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ORIGINAL ARTICLE

A waterfowl seed-dispersal network from the Neotropical region is nested and modular

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Abstract

Seed dispersal by vertebrates is fundamental for the persistence of plant species, forming networks of interactions that are often nested and modular. Networks involving angiosperms and frugivorous birds are relatively well-studied in the Neotropical region, but there are no previous studies of networks involving waterbirds. Here, we describe the structure of a Neotropical waterfowl seed-dispersal network and identify the species that have an important role for the network structure. We used information on 40 plant taxa found in fecal samples of five common waterfowl species to calculate the nestedness (NODF), weighted nestedness (WNODF), modularity, and weighted modularity of the network. We found that the network was nested, with yellow-billed teal showing the highest contribution both to nestedness and weighted nestedness. Twenty-four plant species contributed positively to weighted nestedness, with Salzmann's mille graines presenting the highest influence both to nestedness and weighted nestedness. The network was modular, but the weighted modularity was not significant. These results need to be considered with caution due to incomplete interaction sampling for two species. Ringed teal, Brazilian teal, and yellow-billed teal were considered hub modular species. Among plants, beak sedges and water snowflake were considered modular hub species, while Salzmann's mille graines and spikerush were network connectors. The structure of this Neotropical waterbird seed-dispersal network differed from the only previous waterfowl network study, from Europe, which found similar level of nestedness but no significant modularity. We include several possible explanations for this discrepancy and identified priorities for future research into waterbird–plant interaction networks.

Abstract in Portuguese is available with online material.

KEYWORDS
Anatidae, aquatic plants, endozoochory, network structure, waterbirds, wetlands

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1 | INTRODUCTION

Seed dispersal by vertebrates is fundamental for the persistence of many plant species and to the dynamics of plant populations (Galetti et al., 2001; Jordano, 2010; Wenny et al., 2016). Dispersal interactions between plants and vertebrates are usually arranged in such a way that specialist vectors interact with a subgroup of species, which also interact with generalist vectors, forming a nested pattern (Bascompte & Jordano, 2006; Sebastián-González et al., 2020). Such networks may also be modular, when species are organized in semi-independent groups formed by highly connected species (Guimarães et al., 2017; Sebastián-González et al., 2017). The structure of seed-dispersal networks has important consequences for community stability and their ability to recover from disturbances (Bascompte & Jordano, 2006; Rohr et al., 2014). Thus, it is important to understand the structure of seed-dispersal interactions, especially given ongoing climate change and habitat transformations.

Seed-dispersal networks involving angiosperms and frugivorous birds are relatively well-studied in Neotropical forests (e.g., Emer et al., 2020; Galetti et al., 2001). In contrast, seed-dispersal studies involving waterbirds remain scarce in all biomes (Green et al., 2016, 2022). The only study on the structure of waterbird seed-dispersal networks is from the Palearctic region and found these networks to be similarly nested but less modular than those involving frugivorous birds (Sebastián-González et al., 2020).

The lack of studies on waterbird seed-dispersal networks is surprising given that the transport of diaspores by waterbirds has long been recognized as a fundamental mechanism for the dispersal of aquatic plants (de Vlaming & Proctor, 1968; Green et al., 2016). On the other hand, research into endozoochory by non-frugivorous birds has been discouraged by a dominant paradigm that wrongly assumes that this dispersal mode is exclusive to plants with fleshy fruits (Green et al., 2022). Recent studies have confirmed that herbivorous, granivorous and omnivorous waterbirds may serve as excellent vectors for long-distance dispersal of a wide variety of plant species, most of which lack a fleshy fruit (Green et al., 2016; Hattermann et al., 2019; Silva et al., 2021; Viana et al., 2016). Among waterbirds, waterfowl (Anatidae: ducks, geese and swans) are the best-known dispersers of plant diaspores (Green et al., 2016; Lovas-Kiss et al., 2018; Silva et al., 2018, 2021; Wilkinson et al., 2017).

In this study, we used an exploratory approach to describe the structure of a waterfowl seed-dispersal network in the Neotropical region. We used detailed information on the occurrence of 40 plant taxa in fecal samples of five of the most frequent and abundant omnivorous waterfowl species in the region, including resident and migratory species to (1) investigate the network structure (i.e., nestedness and modularity) of the seed-dispersal network and (2) identify species important to network structure. We expected the network to be nested, but not modular, assuming that the pattern of waterbird seed-dispersal network in the Neotropics was similar to that found for Palearctic networks. The dataset used here was the same dataset used by Silva et al. (2021), but the approach, goals, and analysis are different.

2 | METHODS

2.1 | Sample procedures and studied species

We used data on plant diaspores found in fecal samples from five waterfowl species collected in five wetlands in Santa Vitória do Palmar municipality in the Coastal Plain of southern Brazil (see Silva et al., 2021 for more details in relation to sampling design and data collection). This region is composed of a mosaic of permanent and temporary wetlands inserted in a matrix of native grassland, livestock grazing, and irrigated rice fields and is important to resident and migratory waterbird species (Guadagnin & Maltchik, 2006; Silva et al., 2021). The wetlands sampled were located 1–9 km apart. Birds were constantly moving among them, and sometimes the same flock was seen in different wetlands during the same day. In the warm periods (spring and summer), the water surface area can be drastically reduced, while in the cold period (autumn and winter) overflow is common (Silva et al., 2021).

The five waterfowl species studied are important to plant dispersal in the region (Silva et al., 2018, 2021). Three of them are members of Anatinae subfamily (Brazilian teal *Amazonetta brasiliensis*, ringed teal *Callonetta leucophrys*, and yellow-billed teal *Anas flavirostris*). Brazilian teal and yellow-billed teal are highly abundant medium-sized species (~500 g), with about 1,000,000 individuals per species across their range (Kear, 2005a; Wetlands International, 2021). Both species are resident in the study region (Silva et al., 2021). Ringed teal is the smaller species (~350 g), and its estimated population of 25,000 to 100,000 individuals (Wetlands International, 2021) is partially migratory, although their migration routes are unknown (Silva et al., 2021). The three Anatinae species usually fed by dabbling at the water surface and were often seen feeding together, mainly in shallower water up to 0.5 m depth (Silva et al., 2021).

The other two waterfowl species are from subfamilies Anserinae (coscoroba swan *Coscoroba coscoroba*, estimated population between 10,000 and 25,000 individuals; Wetlands International, 2021) and Dendrocygninae (white-faced whistling-duck *Dendrocygna viduata*, population in South America about 1,000,000 individuals). Coscoroba swan, the largest studied species (~3500 g; Kear, 2005b) is migratory, feeding by submerging the head or neck in the deepest water (above 1 m) and also by grazing in hydromorphic soils and drylands around lake edges (Silva et al., 2021). White-faced whistling-duck (800 g; Kear, 2005b) is a partially migratory species that shared feeding habitat and the foraging mode with the coscoroba swan (Silva et al., 2021).

Fresh droppings were collected from monospecific groups resting or feeding around lake edges. Three collection events were carried out between October 2017 and January 2018, and another four in August 2017, April, May, and June 2018. We located groups of waterbirds resting in a dry area to collect their feces. As birds were located during the displacement to the site where they rest, we looked for the presence of other species in the immediate surroundings for approximately 10 min. Only droppings that were clearly from a single species were collected. We inspected droppings to avoid contamination from the substrate, before storing them individually in plastic tubes. In the laboratory, we washed samples in tap water using a sieve (53 μm) and used a stereomicroscope to separate intact diaspores, such as seeds, oogonia, sporocarps, and megaspores from broken or empty diaspores and other material. We counted intact diaspores and identified them to the lowest possible taxonomic level (see Appendix S1; Silva et al., 2021).

2.2 | Network structure

We analyzed the structure of the seed-dispersal network following the methods used in Sebastián-González et al. (2020), the only previous study on the seed-dispersal network structure for waterbirds. These methods are the same as those used for seed-dispersal networks of frugivorous species. We constructed a bipartite network where the two node levels, waterfowl and aquatic plants, were connected by their seed dispersal interactions. This binary matrix was used to calculate nestedness and modularity. We also created a matrix with the abundance of diaspores found in waterfowl droppings to calculate the weighted nestedness and weighted modularity (Newman & Girvan, 2004). We used the metric NODF to measure nestedness and WNODF to weighted nestedness. Both NODF and WNODF identify how nested a network is by attributing a value that ranges from zero (no nestedness) to 100 (maximum nestedness; Almeida-Neto et al., 2008). We decided to use both nestedness and weighted nestedness because they represent different aspects of the network (Sebastián-González et al., 2020). Nestedness measures whether the interacting partners of specialist species are subsets of those of generalist species, while weighted nestedness incorporates the frequency (or weight) of the interactions, so that generalist species also interact with a higher frequency than specialists. Modularity and weighted modularity were calculated with the metric *M* (Newman & Girvan, 2004) using the annealing algorithm, and the metric Q, using the algorithm QuanBiMo (Dormann & Strauß, 2013).

We compared the statistical significance of the metrics NODF and WNODF against 999 null models using the *null.t.test* function. This function considered random matrices based on r2dtable using Patefields algorithm (Patefield, 1981), which maintains column and row totals. Modularity indices were compared against 999 null models using the *nullmodel* function. We determined the contribution of each species (nodes) to nestedness at the species level using the *nestedcontribution* function, identifying those most important to network structure (Saavedra et al., 2011). In these analyses, *z*-scores were obtained comparing the observed nestedness and values of nestedness from 999 null models of random interactions between waterfowls and plants, with higher positive *z*-scores indicating species that contribute most to network nestedness (Saavedra et al., 2011). Species that actively contribute to nestedness are fundamental to preserve the structure of the seed-dispersal networks, because they have a higher number of ordered interactions than those species with a low contribution. Finally, we extracted the *c* (among modules connectivity) and *z* (within modules degree) metrics using *czvalues* function to analyze the role of the species in modularity, identifying (i) those species highly connected within their own modules (module hubs; $z > 2.5$ and $c \leq 0.62$), (ii) species that only connect modules (connectors; $z \leq 2.5$ and $c > 0.62$); (iii) species considered supergeneralists or network hubs due to their role both as module hubs and connectors (network hubs; $z > 2.5$ and $c > 0.62$), and (iv) those that mostly interact with other nodes within their own module (peripheral; $z \leq 2.5$ and $c \leq 0.62$), (Donatti et al., 2011; Olesen et al., 2007). We calculated all network metrics using the *bipartite* package (Dormann et al., 2009) in *R* version 3.6.1 (R Core Team, 2019).

We evaluated if sampling completeness was sufficient to describe the interactions, following Traveset et al. (2015). We calculated the percentage of plant richness detected in feces as a product of the observed richness divided by the richness estimated via the Chao 2 non-parametric estimator using the function *specpool* of the package *vegan* (Oksanen et al., 2013). We computed sampled-based rarefaction curves for all samples and independently for each species using the package *vegan* (Oksanen et al., 2013), also in R. We found that our sampling effort detected 68% of the estimated interactions. For three of the five waterfowl species, sampling completeness was higher than 70%. Two species, coscoroba swan, and yellow-billed teal might be considered under-sampled, with 46% and 42% of their interactions detected, respectively (Appendix S1).

3 | RESULTS

The 165 fresh droppings sampled (Brazilian teal, $n = 40$; coscoroba swan, $n = 22$; ringed teal, $n = 31$; white-faced whistling-duck, $n = 40$; yellow-billed teal, $n = 32$) resulted in retrieval of 2066 diaspores, from 40 different plant taxa, including 31 identified at species, five at genus and four at family-levels (Appendix S1). Diaspores were mainly angiosperm seeds (88.9%) and fruits (1.1%), but included oogonia (Charophyceae; 9.1%), megaspores (Lycophyta; 0.1%), and sporocarps (Pteridophyta; 0.8%). Of the 35 taxa of angiosperms identified at the species or genus level, 91% have dry fruits such as achenes, capsules, follicles, and utricles (Appendix S1). *Ruppia maritima* was the only species found with a drupe-like fruit, while *Solanum americanum* was the only with a berry.

The structure of the network was significantly nested (NODF = 48.325, $p < .01$; WNODF = 26.075, $p < .01$; Figure 1). Yellow-billed teal was the waterfowl species with the highest contribution both to nestedness (*z*-score = 2.319) and weighted nestedness (*z*-score = 2.320), followed by the Brazilian teal (*z*-score = 1.789 and 1.952, respectively; Appendix S1). Twenty-four plant species (60%) contributed positively to the weighted nestedness (Appendix S1), with the Salzmann's mille graines (*Oldenlandia salzmannii*) presenting the highest influence both to nestedness (*z*-score = 1.175) and weighted nestedness (*z*-score = 1.184).

The network was also modular (*M* = 0.525, $p < .01$), although the weighted modularity was not significant (Q = 0.209, $p > .05$;

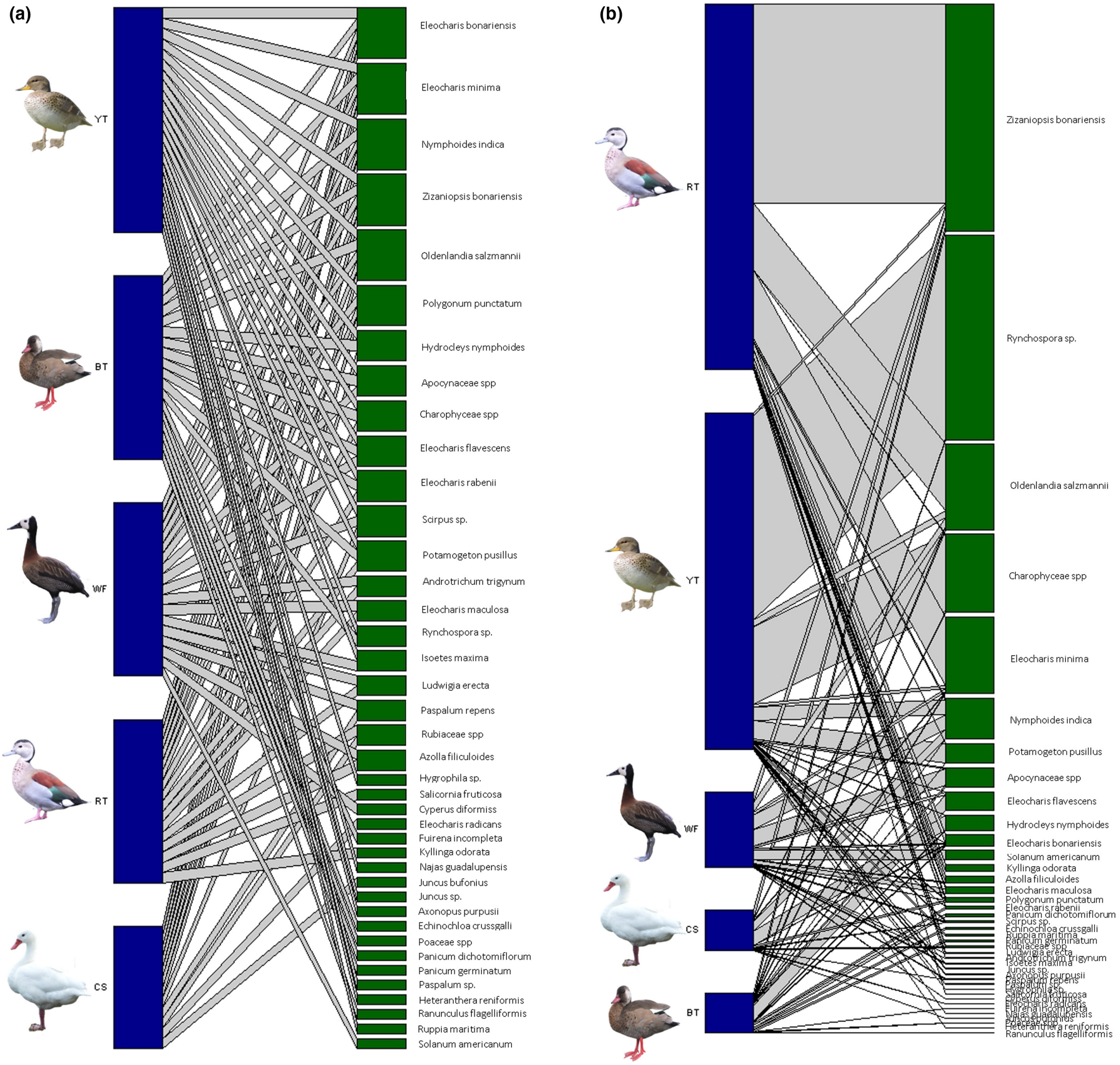

FIGURE 1 Graphic representation of the bipartite networks between waterfowl and plant species in a Neotropical wetland landscape. Unweighted (a) and weighted (b) networks are represented. Black rectangles represent waterfowl species (BT, Brazilian teal; CS, coscoroba swan; RT, ringed teal; WF, white-faced whistling duck; YT, yellow-billed teal), while blue rectangles represent plant species. Gray lines connect a plant species dispersed by a bird species, and the width of the line for the weighted nested represents the proportion of interactions among those two species. Bird images are for illustrative purposes only and are not to scale.

Figure 2). Most of the studied species of plants and waterfowl were classified as peripheral ($z < 2.5$ and $c < .62$), indicating that they had few links in or outside their modules (Appendix S1). Brazilian teal, ringed teal, and yellow-billed teal were waterfowl considered hub modular species ($z > 2.5$ and $c \leq 0.62$), with many links connecting them to plant species inside their modules. Among plants, beak sedge (*Rynchospora* sp.) and water snowflake (*Nymphoides indica*) were also considered modular hub species (Appendix S1). Two other plant species, Salzmann's mille grains and spikerush (*Eleocharis bonariensis*), were connectors ($z \leq 2.5$ and $c > 0.62$), linking modules that would be isolated in their absence, thus being important for network connectivity.

4 | DISCUSSION

We found the dispersal network between waterfowl and plants in a Neotropical area in southern Brazil to be nested, as previously reported for networks between Palearctic waterbirds and angiosperms, and also for seed dispersal networks involving avian

FIGURE 2 Modular (a) and weighted modular (b) network structure of a Neotropical wetland assemblage involving waterfowl and plant species. The intensity of the color in panel B is related to the proportion of interactions among species. Red squares indicate the modules found by the algorithm. Waterfowl species were represented by their initials (BT, Brazilian teal; CS, coscoroba swan; RT, ringed teal; WF, white-faced whistling duck; YT, yellow-billed teal). Bird images are for illustrative purposes only and are not to scale.

frugivores (Bascompte & Jordano, 2006; Sebastián-González et al., 2020). Thus, in our waterfowl assemblage there is a central group of species, which are responsible for most of the interactions, while other birds disperse only a few well-connected plant species (Bascompte et al., 2003; Bascompte & Jordano, 2006). This connection arrangement may confer stability and persistence to the network (Rohr et al., 2014; Thébault & Fontaine, 2010), as attributed to networks of frugivores plants and also to the Palearctic waterbird seed dispersal networks studied previously (Sebastián-González et al., 2020). Network resilience may be especially interesting for the waterfowl seed-dispersal assemblage, as these species are found in permanent and temporary South American wetlands, which are systematically affected by intra and interannual dry periods.

Interestingly, the network we studied also presented a modular pattern, with groups of highly connected species. Brazilian teal, ringed teal and yellow-billed teal and the plants beak sedge and water snowflake were connectors in their modules, suggesting that if they were affected by any negative environmental conditions, the species connected to them may also be affected (Dupont & Olesen, 2009; Stouffer & Bascompte, 2011). The plants Salzmann's mille grains and spikerush were considered important to network connectivity by linking modules that would otherwise be isolated. The network modularity described in our study contrasts to the non-modular waterbird seed-dispersal networks from the Palearctic region (Sebastián-González et al., 2020). This difference occurred even though the group of waterbirds investigated in the present study are phylogenetically, anatomically, and ecologically more homogeneous compared with the assemblages studied by Sebastián-González et al. (2020). The reasons for the differences in modularity between the present and the Palearctic network studied by Sebastián-González et al. (2020) are currently unclear and may be explained by differences in intrinsic factors of each network and/or methodological differences between studies. The analyses of the Palearctic waterbird seed-dispersal networks used datasets from seeds found in the upper digestive tracts of waterbirds collected during the hunting season. In contrast, we retrieved seeds from fecal samples from birds that were resting or feeding at lake shores. Although the presence of seeds in the upper digestive tract is a valid method to estimate seed dispersal, the digestion processes affect seed survival in a species-specific manner, so that larger and softer seeds are less likely to be detected in feces owing to low seed survival during gut passage (Figuerola et al., 2010; Kleyheeg et al., 2018; Lovas-Kiss et al., 2020a). Furthermore, gut processing can vary between waterfowl species and affect relative seed survival (Figuerola et al., 2002; Green et al., 2016). Thus, data on seeds found in fecal samples should be more reliable to identify effective plant dispersal, and the divergence in results on modularity between the two studies might be related to these differences in the methods used to collect seeds. Interestingly, the European study (Sebastián-González et al., 2020) included waterbirds morphologically and phylogenetically more variable, for example, coots and moorhens (Rallidae), in addition to Anatidae ducks, so a more modular pattern would be expected. Thus, more studies in other areas and with different waterbird species are needed to disentangle these different patterns.

Sampling completeness might also be an explanation for the differences found between the European networks and ours. The under-sampling of the coscoroba swan interaction (46%), which is a peripheral species, suggests that the connectivity of this node may increase for larger sample sizes. This may consequently increase overall network connectivity (i.e., the proportion of realized interactions), disrupting the modularity of the network and eventually making the network non-modular, similar to the European ones. However, we consider that the results for nestedness may not change significantly, even if interaction sampling was not complete for two of the species. This is because increasing the number of interactions for the yellow-billed teal (i.e., the other under-sampled species, 42% of the interactions sampled) will only increase network nestedness, as it is the species with the highest degree (i.e., number of interacting partners). More coscoroba swan interactions may both increase or decrease nestedness, but a potential reduction in the pattern by this species may be partially compensated by the increase driven by the yellow-billed teal, thus the overall nestedness is unlikely to change. For the same reason, at the species level, only the results for the coscoroba swan may be taken with caution, while those for the remaining species will likely be robust. The effect of sample size for bipartite networks has recently been evaluated by Llopis-Belenguer et al. (2022), finding that the categorical (but not the quantitative) classification of networks in nestedness and modularity is robust to a reduced sample size.

The structure of avian frugivore seed-dispersal networks is affected by bird and plant traits (Sebastián-González, 2017). In contrast, the Palearctic waterbird seed-dispersal networks were not related to avian traits usually investigated in seed dispersal studies (Sebastián-González et al., 2020). Also, in a review, Almeida et al. (2022) found that different foraging guilds among 29 European waterfowl species disperse plants with different traits, especially those associated with the terrestrial-aquatic continuum. In the studied wetland, some bird characteristics such as body size or foraging depth may be shaping species roles in network structure. However, we could not test which traits of bird and plants were related to their network roles due to the small number of waterbird species in our study and the similarity in their foraging methods and feeding zones and also due to the lack of trait data for Neotropical plant species. The identity of the dispersed plants varies significatively among ringed teals and coscoroba swans, the smallest (*c.* 350 g) and the largest (*c.* 3500 g) species in this study, but not among the other species (500–800 g) (Silva et al., 2021). Body size can allow birds to have access to different depths for feeding, which may lead to greater habitat segregation, and, consequently, to diaspores of different plants (Green, 1998; Guillemain et al., 2002; Ntiamoa-Baidu et al., 1998; Pöysä, 1983). Thus, body size is largely correlated to the depth at which these species forage. Consequently, the low number of nodes, together with the low variability and large correlation of their ecological traits, hinders more in-depth understanding of the species traits that drive the different network roles. Nonetheless, we encourage further studies investigating ecological, morphological, and phenological characteristics of these organisms in Neotropical wetlands, which are important to determine whether the structure of Neotropical waterbird seed-dispersal networks is related to species functional traits. This could shed light on the ecological role of each bird species and how foraging niches are shared or segregated.

Seasonality may influence seed dispersal rates, since the probability that a seed is dispersed increases when the fructification period overlaps with the time migratory waterfowl are present and also due to seasonal changes in bird diet (Green et al., 2002; Silva et al., 2021). For example, using the same dataset from our study, Silva et al. (2021) found differences in the seed species dispersed between bird species and also between seasons (cold vs. warm). Although the effects of seasonality in seed dispersal are complex and poorly understood (Brochet et al., 2010a; Figuerola et al., 2003; Silva et al., 2021), it may have influenced the differences in modularity found between ours and the Palearctic networks. Sebastián-González et al. (2020) used data from birds collected through hunting seasons (fall and winter), while we pooled samples collected during a complete annual cycle. Given the hunting activity in the Palearctic sites, it is also possible that birds in those networks foraged in a great variety of sites and microhabitats, therefore ingesting a greater variety of diaspores. Thus, differences in temporal and spatial scales might have influenced the differences detected between studies.

Here, we demonstrated that a Neotropical waterbird seed-dispersal network is both nested and modular. We highlighted important differences between our study and previous work conducted in the Palearctic region. Although both studies found that networks were nested, conferring a certain long-term stability to them, modularity was only detected in our study, meaning that our network might have an additional resilience to disturbance. Further studies are necessary to confirm the patterns found herein (especially due to uncomplete interaction sampling for two of our waterfowl species) and to expand the comparison of waterbird seed dispersal networks in distinct ecological contexts, as well as to compare them with well-known networks involving frugivorous birds. Likewise, fully investigating the effects of seasonality and the spatial scale of data sampling upon network structure would improve our understanding of dispersal networks in general. To clarify the importance of methodology, additional studies should consider comparing data from upper digestive tracts versus fecal samples. In addition, considering that in our study area wetlands are semi-permanent, it is important to investigate possible effects of landscape dynamics influenced by wetland hydrology on the production of seeds and their availability to birds, which can influence the network structure. Thus, short-term studies are necessary to understand the waterbird seed-dispersal network specificities in different wetland systems, while long-term studies would be necessary to understand such patterns over time. Finally, in order to understand the processes underlying the dynamics of wetland biodiversity and, consequently, wetland conservation, it is important to integrate networks for waterbird seed-dispersal by endozoochory with other mechanisms of plant dispersal, such as endozoochory of whole plants or viable fragments, or epizoochory (Green et al., 2022; Lázaro et al., 2021; Silva et al., 2018; Wilkinson et al., 2017). Likewise, there is a need to investigate dispersal networks for other organisms dispersed by waterbirds, as shown for many aquatic invertebrates (Brochet et al., 2010b; Green & Figuerola, 2005; Martín-Vélez et al., 2022; Silva et al., 2022) and recently for fishes (Lovas-Kiss, Vincze, Löki, et al., 2020; Silva et al., 2019).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data used in this study are available online at https://doi.org/10.5061/dryad.9w0vt4bkf. A summary of the data is available as Supporting Information.

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