all plots and were present in at least three of the habitats.

(Figure 3, Table 1). Seven species (3.3% of all species) classified as oligarchs (*Myiopsitta monachus*, *P. tapera*, *Vanellus chilensis*, *Paroaria coronata*, *Furnarius rufus*, *Patagioenas picazuro*, and *Phacellodomus ruber*) were also local dominants in the four habitat types (Table 1).

Habitat type contributed to significantly explain differences in the proportion of oligarch species among sites (ΔAICcM$_{hab}$-M$_{null}$=10.05 units). Anthropized sites showed the highest contribution of oligarch species to the relative abundance, and significantly different from the other three natural habitats (Tukey's tests: anthropized/grasslands, $p=.039$; anthropized/riparian forests, $p<.001$; anthropized/savannas, $p=.019$). The three natural habitats showed a similar contribution and nonsignificant difference of oligarch species (Figures 4 and S2).

Nonmetric multidimensional analysis (NMDS, stress value=0.1789) showed that assemblages in palm savannas had a high degree of overlap with the other three habitat types (Figure 5). Forest assemblages showed a distinct pattern of composition relative to grassland and anthropized habitats, while the latter also showed significant overlap (Figure 5). NMDS analyses showed similar configurations for dry and wet seasons (Figures S3 and S4). The PERMANOVA test showed a significant difference in composition of bird assemblages among habitats (df=3, F=2.40, $p<.001$) and the

adjusted *p*-values of pairwise tests showed significant differences among all of them ($p<.05$) except between savanna/grassland and savanna/anthropized comparisons. Table S1 lists the contribution of each species to the overall mean Bray–Curtis dissimilarity. In general, only between 11.0%–26.2% of the total dissimilarity was attributed to significant differences between species, with oligarch species contributing between 39.1% and 76.8% of this dissimilarity (Table S1). For example, in the case of anthropized habitats and grasslands, three (*P. tapera*, *Molothrus bonariensis*, and *Tyrannus melancholicus*) and one oligarch species (*Guira guira*), respectively, always showed a significant contribution to their dissimilarity with other habitats. On the other hand, local dominants, such as *Cyclarhis gujanensis*, and to a lesser extent *Cyanocorax chrysops*, contributed significantly to dissimilarity in riparian forest habitats (Table S1).

The analysis of beta diversity showed that total dissimilarity among habitats was dominated by the balance component (Figure 6), where increases in abundance in some species were compensated for by decreases in abundance in other species from one habitat to another. Although there were no marked differences in total dissimilarity among habitats, the results are consistent with the NMDS analysis, with the palm savanna habitat showing the lowest mean dissimilarity with the other three, and the highest dissimilarity between the forest habitat and the grassland and anthropized habitats (Figure 6).

4 | DISCUSSION

In Paraguay, 688 bird species have been described (Birdlife International, 2023), while 330 and 356 species have been documented for the Ñeembucú region according to Hicks et al. (2022) and eBird Paraguay (2023), respectively. This study recorded 30.1% of the birds distributed in Paraguay and around 60% of those described for the Ñeembucú region. In contrast to the great richness of bird species in the study region, our results showed a clear pattern of dominance of a small set of 16 oligarchic species (7.7% of all species recorded) comprising half of the abundance of birds in the Ñeembucú Wetlands Complex. Patterns of relatively few frequently reported species and many rarely reported species are typical of many tropical assemblages at local scales, even when sampling methods differ (e.g., observations vs. captures) (Robinson et al., 2000; Blake, 2007; Azpiroz & Blake, 2009; Blake & Loiselle, 2009; Borges et al., 2019; dos Anjos et al., 2023.). However, our results clearly support the validity of the "oligarch hypothesis" (Pitman et al., 2013) to explain the structure of bird assemblages at larger scales (Blake, 2007; Naka, 2004), as there was a consistent pattern of dominance by a relatively small but abundant assemblage of bird species across different habitats in the Ñeembucú Wetlands Complex.

A subset of seven species was classified as being oligarchic and locally dominant in all four habitats. This core of seven species consists of generalist species that exploit a wide variety of habitats, are well adapted to human disturbance, and have a wide geographical distribution ranging from the Southern Cone

TABLE 1 Species that contributed to the accumulated 50% of abundance in each habitat. Species were ordered from the highest to the lowest relative abundance of all sampled points combined, and relative abundance is shown only when this value contributed to the accumulated 50%.

Species	Type	Savannas	Riparian forests	Grasslands	Anthropized sites	All sites combined
Myiopsitta monachus	N-W	0.1023	0.0600	0.0751	0.1103	0.0888
Vanellus chilensis	N-W	0.0527	0.0371	0.1031	0.0725	0.0608
Progne tapera	W	0.0315	0.0643	0.0310	0.0803	0.0524
Patagioenas picazuro	N-W	0.0421	0.0305	0.0240	0.0318	0.0337
Paroaria coronata	N-W	0.0346	0.0262	0.0240	0.0354	0.0309
Furnarius rufus	N-W	0.0270	0.0311	0.0350	0.0318	0.0305
Phacellodomus ruber	N-W	0.0275	0.0262	0.0350	0.0275	0.0290
Guira guira	N-W	0.0199	0.0278	0.0561		0.0269
Columbina picui	N-W	0.0261		0.0300		0.0220
Sicalis flaveola	N-W	0.0204	0.0240		0.0228	0.0217
Aramides ypecaha	WB	0.0168	0.0251	0.0330		0.0210
Saltator coerulescens	N-W	0.0182	0.0305			0.0194
Tyrannus melancholicus	N-W				0.0306	0.0188
Molothrus bonariensis	N-W	0.0182		0.0300	0.0318	0.0185
Coragyps atratus	N-W	0.0168	0.0294			0.0183
Pitangus sulphuratus	N-W	0.0186				0.0178
*Cyanocorax chrysops**	N-W		0.0365			0.01657
*Ortalis canicollis**	N-W		0.0180			0.01346
*Forpus xanthopterygius**	N-W		0.0180			0.01287
*Phimosus infuscatus**	WB				0.0258	0.0121
*Machetornis rixosa**	N-W				0.0228	0.0121
*Chauna torquata**	WB	0.0266				0.0121
*Agelasticus cyanopus**	W	0.0253				0.0109
*Cyclarhis gujanensis**	N-W		0.0180			0.0078
*Mycteria americana**	WB			0.0250		0.0067
*Bulbucus ibis**	N-W			0.0250		0.0037

Note: All species were oligarch, except local dominant species that were indicated with an asterisk (*). Species were classified as waterbirds (WB), wetland dependent (W) and non-wetland dependent (N-W) following Lorenzón et al. (2019).

(typically an area covering northern Argentina, Bolivia, Paraguay, Uruguay, and southern Brazil) to almost all South America and part of Mesoamerica, with one of them (*M. monachus*) being an invasive species in many parts of the world (IUCN, 2023). Except for *P. tapera*, a migrant species that arrives for the breeding season, all are resident species. However, these seven common and abundant species have different survival strategies in the Ñeembucú Wetlands Complex, where *P. picazuro* is a specialist granivorous species that feed on the ground (Quiroga et al., 2018), *M. monachus* feeds on seeds and fruits showing a marked plasticity to feed on the ground of grasslands and cultivars as well as in trees (Aramburú & Corbalán, 2000), *P. coronata* is an omnivorous species that feeds mainly on insects, seeds, and fruits and typically forages low in the shrub layer or on the ground (Quiroga et al., 2018; Segura & Arturi, 2012), *P. tapera* is an aerial insectivore species (Oniki-Willis et al., 2022), *P. ruber* mainly feeds on insects in the shrub/tree stratum (Quiroga et al., 2018), and *F. rufus* and *V. chilensis* feed on

invertebrates (insects, earthworms, etc.) but mainly on the ground (Faria et al., 2018; Gantz et al., 2009; Quiroga et al., 2018). The other nine species are also generalist species well adapted to open areas and anthropized habitats, although in some cases they prefer some habitats to others. For example, *Saltator coerulescens* was more abundant in forest and palm savannas in accordance with their habitat requirements (Beltzer et al., 2004), while the brood parasite *M. bonariensis* was almost absent in forests, probably because host nests are more easily and quickly detected in open areas than under dense cover (Sharp & Kus, 2006).

Moreover, of the 16 oligarchic species, 14 are considered terrestrial species, only one is a typical waterbird, *A. ypecaha*, and the last one, *P. tapera* is strongly associated with rivers and wetlands. The dominance in the abundance of terrestrial species is partly explained by the fact that we did not focus our surveys on open water habitats, but also because they are generalist species that exploit diverse upland habitats during the high-water periods and expand
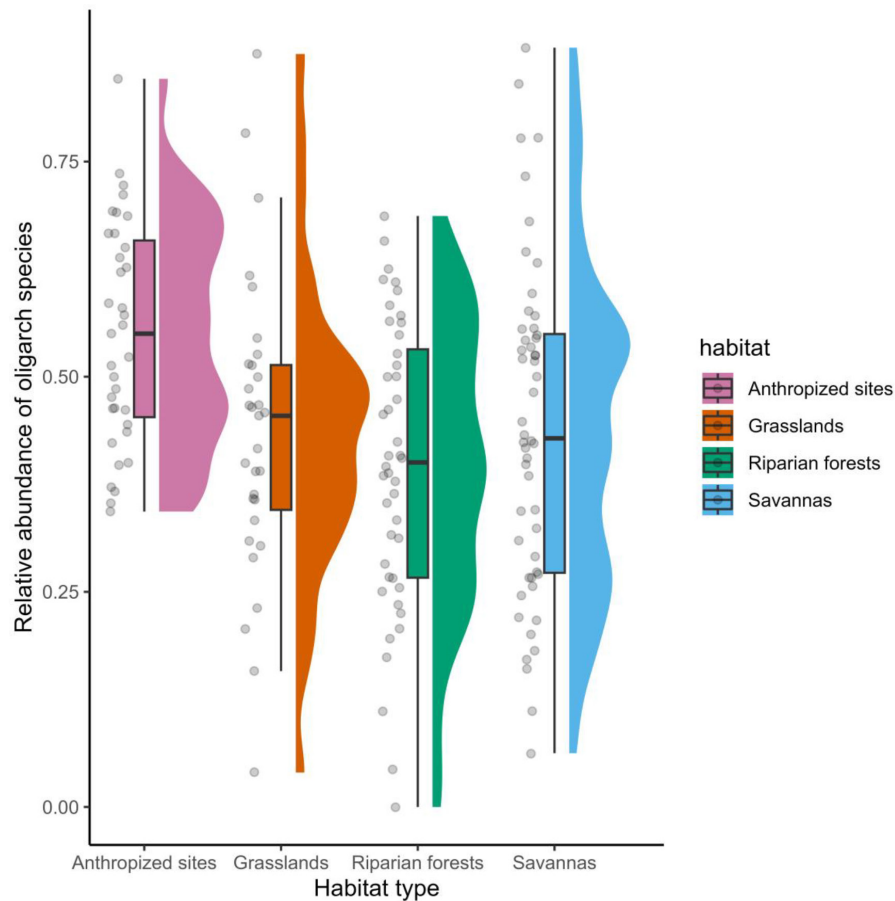
FIGURE 4 Raincloud plots (from left to right: The raw data, a box plot, and halved violin plot) of the relative abundance of oligarch species per site and habitat type.
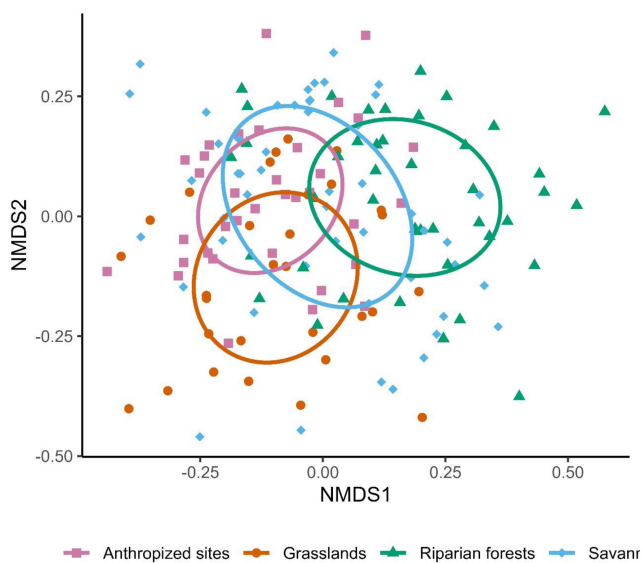

FIGURE 5 Non-metric Multidimensional Analysis of the bird assemblages sampled at each point counts (dots) for the four habitat types. Solid lines of the ellipsoids indicate standard deviations of the centroids. Stress value: 0.1789.

opportunistically during low-water periods (Lorenzón et al., 2017, 2019). The wetlands of the Paraná basin show high intra- and inter-annual oscillations in water levels so that predominantly aquatic and terrestrial phases alternate relative to the seasonality and amount of rainfall throughout the basin. Similarly, some species, such as the omnivorous terrestrial bird, *Pitangus sulphuratus*, although not dependent on wetlands, can exploit aquatic environments where they dive directly into the water to catch fish (Lorenzón et al., 2016).

When considering differences in diversity parameters, the more structurally complex habitats, the riparian forests and palm savannas, presented larger values than the more simple structural grasslands (da Frota et al., 2020; Macchi et al., 2013; Petit et al., 1999; Sam et al., 2019). This occurs because the lower vertical stratification is associated with less habitat complexity and food resource diversity, and the number of potential niches is correspondingly smaller (Arriaga-Weiss et al., 2008; da Frota et al., 2020; Macchi et al., 2013; Maya-Elizarrarás & Schondube, 2015). Also, all natural habitats showed higher diversity values than anthropized sites, with the only exception of a similar species richness between grasslands and anthropized sites. In fact, anthropized sites showed the highest proportion of oligarch species, with only 3 species (2.3%
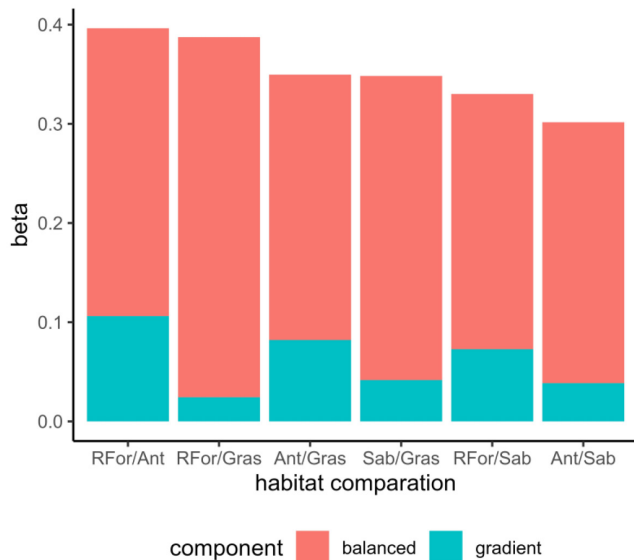
FIGURE 6 Beta diversity between all habitat pairs using the Bray-Curtis distance. Beta diversity is divided into two components: Balance and abundance gradient.

of species) accounting for 26.3% of the abundance, indicating that only a few opportunistic species (*M. monachus*, *V. chilesis* among others) consume most of the resources in human-modified habitats (MacGregor-Fors & Schondube, 2011; Domínguez-López & Ortega-Álvarez, 2014). It has been shown that in many cases bird richness and abundance have not been affected by land-use change (i.e., forest loss) at the landscape scale, as bird assemblages are composed of species that have different responses to environmental variables and anthropogenic impact, with bird species from sensitive habitats being replaced by those favored by human activity and habitat modification (Morante-Filho et al., 2015). However, our results argue against richness as the sole measure of diversity, as anthropized sites showed a relatively high species richness but more uneven distribution of abundance of individuals. This indicates dominance by a smaller set of species than in natural habitats that probably consume a larger proportion of available resources.

Parallel to the dominance of the subset of oligarchic species, we found that, in general, there was a significant overlap in the composition of assemblages among habitats, especially with palm savannas that were less dissimilar to the other habitats. Palm savannas are heterogeneous habitats with forest, shrub, and grassland elements that allow the coexistence of a rich bird diversity shared with the rest of the habitats of the Ñeembucú Wetlands Complex. Nevertheless, despite the overall similarity among the habitats, there is still sufficient differentiation between some bird assemblages, as beta diversity was dominated by the substitution in abundance of some other species (the balanced component of beta diversity), with nestedness playing an extremely minor role. In fact, the composition and abundance of bird assemblages usually respond to the wetland habitat type, with habitat availability being the major factor explaining variation in bird community structure, especially during the wet season (da Frota et al., 2020; de Deus et al., 2020). During the dry season, with the withdrawal of water, many understory and

terrestrial species expand their distribution, resulting in a reduction of habitat dissimilarity (da Frota et al., 2020; Lorenzón et al., 2017, 2019). In our study, the habitats that showed the highest level of dissimilarity were the most contrasted in physical structure: riparian forest and grassland habitats (Filloy et al., 2010; Maya-Elizarrarás & Schondube, 2015; Morante-Filho et al., 2015; Petit et al., 1999). The riparian forest had more weight for the local dominant species, relative to oligarch species, than the other habitats, with species such as *Cyclarhis gujanensis*, *C. chrysops*, *Cacicus chrysopterus*, *Cacicus haemorrhous*, *Crotophaga major*, and *Myiarchus tyrannulus* characterizing the bird assemblages in this habitat. Although none of these species were exclusively forest-dependent, they showed a clear preference for riparian forests, indicating that they can be susceptible to land conversion due to forest loss (de Deus et al., 2020; Morante-Filho et al., 2015; Yabe et al., 2010). On the other hand, grasslands are mainly identified by species typical of seasonally flooded lowlands and marshes such as *Certhiaxis cinnamomeus*, *Donacobius atricapilla*, and *Mycteria americana* (Beerens et al., 2015; Nunes, 2011; Restall et al., 2006). Additionally, other species characteristic of open grasslands were *Anthus chii*, *Athene cunicularia*, *Embernagra platensis* and *G. guira*, the latter an oligarchic species common across the landscape but which attained the highest relative abundance in grasslands. *G. guira* is a social species and group size has been explained mainly by grass cover alone as Guira Cuckoos are ground foragers, preying on insects and small invertebrates in the grass (Macedo & Bianchi, 1997). Finally, anthropized habitats showed the highest weight for oligarchic species, with several oligarch species like *P. tapera*, *M. bonariensis*, and *T. melancholicus* that are well adapted to open areas and human disturbance (Cristaldi et al., 2017; Domínguez-López & Ortega-Álvarez, 2014; Leveau, 2019; Sharp & Kus, 2006) and where anthropized habitats account for around the 40% of their total abundance. Interestingly, the American Kestrel (*Falco sparverius*) was also more associated with anthropic habitats, as traditional farmland has been found to have a positive impact on the breeding success and productivity of this species (Orozco-Valor & Grande, 2020). Recent evidence also indicates that, although this species is traditionally linked to agroecosystems, it is somewhat sensitive to agricultural intensification, especially soybean expansion in South America (Carrete et al., 2009; Orozco-Valor & Grande, 2020).

5 | CONCLUSIONS

The Ñeembucú Wetlands Complex showed a high bird richness (209 species) that contrasted with a pattern of dominance by a small set of 16 species that comprised half of the bird abundance. Therefore, our results support the validity of the "oligarch hypothesis" (Pitman et al., 2001) to explain the structure of the bird assemblages in the different habitats of our study region. This set of oligarchic species consists of generalist species that exploited a wide variety of habitats and were well adapted to human disturbance. Parallel to the dominance of the oligarchic species, there was significant overlap in the composition of assemblages across habitats, especially within palm savannas. However, despite this overall similarity, there is still

significant differentiation in bird composition among habitats, especially between the habitats with the most contrasting physical structure, the riparian forests and grasslands, as beta diversity was dominated by the balance component, with nestedness playing a rather minor role. In addition, the more structurally complex habitats, riparian forests and palm savannas, showed higher diversity values, and oligarchic species had a lower weight in abundance, than in the more structurally homogeneous grasslands and anthropized habitats. While most of the Ñeembucú Wetlands Complex is still in an almost pristine state of conservation due to a low human population density, there is an increasing trend of farmland and urban development. So, although our data suggest that most of the species in the Ñeembucú Wetlands Complex are generalist species that can be found in most of the habitats, and bird richness can be relatively resistant to an increase in human impact, it also showed that anthropized environments have the most uneven distribution of abundance between species, indicating the dominance by a smaller assemblage of species and the loss of ecological diversity.

CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to disclose.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad. rfj6q57jq.

ORCID

Fernando Silla https://orcid.org/0000-0001-9943-2572

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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