



WATERBIRD ANNUAL ASSEMBLAGE IN A ZONE OF THE VENEZUELAN LLANOS REGION

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Abstract · The Venezuelan Llanos is a floodplain region of global importance for waterbirds, but comprehensive surveys of waterbird assemblages that encompass the entire annual cycle are lacking. We conducted monthly fixed-point surveys of waterbirds at eight permanent lagoons within an agro-forestry landscape in the Llanos over an entire annual cycle, from April 2022 to March 2023. We recorded species richness and abundance and evaluated diversity, dominance, turnover patterns, and spatio-temporal variation to characterize assemblages and assess the conservation value of these wetlands. We recorded a total of 54 waterbird species, with greatest species richness and abundance at the largest Samancito lagoon. Month of the year significantly influenced species richness and abundance, peaking during the dry season. Structural traits (diversity, dominance, and species turnover) varied among lagoons, reflecting distinct ecological values and assemblages, with certain lagoons serving as functional hotspots for specific guilds, such as Gandaria lagoon for waders. Migratory species comprised a modest percent of species richness and total bird counts, peaking in the month of September (20% species richness; 12% abundance). Our findings underscore that wetlands within the Venezuelan Llanos were not functionally uniform, including also temporal dynamics of waterbird assemblages. Conservation and management strategies should recognize the complementary roles of different wetlands and account for seasonal variability in species use, thereby preserving permanent wetlands to support waterbird assemblages year-round, particularly during resource-scarce dry season.

Resumen · Los Llanos venezolanos constituyen una llanura de inundación de importancia global para las aves acuáticas, pero faltan estudios exhaustivos de las comunidades de estas aves que abarquen todo el ciclo anual. Realizamos censos mensuales de aves acuáticas desde puntos fijos en ocho lagunas permanentes dentro de un paisaje agroforestal en los Llanos a lo largo de un ciclo anual completo, desde abril de 2022 hasta marzo de 2023. Registramos la riqueza y abundancia de especies y evaluamos la diversidad, la dominancia, los patrones de recambio y la variación espacio-temporal para caracterizar las comunidades, así como valorar la importancia de conservación de estos humedales. Detectamos 54 especies de aves acuáticas, siendo la laguna de Samancito la que registró más especies y ejemplares. El mes del año influyó significativamente en la riqueza y abundancia de especies, alcanzando su máximo en la estación seca. Los rasgos estructurales (diversidad, dominancia y recambio de especies) variaron entre lagunas, reflejando valores ecológicos y comunidades distintas, con ciertas lagunas actuando como puntos funcionales clave para gremios específicos, como la laguna Gandaria para las aves limícolas. Las especies migratorias representaron un porcentaje modesto de la riqueza y abundancia, con un máximo en el mes de septiembre (20% de riqueza de especies; 12% de abundancia). Nuestros resultados subrayan que los humedales de los Llanos venezolanos no fueron funcionalmente uniformes, y presentaron dinámicas temporales en las comunidades de aves acuáticas. Las estrategias de conservación y gestión deben reconocer las funciones complementarias de los diferentes humedales, y tener en cuenta la variabilidad estacional en el uso de las especies, preservando así los humedales permanentes para sostener las comunidades de aves acuáticas durante todo el año, especialmente durante la estación seca con escasez de recursos.

Keywords: *bird counts · boreal migrants · community structure and diversity · waterbird community composition · wetlands*

INTRODUCTION

Waterbird assemblages are key indicators of the ecological health of wetlands (Bellamy 1993, Weller 1999, Zwarts et al. 2009). Waterfowl play vital roles in ecosystem functioning such as nutrient cycling, seed dispersal or pest control (Green and Elmberg 2014, Winton and Richardson 2017), also acting as indicators for monitoring environmental changes, habitat degradation and the impacts of climate change (Wrona et al. 2006, Amano et al. 2019). Regular monitoring of waterbirds provides critical data for understanding their distribution patterns, population dynamics and habitat use, which are pivotal for conservation policies and sustainable management of wetlands (Bildstein et al. 1991, Aarif et al. 2014, McFadden et al. 2017). This is particularly relevant in zones undergoing rapid human-induced changes, where wetlands face escalating threats from agriculture development, urbanization and climate-related hydrological shifts.

Waterbird assemblages have been widely studied across a broad range of humid zones worldwide (Weller 1999). A consistent finding across regions is that waterbird abundance, richness and community structure often show strong seasonal variations, driven by changes in flooding levels, food availability and migratory movements (Paracuellos 1996, Villarán Adánez 2000, Green et al. 2002,

Ramo et al. 2013). Consequently, many studies have emphasized the importance of accounting for seasonality when assessing wetland value for conservation (Weller 1999). Nevertheless, a substantial proportion of waterbird surveys are limited to specific periods of the year, commonly focusing on peak seasons such as the breeding period, the dry season, or migration windows, rather than covering complete annual cycles (Marchowski et al. 2025, Martínez-Curci et al. 2025, Zhang et al. 2025). Thus, comprehensive annual studies remain comparatively scarce in tropical floodplain areas, where hydrological dynamics are especially pronounced (Vilella and Baldassarre 2010). In the Venezuelan Llanos, despite their recognised importance for waterbirds at regional and continental scales, systematic surveys spanning an entire annual cycle are still very limited (Vilella and Baldassarre 2010), resulting in an incomplete understanding of how seasonal processes shape waterbird assemblages at the scale of individual wetlands.

Venezuela is a South American biodiversity hotspot with important waterbird populations due to its extensive network of aquatic ecosystems, including forested peatland, mangrove swamps, coastal marshes, riverine wetlands, seasonal floodplains or freshwater permanent wetlands (Galán de Mera and Linares Perea 2008). Los Llanos is a vast tropical herbaceous plain that hosts an extraordinary rich waterbird diversity including both resident and migrant species, hence being a region of international importance for the conservation of waterbirds (Vilella and Baldassarre 2010). Despite its ecological importance, Los Llanos is under increasing pressure from agro-forestry activities, with extensive areas being converted from natural savanna to agricultural land, and hydrological exploitation and alteration, which threaten its wetlands and the waterfowl depending on them (Chacón 2007). In parallel, waterbirds have been relatively poorly studied within the region, with the chief exception being the Neotropical Waterbird Census (Sainz-Borgo et al. 2023). However, this census is based on just two sampling days per year, in the dry (February) and the wet season (July), a protocol that is insufficient for a detailed characterization of wetlands due to the seasonal variation of waterbird assemblages over the annual cycle (Vilella and Baldassarre 2010). Comprehensive surveys of waterbirds in the Llanos region are therefore essential for identifying key wetlands, and to evaluate their relative contribution for waterbird conservation in this region.

We therefore aimed to evaluate waterbird assemblages at several permanent lagoons within a region of Los Llanos in Venezuela, with the goal of determining their value for conservation. We hypothesized that wetlands would be structurally distinct, and these differences could be reflected, even inferred, in the assemblage of waterbirds that use such environments. In this way, we provide data from one of the most iconic and ecologically dynamic landscapes to contribute to regional and national conservation priorities, and evaluate the importance of these wetlands from a flyway perspective, given the presence of migratory waterbird populations.

METHODS

Survey lagoons. We carried out surveys at eight wetland sites located within the Llanos region of Venezuela, within a property owned by Desarrollos Forestales San Carlos II, S.A., situated 12 km south of San Carlos city in the state of Cojedes, central-western Venezuelan Llanos (Figure 1). The wetlands were situated within a 11,742 ha fragmented habitat mosaic, originally covered by savannah-like habitat, but now comprising *Eucalyptus* and *Corymbia* timber plantations (55.6%), together with patches of natural habitat of forests and lagoons (36.25%) and areas of other uses (8.2%) like pastures, small urban areas, and roads (Leite De Souza et al. 2014). The region has average temperatures between 27°C and 32°C, and two marked climatological periods: the dry (November–April) and the rainy (May–October) season (Leite De Souza et al. 2014).

The eight survey wetlands were permanent freshwater bodies, all of which were protected, except for Ganadería that was only partially protected. Hunting and fishing were prohibited in all the lagoons, which remain in a relatively well-preserved ecological condition, thus potentially harbouring representative waterbird assemblages. The lagoons occurred within an altitudinal range of 114–132 m asl, with an average water surface area of 30 ± 41.8 ha (range: 0.4–99.9 ha). The smaller lagoons were Ganadería, Laguna 25, Laguna 11, and Topochal, ranging from 0.4–2.1 ha; the large lagoons were Cocos, Polvosito, and Samancito (58.6–99.9 ha), and Monos at 23.6 ha was in the mid-range.

Waterbird surveys. At each wetland site, we surveyed waterbirds once a month over the entire annual cycle, starting in April 2022 through to March 2023. We conducted one survey per site each month, with a mean 30 ± 8.5 days (range: 12–50 days) elapsed between subsequent surveys at the same site. When possible, more than a single site was surveyed on a given date.

We conducted counts from fixed survey points, except in the largest wetland of Samancito, where we surveyed a 50 m line-transect along the western shore of the lagoon. We carried out surveys from 07:00 to 09:00 am, on sunny and calm days with no wind, even during the wet season. One person (JCO) conducted counts, accompanied by a second observer who tallied the counts. Counts were conducted for approximately 15 min per wetland with the aim of registering all waterbirds occurring at each site, dedicating as much time as required, though being as rapid as possible to avoid over-counting individuals. All settled birds detected within 100 m from the observer were counted, without distinguishing between age classes. Flying individuals were omitted unless they landed on the water or in the nearby vegetation associated with the wetland.

We used the South American Classification Committee list as a taxonomic reference (Remsen et al. 2026). Each species was assigned a category of either sedentary or migratory (Supplementary Material 1). For sedentary, we considered all species that were strictly resident or that could have intra-tropical dispersal, although their movements remain unknown. We classified as migratory species all the boreal (Northern American) migrants that overwinter in Venezuela or other Southern American regions.

Statistical analyses. To determine whether month of the year influenced species richness or bird abundance we conducted Generalized Linear Mixed Models (GLMM), with one model for number of species and another for bird counts as dependent variables. We included month as a fixed factor and lagoon (site) as a random factor in models, and considered a Poisson error distribution. We used the function ‘glmer’ provided by package ‘lme4’ (Bates et al. 2014) run on the R environment (R Core Team 2025).

To disentangle potential structural patterns that may highlight the existence of variation between the sampled wetlands, we conducted a hierarchical analysis of clusters, based on an index of similarity (Morisita) and the UPGM method of ordination. We also conducted a Correspondence Analysis to visualize structural species-wetland relationships, and determine which species explained the degree of differentiation among sites. These multivariate analyses were carried out with PAST software (Hammer et al. 2001).

We also calculated a number of β -diversity-associated ecological parameters to describe additional structural patterns of waterbird assemblages at each wetland site, including: observed species richness, abundance (bird counts), diversity, dominance, and turnover patterns. We used the Shannon and

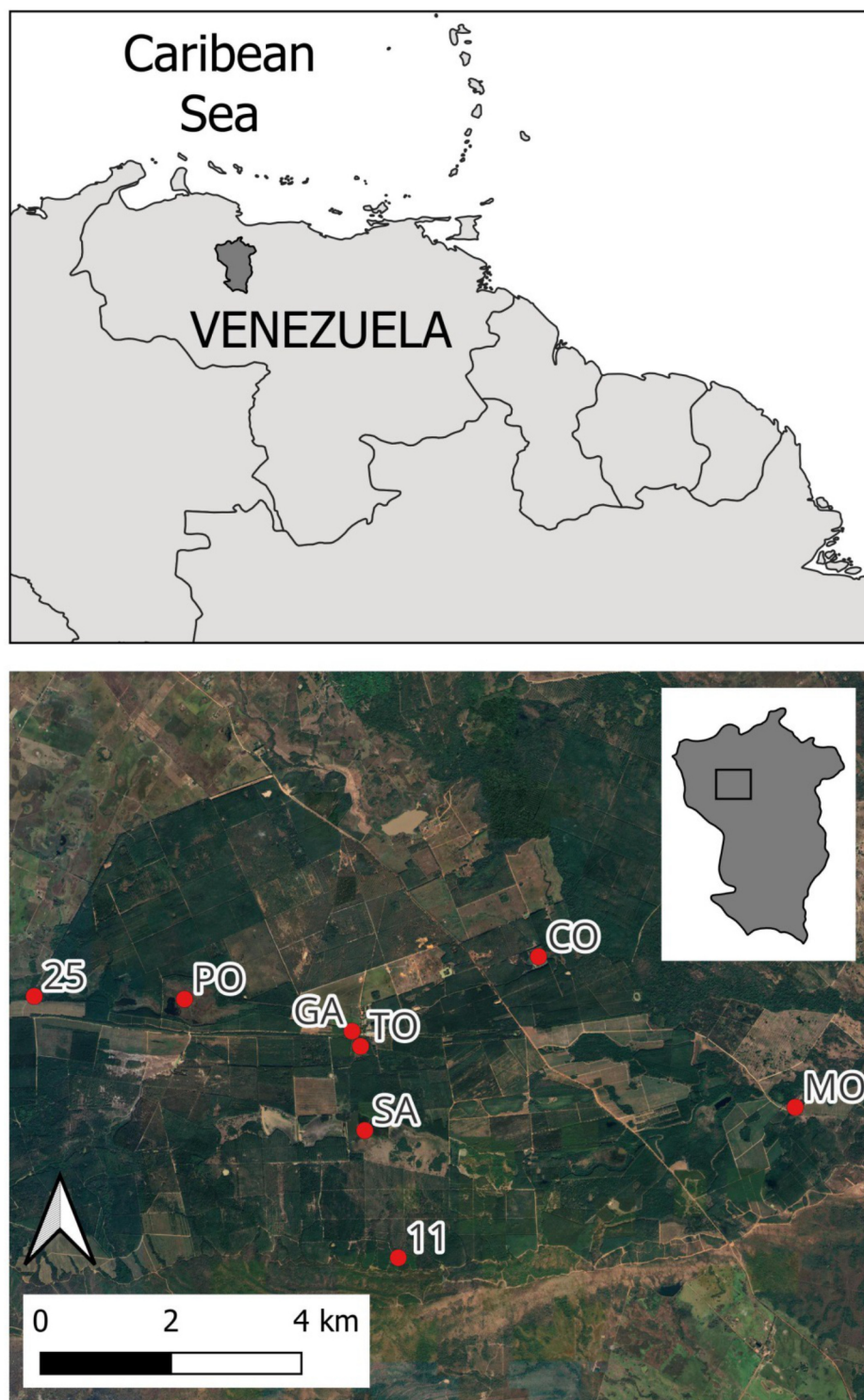


Figure 1. Distribution of eight surveyed wetlands, within the Cojedes State, Venezuela. Wetland codes: 11 – Laguna 11, 25 – Laguna 25, CO – Cocos, GA – Ganadería, MO – Monos, PO – Polvosito, SA – Samancito, TO – Topochal.

Simpson indices to calculate diversity and dominance, respectively (Magurran and McGill 2011). Variation of site-related species composition can be caused by two different phenomena (Baselga 2012): the replacement of several species by others from site to site (turnover), and a pattern where poorest sites are species subsets of the richest ones (nestedness). Using the ‘betapart’ package (Baselga and Orme 2012) in R, we calculated separately the turnover and nestedness components of β -diversity, with the aim of obtaining a mean turnover estimate for each wetland site. The turnover was calculated with the Jaccard index of dissimilarity (Baselga 2012).

RESULTS

Species richness and abundance. We registered a total of 5,653 waterbirds of 54 species from 11 Orders (Supplementary Material 1). Species richness per site varied from 22 species at Laguna 11 to 49 species at the largest Samancito lagoon (Table 1). Eight species were each recorded at only one site, whilst five species were present in all eight wetlands.

Most detected species belonged to the ‘resident’ category (45 resident species vs. 9 migratory species). Only five out the eight wetland sites hosted migrant species, with Ganadería hav-

Table 1. Main ecological indices related to β -diversity of each lagoon. The turnover rate is calculated considering nestedness (nest.) and replacement (repl.).

Ecological parameters	Laguna 11	Laguna 25	Cocos	Ganadería	Monos	Polvosito	Samancito	Topochal
Species richness	22	24	26	24	27	31	49	30
Counts (total birds)	423	370	519	274	359	571	2,855	282
Diversity	1.81	1.68	2.27	2.76	2.21	2.61	2.30	2.80
Dominance	0.28	0.30	0.15	0.08	0.19	0.13	0.19	0.09
Turnover (nest.)	0.13	0.10	0.09	0.08	0.09	0.11	0.33	0.10
Turnover (repl.)	0.33	0.34	0.34	0.47	0.32	0.31	0.13	0.29

ing an assemblage with slightly more than 20% of migrant species, followed by Samancito (14% migrants), Topochal (ca. 10%), Monos (7.4%) and Cocos (3.8%).

The two most abundant species were the Hoatzin *Opisthocomus hoazin* (20.6%) and the Black-bellied Whistling-Duck *Dendrocygna autumnnalis* (20.2%; Figure 2). The two second-most abundant species were the Cattle Egret *Ardea ibis* (12.6%) and Greater Ani *Crotophaga major* (7.3%), with the remaining species accumulating less than 5% of the counts in each case (Figure 2). The site that hosted the largest bird numbers was Samancito, with almost 3,000 counts (Table 1). By comparison, the other wetland sites totalled just a few hundreds of birds, from 282 counts in Topochal to 571 in Polvosito (Table 1).

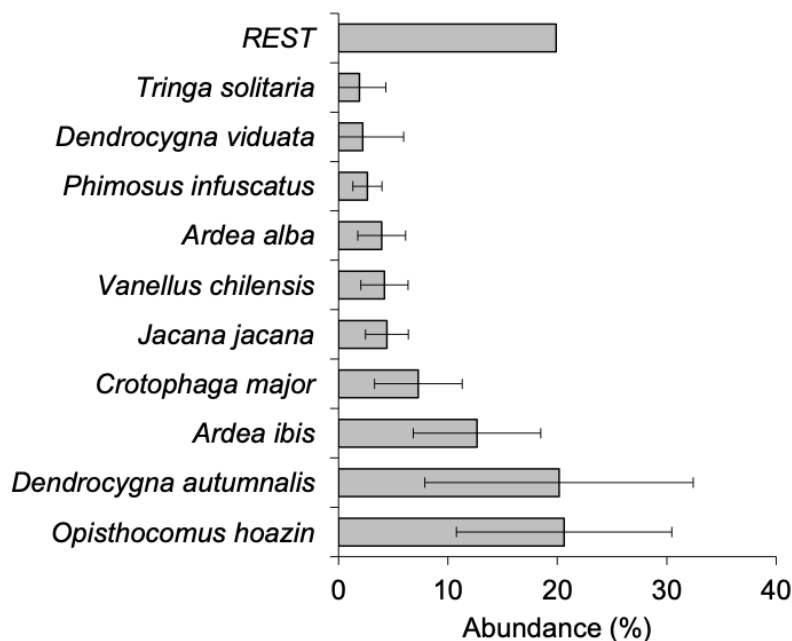
Temporal variation. After controlling for a random site-effect, GLMM showed that month of the year influenced species richness ($F_{11} = 3.706$, $P < 0.001$; R^2 : conditional 0.64, marginal 0.16), and waterbird abundance ($F_{11} = 108.25$, $P < 0.001$; R^2 : conditional 0.96, marginal 0.30). Greater species richness was registered in October, November, and December at the start of the dry season, and a minimum in April and July during the rainy season (Figure 3). Regarding abundance, we again found a peak in the dry season month of January, and a minimum in July during the rainy season (Figure 3).

The percentage of migrant species in waterbird assemblages showed two peaks in contribution of migrants during

February–April (10–12%) and in September (almost 20%; Figure 4). After the first initial peak in September, a decreasing percent of migrants was registered from October to January (Figure 4). Lowest percent of migrants occurred from May to August, with no migrants registered in May and <4% during the months of June to August (Figure 4). This pattern was similar when considering species richness or abundance, although percent contribution of migrants was lower when considering abundance (Figure 4).

Assembly-related structural traits. Cluster analysis revealed that the waterbird assemblage of Ganadería was distinct to the other lagoons (Figure 5). Correspondence analyses showed that this difference was due to species such as the Least Sandpiper *Calidris minutilla*, White-rumped Sandpiper *C. fuscicollis*, Spotted Sandpiper *Actitis macularius*, and Solitary Sandpiper *Tringa solitaria* (Figure 6) that were migratory waders registered mainly in this lagoon (Supplementary Material 1). Samancito also showed some degree of differentiation, mainly due to the presence/abundance of White-faced Whistling-Duck *Dendrocygna viduata*, Lesser Yellowlegs *Tringa flavipes*, and Greater Yellowlegs *Tringa melanoleuca* (Figure 6).

Diversity indices fluctuated between 1.68 and 2.80, showing the greatest diversity in Topochal (Table 1). By contrast, dominance was inversely related to diversity, ranging from 0.08 to 0.30, with Ganadería exhibiting the lowest value (Table 1). Nested turnover values remained relatively consistent,

**Figure 2.** Mean percent abundance ($\pm 95\%$ confidence interval) of the ten most frequent species detected at eight wetland sites of the Venezuelan Llanos region. REST: all remaining species.

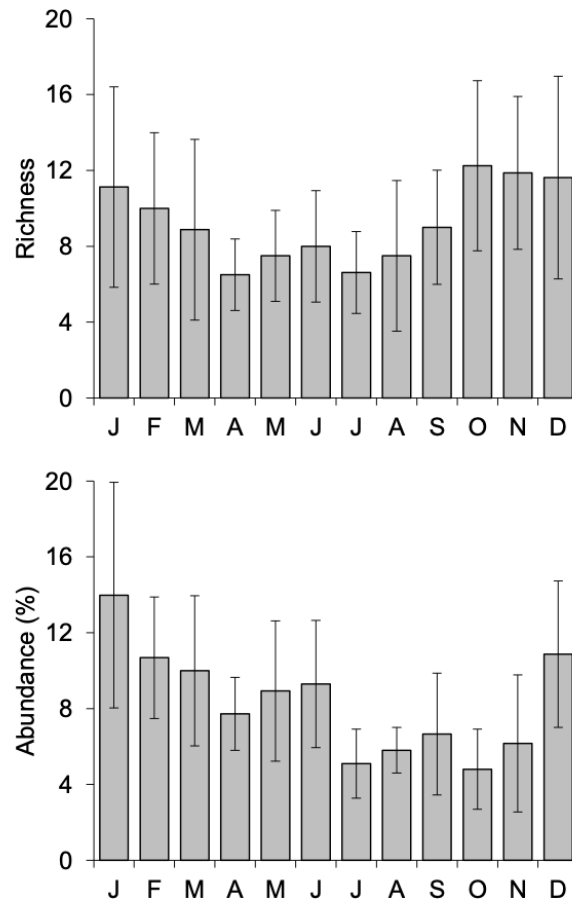


Figure 3. Monthly mean ($\pm 95\%$ confidence interval) species richness and percent waterbird abundance at eight wetland sites of the Venezuelan Llanos region, from April 2022 to March 2023.

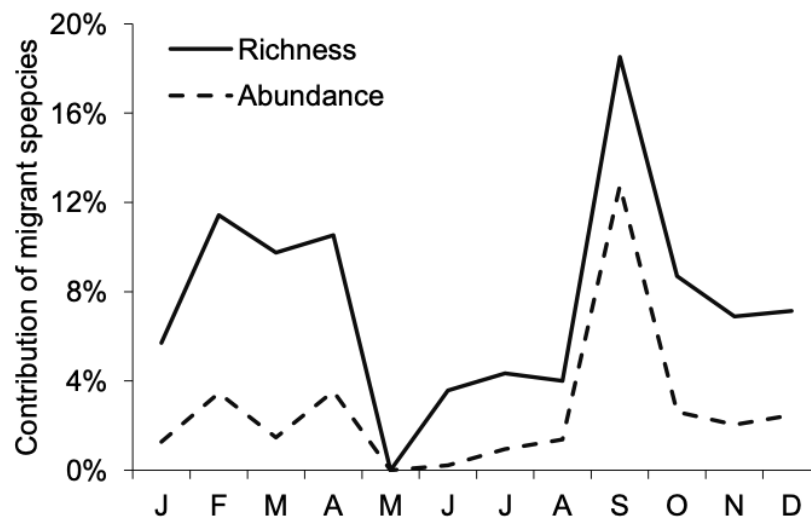


Figure 4. Monthly percent contribution of boreal migrants to species richness and abundance of waterbirds at eight wetland sites at Llanos region, Venezuela, from April 2022 to March 2023.

between 0.08 and 0.13, except for a spike at 0.33 in Samancito (Table 1). Replacement turnover was more variable, ranging between 0.13 and 0.47, with Ganadería displaying the greatest replacement turnover (Table 1).

DISCUSSION

Our results provide a comprehensive overview of waterbird assemblages in the Venezuelan Llanos over an entire annual cycle, revealing a significant influence of month on species richness and waterbird abundance. This adds to previous studies that, al-

though they covered larger spatial scales (Sainz-Borgo et al. 2023), did not consider sufficient temporal coverage to consider monthly or seasonal variations.

We found that both species richness and waterbird abundance peaked in the dry season months of November to January, with lowest values in July in the middle of the rainy season. These fluctuations align with known ecological dynamics of Llanos region, where hydrological fluctuations shape population dynamics and territory use of waterbirds (Vilella and Baldassarre 2010). Such findings also fit with the dynamics ob-

served in other American tropical wetlands (Lorenzón et al. 2019). During the dry season, wetlands become critical refuges for waterbirds as vast areas across the floodplain dry out, concentrating bird populations in remaining water bodies. Conversely, the wet season facilitates dispersal of waterbirds throughout newly inundated areas (Chacón 2007). These findings underscore the importance of keeping permanent wetland sites within the region to support waterbirds through the entire annual cycle, particularly during the dry season, when resources are scarce and concentrated at specific permanent water-bodies (Lorenzón et al. 2019). Alternatively, it may be that during the wet season the water level increases, reducing available shore-line for waterbird species that tend to rest and feed in this habitat.

Multivariate analysis also highlighted notable differences among the surveyed wetlands. In particular, the assembly of waterbirds detected in Ganadería lagoon was structurally distinct, primarily due to the presence of migratory waders. This suggests that certain lagoons serve specialized roles within the larger eco-

system, supporting specific guilds of waterbirds. Identifying such functional hotspots is of key importance for targeted conservation policies, ensuring that habitat management focuses on diverse species-specific ecological requirements given that these wetlands do not seem to be interchangeable.

Migratory birds comprised up to 12–20% of species richness, although their contribution in terms of abundance was modest, with less than 5% of all bird counts corresponding to boreal migrants, except in September (12% migrants). From a flyway perspective, the contribution of boreal migrants to species richness and abundance raises the importance of the Llanos region for conservation of American waterbirds. Protecting these wetlands helps to contribute to regional biodiversity as well as to broaden conservation efforts under an umbrella of international agreements (Sainz-Borgo et al. 2023). Given the vulnerability of the Llanos region to climatic change (García Montero 2022) and increasing agricultural pressure (Huber et al. 2006), our findings advocate for measures to safeguard these permanent wetlands. This includes integration of

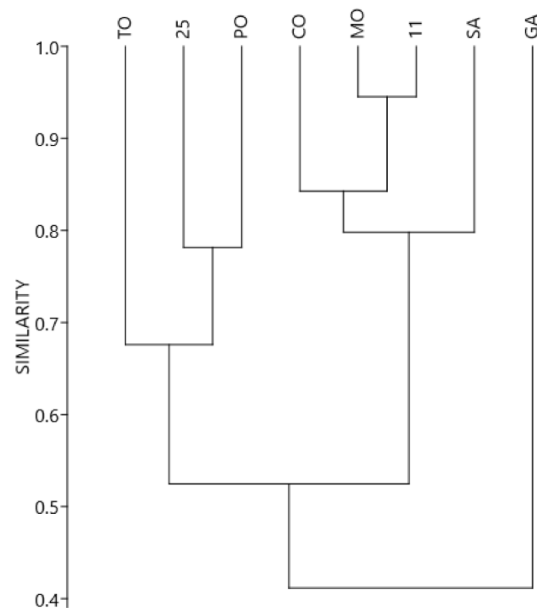


Figure 5. Hierarchical clustering ordination plot of eight surveyed wetlands based on a quantitative similarity analysis (UPGMA method using Morisita index). Site codes: 11 – Laguna 11, 25 – Laguna 25, CO – Cocos, GA – Ganadería, MO – Monos, PO – Polvosito, SA – Samancito, TO – Topochal.

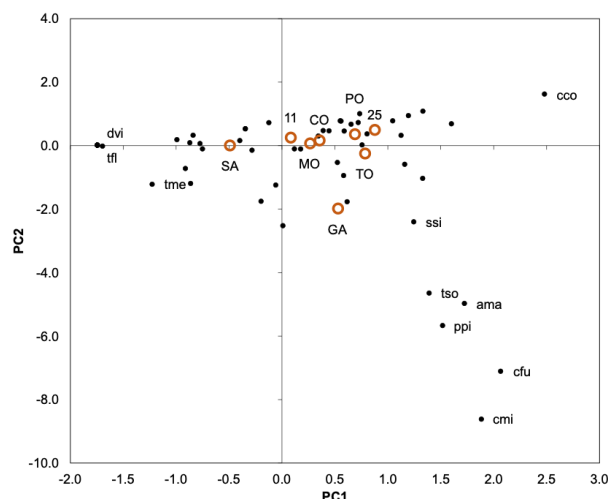


Figure 6. Correspondence Analysis to detect structural traits separating wetlands (orange open circles) associated with waterbird abundance. Species codes are shown for those situated at extremes of the PC1 and PC2 axes that generate the observed structural differences. dvi: *Dendrocygna. viduata*; tfl: *Tringa flavipes*; tme: *Tringa melanoleuca*; cco: *Cochlearius cochlearius*; ssi: *Syrigma sibilatrix*; tso: *Tringa solitaria*; ama: *Actitis macularius*; ppi: *Ptilinopus pileatus*; cfu: *Calidris fuscicollis*; cmi: *Calidris minutilla*.

wetlands conservation into agro-forestry management and the establishment of buffer zones around lagoons to minimize habitat degradation.

The temporal pattern we observed in the contribution of migratory species corresponded with the main phenological periods of boreal migrant species in South America (Greenberg and Marra 2005). After the boreal breeding season, migrant species started to appear in Venezuela by June, progressively increasing up to September, when we detected peak richness and abundance of migrants. However, we detected a decreasing contribution of migrant species from October onwards, suggesting that the bulk of migrants passed over the region, but did not remain to over-winter in this area. The second more modest peak from May to August may be due to spring migrants moving North. This more modest contribution as compared to September may reflect winter mortality or the use of alternative migratory routes in spring (Newton 2007). It appears, therefore, that the Llanos region functions mainly as a stopover area for boreal migrants that spend the winter in areas further south, such as Brazil, Uruguay, Argentina or Chile.

While we provide valuable baseline data on the annual cycle of waterbird assemblages in the Venezuelan Llanos, future research is needed to deepen our understanding of the function and conservation importance of Los Llanos for waterbirds. Further research could expand the temporal coverage to evaluate inter-annual variations driven by climatic events (Brabata et al. 2019). Studies could also evaluate the ecological role of abundant or less abundant species and their contribution to ecosystem functioning or from a conservation standpoint. Finally, studies need to assess the impact of agroforestry activities on wetland health and bird populations (Shuford et al. 2019, Eloegi et al. 2020, Wang et al. 2021).

In conclusion, our study underscores the ecological importance of permanent wetlands in the Venezuelan Llanos, demonstrating their role in supporting diverse waterbird assemblages across seasons. By identifying the key patterns of richness, abundance, β -diversity and structural differentiation among lagoons, we lay the groundwork for informed conservation policies that could be adopted locally. The continued monitoring and protection of these wetland sites are imperative for sustaining the waterbird diversity of the region and its contribution to global ecological networks.

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