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Original Article

Invertebrate dispersal by waterbird species in neotropical wetlands

A dispersão de invertebrados por aves aquáticas na região neotropical

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Abstract

Endozoochory by waterbirds is particularly relevant to the dispersal of non-flying aquatic invertebrates. This ecological function exercised by birds has been demonstrated in different biogeographical regions, but there are no studies for the neotropical region. In this work, we identified propagules of invertebrates in faeces of 14 syntopic South American waterbird species representing six families, and hatched additional invertebrates from cultured faeces. We tested whether propagule abundance, species richness and composition varied among bird species, and between the cold and warm seasons. We found 164 invertebrate propagules in faecal samples from seven different waterbirds species, including eggs of the Temnocephalida and Notonectidae, statoblasts of bryozoans (*Plumatella* sp.) and ephippia of Cladocera. Ciliates (including *Paramecium* sp. and Litostomatea), nematodes and rotifers (*Adineta* sp. and Nottomatidae) hatched from cultured samples. Potential for endozoochory was confirmed for 12 of 14 waterbird species. Our statistical models suggest that richness and abundance of propagules are associated with bird species and not affected by seasonality. Dispersal by endozoochory is potentially important to a broad variety of invertebrates, being promoted by waterbirds with different ecological and morphological traits, which are likely to drive the dispersal of invertebrates in neotropical wetlands.

Keywords: zoochory, waterbirds, aquatic invertebrates, propagules, neotropical region.

Resumo

A endozoocoria promovida por aves aquáticas é particularmente relevante para a dispersão de invertebrados aquáticos não-voadores. Essa função ecológica exercida pelas aves tem sido demonstrada para diferentes regiões biogeográficas, porém, não existem estudos para a região neotropical. Neste trabalho nós identificamos propágulos de invertebrados encontrados em fezes de 14 espécies sintópicas de aves aquáticas da América do Sul, representando seis famílias de aves, e também invertebrados emergidos de amostras fecais cultivadas em laboratório. Testamos se a abundância, riqueza de espécies e composição de propágulos de invertebrados variavam entre as espécies de aves e entre estações. Nós encontramos 164 propágulos de invertebrados em amostras fecais de sete espécies de aves, incluindo ovos de Temnocephalida e Notonectidae, estatoblastos de briozoários (*Plumatella* sp.) e efípios de Cladocera. Ciliados (incluindo *Paramecium* sp. e Litostomatea), nematóides e rotíferos (*Adineta* sp. e Nottomatidae) eclodiram de amostras cultivadas. O potencial para endozoocoria foi confirmado para 12 das 14 espécies de aves aquáticas investigadas. Nossos modelos estatísticos sugerem que a riqueza e abundância de propágulos estão associadas às espécies de aves e não são afetadas pela sazonalidade. A dispersão por endozoocoria é importante para uma ampla variedade de invertebrados, sendo promovida por aves aquáticas com diferentes características ecológicas e morfológicas as quais provavelmente regulam a dispersão de invertebrados entre áreas úmidas neotropicais.

Palavras-chave: zoocoria, aves aquáticas, invertebrados aquáticos, propágulos, região neotropical.

1. Introduction

The wide geographic distribution of non-flying freshwater invertebrates is an intriguing ecological issue (Bilton et al., 2001; Brochet et al., 2010). Aquatic invertebrates inhabiting isolated wetlands, such as lakes and temporary ponds, are surrounded by a terrestrial matrix that limits their dispersal in the landscape (Figuerola and Green, 2002). Passive dispersal of whole individuals or their propagules through a transport vector such as air, water or animals is key to understanding how many species are able to move between isolated wetlands (Figuerola and Green, 2002; Brochet et al., 2010; Vanschoenwinkel et al., 2011). Zoochory, when an animal

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acts as a transport vector, is an important ecological process facilitating long-distance dispersal of aquatic invertebrates (Frisch et al., 2007; Brochet et al., 2010; Okamura et al., 2019). In this process, invertebrate propagules or whole individuals are transported attached to external parts of the vector (epi- or ectozoochory) or inside the vector's digestive tract (endozoochory), and both processes are fundamental to the dispersal of many aquatic invertebrates between isolated wetlands (Figuerola and Green, 2002; Vanschoenwinkel et al., 2011).

Waterbirds are particularly relevant to the dispersal of aquatic invertebrates due to their abundance, global distribution and their flight capacity (Figuerola et al., 2003; Brochet et al., 2010). Invertebrate dispersal by avian endozoochory has been confirmed for a wide spectrum of taxa, including crustaceans (notably Branchiopoda and Ostracoda), rotifers, nematodes, dipteran larvae, beetle eggs, leech eggs, and snails (Brown, 1933; Proctor, 1964; Malone, 1965a, b; Green and Figuerola, 2005; Brochet et al., 2010; Laux and Kolsch, 2014; Rogers, 2014; Simonová et al., 2016; Lovas-Kiss et al., 2019; Moreno et al., 2019). The underlying factors explaining variation in the dispersal ability of invertebrates among waterbirds are unclear (van Leeuwen et al., 2012). As for plant diaspores, dispersal of invertebrate propagules may be affected by bird morphology, foraging behaviour, gut anatomy, movement patterns, as well as propagule characteristics such as size, shape and chemical and mechanical resistance (Figuerola et al., 2003; Green et al., 2016; Reynolds and Cumming, 2015; van Leeuwen et al., 2012). Seasonality is also expected to influence invertebrate dispersal, especially for species with seasonal propagule production, and the phenological match between propagule availability and the presence of migratory waterbirds may be crucial to long-distance dispersal (Clausen et al., 2002; Lovas-Kiss et al., 2020). However, studies addressing seasonal effects on the dispersal of invertebrate and plants indicate divergent results (Figuerola et al., 2003; Sánchez et al., 2007; Brochet et al., 2010; Lovas-Kiss et al., 2020; Silva et al., 2021). Furthermore, previous studies of invertebrate dispersal by waterbirds have focussed mainly on the Anatidae (especially ducks), and little is known about potential dispersal by other waterbird families (see Lovas-Kiss et al., 2019; Sánchez et al., 2007; Moreno et al., 2019 for exceptions).

Dispersal of aquatic invertebrates through waterbird zoochory has been demonstrated in different biogeographical regions (Figuerola et al., 2005; Green and Figuerola, 2005, Green et al., 2008; Brochet et al., 2010; Green et al., 2013; Reynolds and Cumming, 2015), but none were previously undertaken in neotropical wetlands. Here, we extracted and identified propagules of aquatic invertebrates from faecal samples of 14 syntopic South American waterbird species, representing six different families. We tested hatchability of the invertebrate propagules found, and also cultured the residual organic material from faeces to look for other invertebrates. We tested whether invertebrate propagule abundance, richness and composition varied among bird species, and between cold and warm seasons. We expected important variation among bird species and taxonomic groups (ranging from ducks to herons and ibis), due to their different morphology and foraging ecology. We also expected seasonal changes in invertebrate dispersal due to the temporal variation in invertebrate communities throughout the annual cycle in wetlands of the region (Stenert et al., 2008).

2. Material and Methods

2.1. Sampled area

The study was conducted in southern Brazil (Figure S1, Supplementary material), one of the most important regions for waterbird conservation in South America (Silva et al., 2021). We collected faecal samples of 14 waterbird species in five different wetland sites separated from each other by 100-600 km (Figure S1, Table S1 - Supplementary material). From August 2017 to December 2019, eight collecting events were carried out, distributed between the cold (n=4) and warm (n=4) periods. Samples collected during the austral autumn and winter were grouped as the cold period (April to September). Samples collected during austral spring and summer (October to March) were grouped as the warm period. The warm period is the main breeding season in the study region, except for some occasional breeding during the cold period. All bird species studied can nest in the early warm period, and raise their offspring before the end of the warm period (Calabuig et al., 2010; Dias and Fontana, 2002; Mauricio et al., 2013; Silva et al., 2021).

2.2. Sampling procedures

We obtained 209 faecal samples (Table S1) from two distinct methods. We collected fresh droppings of 11 waterbird species from on top of grass: Brazilian teal (*Amazonetta brasiliensis,* Gmelin, n = 28), yellow-billed teal (*Anas flavirostris*, Vieillot, n= 18), silver teal (*Anas versicolor*, Vieillot, n = 3), ringed teal (*Callonetta leucophrys*, Vieillot, n = 31), coscoroba swan (*Coscoroba coscoroba,* Molina, n = 27), white-faced whistling-duck (*Dendrocygna viduata,* Linnaeus, n = 35), southern screamer (*Chauna torquata,* Oken, n = 18), red-gartered coot (*Fulica armillata*, Vieillot, n = 7), limpkin (*Aramus guarauna,* Linnaeus, n = 3), buff-necked ibis (*Theristicus caudatus,* Boddaert, n = 14) and plumbeous ibis (*T. caerulescens*, Vieillot, n = 2). We located individuals or monospecific groups of each species resting or feeding around lake edges, and collected fresh droppings from the grass, with a minimum distance of one meter between samples to prevent resampling of the same individuals. Samples were stored individually in plastic tubes and frozen (- 4 °C) to avoid fungal infestation prior to arrival at the laboratory.

We used a second method to collected faecal samples of another three waterbird species: black-crowned night-heron (*Nycticorax nycticorax,* Linnaeus, n= 13), roseate spoonbill (*Platalea ajaja,* Linnaeus, n= 4) and *Egretta* spp. (indistinguishable faeces of a mixed group of little blue heron *Egretta caerulea,* Linnaeus and snowy egret *E. thula*, Molina, n = 6). After identifying roosts of these species, we used tweezers to scrape faeces from branches, avoiding any contact with soil. The samples were collected with a minimum distance of one meter apart to prevent resampling, stored individually in plastic tubes and frozen (- 4 °C) to avoid fungal infestation.

2.3. Laboratory procedures

The samples were defrosted, weighed and washed in tap water (well water) using a sieve (53 µm) in the laboratory at UNISINOS University. Some resting eggs smaller than 53 µm may have been lost during washing. We used a Bogorov chamber in a stereomicroscope (10x to 1.6x - 5 x of total magnification) to separate the visible propagules from other materials. We only considered intact propagules, discarding broken ones.

With the exception of a morphotype with grouped eggs highly adhered to each other, and for that reason kept together, all other eggs and statoblasts recovered were placed individually in plastic tubes with 10 ml of deionised water (pH 7.5) and maintained for 21 days in a controlled chamber (12 h dark at 16ºC + 2ºC, 12 h light at 26ºC + 2ºC). The remaining organic material of each sample (n= 209) was individually separated in independent pots, hydrated with 100 ml of deionised water, and placed in an air- tight plastic box to record later hatching of invertebrates whose propagules were not detected during the first separation process (mainly because they were very small). Then, these boxes were also maintained for 21 days in the above controlled chamber. Both propagules and pots with organic material were inspected at three intervals in order to quantify hatching. When emerged invertebrates were found, they were inspected under the microscope (10x - 100x of total magnification). We identified invertebrate eggs (68%) and all hatchlings using specimens from the LECEA collection, and specific literature (Koste, 1978; Lopretto and Tell, 1995; Domínguez and Fernández, 2009; Gazulha, 2012).

2.4. Data analyses

We analyzed effects of bird species and sample weight on the total richness and abundance of invertebrate found in the faeces using Generalized Linear Mixed Models (GLMMs), with the sampling site (five levels) and sample event (eight levels) as random factors. In our richness models, we combined both the propagules found in the faeces and hatchlings from the organic material experiment. In the abundance models, only propagules were considered, since hatchlings from the organic material were uncountable due to their rapid asexual reproduction. We ran separate GLMMs to analyze the influence of the season using only samples of five Anatidae species (excluding silver teal), since the adequate temporal repetition was only possible for these species. In seasonal models, we considered the factors bird species, sample weight, season and the interaction between bird species and seasons.

Model parameters were estimated by maximum likelihood (Laplace approximation). All models fitted best with a negative binomial error distribution. We used the *overdisp_fun* function (*lme4* package, Bates et al., 2014) to certify that our models have no overdispersion. We compared the effects against null models (intercept only) and performed model selection using the Akaike information criterion (AIC) (Burnham and Anderson, 2002), retaining only models with delta AIC < 2.0 for further inference. We fitted all the GLMMs in the R statistical environment v. 3.6.1 (R Development Core Team, 2019) using the function *glmer.nb* of the package *lme4* (Bates et al., 2014).

We combined data on invertebrate richness found in the faeces and hatchlings from organic material in order to assess variation in invertebrate composition among all bird species through Principal Coordinates Analysis (PCoA) and Permutational Multivariate Analysis of Variance (PERMANOVA), using the Jaccard distance matrix and 999 permutations to validate the model significance. PCoA and PERMANOVA were analysed through the funcions *cmdscale* and *adonis2* of the package Vegan (Oksanen et al., 2020), respectively. In these analyses, we used the 81 samples with propagules or hatchlings. In order to investigate the variation in invertebrate composition among seasons we considered only data from the 51 Anatidae samples with propagules or hatchlings. The homogeneity of multivariate dispersions was tested (PERMDISP) through the function *betadisper* because the PERMANOVA analysis is sensitive to data dispersion (Anderson and Walsh, 2013).

We ran pairwise tests (*pairwise.adonis* function, Oksanen et al., 2020) with Bonferroni adjust for multiple comparisons of invertebrate composition variation among bird species.

Finally, we calculated the frequency of occurrence of hatchings from waterbird species for the samples with remaining organic material. For this purpose, we considered the number of samples with invertebrate hatching, divided by the total samples for that waterbird species, and multiplied the result was by 100.

3. Results

3.1. Invertebrate propagules recovered from faecal samples

We recovered 164 invertebrate propagules in faecal samples from seven different waterbird taxa (Table 1). Eggs of the Platyhelminthes Temnocephalida (n=61) were the most abundant, following by a non-identified morphotype I (n = 58, Figure S2, Supplementary material). We also found 32 Notonectidae eggs (Insecta), nine statoblasts of *Plumatella* sp. (Bryozoa), one ephippium of Cladocera and three eggs from three other unidentified morphotypes. At least one invertebrate propagule was recorded in 15% of the faecal samples, with a higher frequency in droppings of coscoroba swan (48%), following by yellow-billed teal (23.5%). Seven bird species had no propagules in their faeces (Brazilian and silver teals, limpkin, black-crowned night-heron, plumbeous ibis, red-gartered coot and roseate spoonbill).

Non-identified ciliates were the most frequent taxa hatched, found in samples of all bird species except limpkin and roseate spoonbill (Table 2). We found ciliates *Paramecium* sp. in samples of six waterbird species and Litostomatea in four species. Nematodes hatched from samples of Brazilian teal and buff-necked ibis, and Rotifera (*Adineta* sp. and Nottomatidae) emerged from samples

Table 1. Invertebrate propagules recovered from waterbird faecal samples. n = total number of samples per waterbird species, (s) = number of samples with propagules, a= number of propagules found in the samples.

			YT		**RT**		**SC**		**CS**		**WF**		**ES**		**BI**	
			n (s) = 17 (4)		**n (s) = 29 (2)**		**n(s) = 18 (3)**		**n (s) = 27 (13)**		**n (s) = 34 (6)**		**n (s) = 6 (1)**		**n (s) = 14 (2)**	
			a	**(s)**	**a**	**(s)**	**a**	**(s)**	**a**	**(s)**	**a**	**(s)**	**a**	**(s)**	**a**	**(s)**
Cladocera																
	Daphnia sp.	Ephippia							1	(1)						
Insecta																
	Notonectidae	Egg	9	(4)			6	(2)	10	(3)	5	(5)			2	(1)
Bryozoa																
	Plumatella sp.	Statoblast			2	(2)	1	(1)	2	(2)	2	(2)	1	(1)	1	(1)
Platyhelminthes																
	Temnocephalida	Egg							61	(8)						
Non identified																
	Morphotype 1								58	(1)						
	Morphotype 2	Egg							1	(1)						
	Morphotype 3	Egg							1	(1)						
	Morphotype 4	Egg							1	(1)						

Bird species are represented by initials: YT = yellow-billed teal; RT = ringed teal; SC = southern screamer; CS = coscoroba swan; WF = white-faced whistling-duck; ES = *Egretta* spp; BI = buff-necked ibis.

Table 2. Frequency of invertebrate hatchings (samples in which hatching was observed, divided by the total samples for each waterbird species, multiplied by 100) from organic material remaining after waterbird faeces had been sieved, and after intact propagules seen under the binocular microscope had been removed (i.e. those from Table 1).

Taxa	**BT**	**YT**	**ST**	**RT**	**SC**	**CS**	**WF**	**ES**	**RC**	**BH**	**PI**	**BI**
	n = 28	**n = 17**	**n = 2**	**n = 29**	**n = 18**	**n = 27**	**n = 34**	**n = 6**	**n = 7**	**n = 13**	**n = 2**	**n = 14**
Ciliophora												
Paramecium sp.	0.0	0.0	50.0	3.4	0.0	3.7	2.9	33.3	0.0	0.0	0.0	14.3
Litostomatea	0.0	11.8	0.0	3.4	0.0	3.7	0.0	0.0	0.0	0.0	0.0	7.1
Non-identified	17.9	41.2	0.0	17.2	27.7	14.8	23.5	33.3	71.4	30.8	50.0	35.7
Nematoda												
Non-identified	3.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	21.4
Rotifera												
Adineta sp.	3.6	0.0	0.0	3.4	0.0	7.4	0.0	0.0	0.0	0.0	0.0	14.3
Nottomatidae	3.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Bird species are represented by initials: BT = Brazilian teal; YT = yellow-billed teal; ST = Silver teal; RT = ringed teal; SC = southern screamer; CS = coscoroba swan; WF = white-faced whistling-duck; ES = *Egretta* spp; RC = red-gartered coot; BH = black-crowned night-heron; PI = plumbeous ibis; and BI = buff-necked ibis.

of four waterbird species. No invertebrates (whether propagules or hatchlings) were found in the three samples of limpkin or in the four samples of roseate spoonbill.

3.2. *Effects of bird species, sample weight and seasonality on invertebrate taxon richness and abundance*

The best fitted models showed that the bird species factor explained both invertebrate richness ($p = 0.005$) and abundance ($p < 0.001$), and these variables were not affected by the sample weight (Table 3). In the model selection to analyse the seasonality effect in the richness, considering only Anatidae species (except silver teal), the best fitted model showed that the interaction between bird species and seasons was significant ($p = 0.003$, Table 4). Regarding the abundance, there was no effect of the seasonality in the models selected (Table 4).

Table 3. Summary of all run models explaining Richness and Abundance of invertebrates found in faeces of waterbirds in southern Brazil. Both variables were affected by the bird species and not by sample weight. All models included wetlands as random factors (1 | Wetland) and (1 | Collect Event). Richness models considered both invertebrate eggs and uncountable hatchlings from organic material of individual samples. Abundance models considered only the eggs found in the faeces (countable). Details are only shown for models with ΔAIC<2.

Variable	Models	ΔAIC	Weight (AIC)	Factor	AIC	*df*	LR Chisq	*P*-value
Richness								
Model 1	~Bird	0.0	0.45		419.73	17	29.503	0.005
Model 2	~Bird+ Weight	1.1	0.27		420.79	18		
				Bird	423.84		29.046	0.006
				Weight	419.73		0.941	0.332
Model 3	~1	2.1	0.16					
Model 4	~ Weight	2.7	0.12					
Abundance								
Model 1	~Bird + Weight	0.0	0.59		292.96	18		
				Bird	322.48		55.517	<0.001
				Weight	294.18		3.221	0.073
Model 2	~Bird	0.7	0.41		293.68	17	80.551	<0.001
Model 3	~Weight	20.3	<0.01					
Model 4	~1	38.0	<0.01					

Table 4. Summary of the best fitted models explaining Richness and Abundance of invertebrate eggs found in faeces of waterbirds in southern Brazil, using only Anatidae species with adequate temporal repetition in order to analyse the effect of seasonality. All models included wetlands as random factors (1 | Wetland) and (1 | Collect Event). Richness models considered both invertebrate eggs and uncountable hatchlings from organic material of individual samples. Abundance models considered only the eggs found in the faeces (countable). Details are only shown for models with ΔAIC<2.

Variable	Model	ΔAIC	Weight (AIC)	Factor	*df*	AIC	LR Chisq	*P*-value
Richness								
Model 1	~Bird + Season + Weight + Bird*Season	0.0	0.89		14	265.13		
				Weight		264.94	1.808	0.179
				Bird*Season		273.46	16.331	0.003
Model 2	~Bird	5.5	0.06					
Model 3	~Bird + Weight	6.4	0.04					
Model 4	~Weight	8.4	0.01					
Model 5	~1	10.9	<0.01					
Model 6	~Season	12.8	<0.01					
Abundance								
Model 1	~ Bird +Season + Weight +Bird *Season	0.0	0.38		14	225.15		
				Weight		228.57	5.415	0.020
				Bird *Season		224.70	7.544	0.110
Model 2	~ Bird+ Weight	0.2	0.34		9	225.37		
				Bird		248.85	31.481	<0.001
				Weight		225.92	2.548	0.110
Model 3	~Bird	0.6	0.28		8	271.23	53.481	<0.001
Model 4	~Weight	19.0	<0.01					
Model 5	~Season	32.6	<0.01					
Model 6	~1	35.3	<0.01					

3.3. Variation in the taxonomic composition of invertebrate propagules among waterbird species and seasons

According to PERMANOVA tests, invertebrate composition differed among waterbirds when considering all bird species, and combining propagules and hatchlings (R^2=0.25, F=2.123, P=0.001) (Figure 1). However, adjusted pairwise tests showed no difference among species, although Coscoroba swan differed marginally from Brazilian teal and Ringed teal (P = 0.063). There were also differences in invertebrate composition according to seasonality, considering only data from Anatidae species (R^2=0.07, F=3.640, P=0.005) (Figure 2). The PERMANOVA result was affected by multivariate dispersion within waterbird species (F=2.887, P=0.003), but not by multivariate dispersion within seasons (F=3.360, P=0.073).

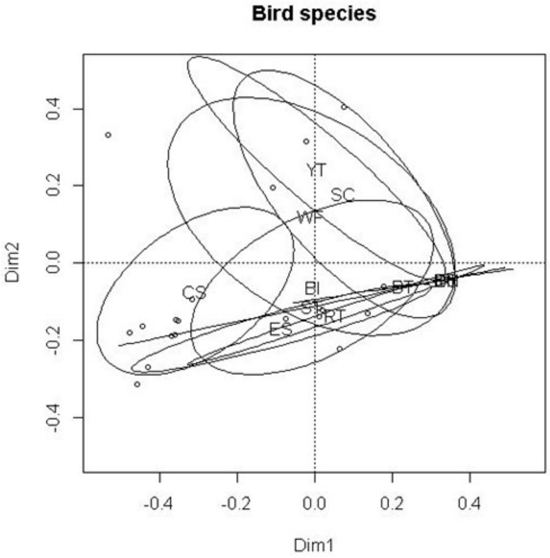

Figure 1. Ordination (Principal Coordinate Analysis) of invertebrate taxonomic composition (propagules and hatchlings) and how it varied among bird species (based on data from Table 1 and 2). The combined amount of variation explained by the axes was 57% (Axis 1 = 39% and Axis 2 = 18%). Bird species are represented by initials: CS = coscoroba swan; RT = ringed teal; WF = white-faced whistling-duck; YT = yellow-billed teal; SC = southern screamer; ST = silver teal; ES = *Egretta* spp; and BI = buff-necked ibis. Dots represent samples.

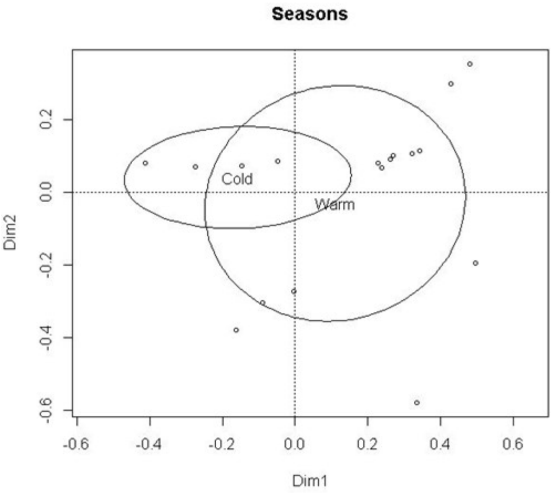

Figure 2. Ordination (Principal Coordinate Analysis) of taxonomic composition of invertebrate propagules and how it varied among Cold and Warm periods, considering only Anatidae species (based on data in Table 1 and 2). The total variation explained by the axes was 56% (Axis 1 = 36% and Axis 2 = 20%). Dots represent samples.

4. Discussion

Our work is the first to address invertebrate dispersal through waterbird endozoochory in the neotropical region. We recorded ciliates, nematodes and rotifers emerging from faeces of 12 of 14 waterbird species studied, and recorded eight different types of invertebrate propagules from seven of these species. Coscoroba swan, a migratory species, showed more propagule abundance and richness in their faeces than other bird species. Considering the known wide spectrum of invertebrate taxa dispersed by endozoochory of waterbirds (Green and Figuerola, 2005; Brochet et al., 2010; Laux and Kolsch, 2014; Rogers, 2014; Simonová et al., 2016; Lovas-Kiss et al., 2019; Moreno et al., 2019), it is likely that the propagules found did not hatch because they had all been frozen, although the effect of freezing in propagules is unknown for invertebrates found in this study. Except for high altitudes, in the neotropical region wetlands rarely freeze, so invertebrate eggs might not be adapted to survive freezing. Only limpkin and roseate spoonbill showed no propagules in their faeces or hatching from cultures, and this may be explained by the small number of samples obtained for each species (three and four samples, respectively).

Dispersal of rotifers, nematodes and ciliates by waterbirds was demonstrated previously (Frisch et al., 2007; Green et al., 2008). In our study, we found ciliates hatched from 12 of the 14 species analysed. As our cultures were in closed plastic recipients that were opened only during the inspection under the stereomicroscope, we think it unlikely that this hatching could be explained by contamination such as the arrival of invertebrate propagules by air. We did not find previous references of waterbird endozoochoric dispersal of the ciliates *Paramecium* sp. and Litostomatea, or of the rotifers *Adineta* sp. and Notommatidae, and our study is likely the first to find such evidence. This is despite the fact that dispersal of a variety of rotifers by waterbird endozoochory has been reported in Europe (Conde-Porcuna et al., 2018; Moreno et al., 2019).

The most abundant invertebrate propagule found in faeces was eggs of the Platyhelminthes Temnocephalida. These eggs were found in faeces of coscoroba swan among some intact shells and uncountable fragments of snails (Hydrobiidae and Planorbidae). Temnocephalida species are ectosymbionts of snails and other aquatic organisms (Amato and Amato, 2005; Seixas et al., 2010), and the presence of these eggs in the samples may be due to accidental ingestion, when birds were feeding on snails. We did not find previous references of Temnocephalida eggs dispersed by endozoochory, thus the viability of these eggs needs to be appropriately tested to confirm that they can disperse internally by a waterbird.

Bryozoans have been shown to be dispersed by waterbirds in several continents (Macias et al., 2004; Okamura et al., 2019), and here we made the first observation of zoochory in the neotropics. *Plumatella* sp. statoblasts were found in faeces of coscoroba swan, southern screamer, ringed teal, white-faced whistling-duck, *Egretta* spp., and buff-necked ibis. There have been few studies of neotropical bryozoans, and a lot of future work is needed to understand their ecology and distribution (Wood and Okamura, 2017; Wood and Liebbe, 2020). Considering that bryozoan statoblasts are known to survive passage through waterbird digestive systems, and that they can stay inside the vector for hours (Brown, 1933; Charalambidou et al., 2003), our findings suggest that bryozoans disperse readily via endozoochory between neotropical wetlands. Our findings that *Plumatella* sp. statoblasts can be transported inside the bodies of egrets and buff-necked ibis demonstrated that even non-migratory species may be important to bryozoan dispersal, since the samples of these birds were collected in their roosts, located usually several kilometres from their feeding sites. Furthermore, this illustrates how even predatory waterbirds can be important vectors of statoblasts and other propagules, ingested together with their prey, this being secondary dispersal (van Leeuwen et al., 2017; Lovas-Kiss et al., 2019).

The presence of Notonectidae (Heteroptera) eggs in samples of coscoroba swan, white-faced whistling-duck, yellow-billed teal, southern screamer and buff-necked ibis suggest that backswimmer species are potentially dispersed by endozoochory, but this requires further investigation. Similar Corixidae (Heteroptera) eggs have been recorded from Anatidae faeces in Europe (Figuerola et al., 2003). Carbonell et al. (2021) found that eggs of boatman (*Trichocorixa verticalis,* Corixidae) showed low resistance to chemical treatment and no resistance to scarification in simulated digestion, and were unable to hatch a number of intact eggs recovered from Eurasian coot (*Fulica atra*) droppings. Given that we froze samples in the field, and our field sites are not subjected to low temperatures, it is no surprise that we failed to hatch any of the propagules we extracted in the laboratory. Nevertheless, eggs of an aquatic coleopteran were hatched after gut passage through ducks (Laux and Kolsch, 2014), so the dispersal of Notonectidae by avian endozoochory is plausible, but remains to be demonstrated.

The best fitted models showed invertebrate propagule richness and abundance varying according to bird species and not affected by the sample weight or seasonality. The variation we recorded is likely associated to intrinsic characteristics of bird species not addressed in our study. For example, the foraging strategy and the body size may lead to differences in access to alimentary resources and habitat segregation, and result in differences in diaspore dispersal (Ntiamoa-Baidu et al., 1998; Pöysä and Poysa, 1983; Green, 1998; Guillemain et al., 2002; Silva et al., 2021). The lack of seasonal effects for abundance and richness, and the weak effect in the propagule composition should be investigated. General seasonal patterns of invertebrate endozoochory are inconsistent in the literature. For example, Sánchez et al. (2007) found that rates of *Artemia* cyst endozoochory were high in both spring and autumn, and almost inexistent in midwinter. Brochet et al. (2010) reported a lack of seasonal patterns in endozoochory of branchiopods, ostracods and bryozoans. Studies carried out in wetlands in the region with aquatic macroinvertebrates showed that the community varies temporally (Stenert et al., 2008; Moraes et al., 2014) suggesting the availability of invertebrates in our study ponds may influence what is dispersed by birds. Moreover, low sample sizes might have influenced our results, and studies with higher numbers of samples are necessary to corroborate the patterns found.

The factors that regulate variations in the richness, abundance and composition of invertebrates dispersed by birds need to be clarified. Ecological and morphological characteristics of birds may influence what propagules they disperse (Green et al., 2002; Kleyheeg et al., 2017). For example, waterfowl can change their diet and gizzard biomass according to the time of year, which can affect the destruction and consequently the survival of propagules that pass through the digestive tract (Piersma and Lindstrom, 1997; Figuerola and Green, 2002). Differences in foraging techniques and ecological niche may lead to birds to access different resources, and therefore influence what they disperse (Green et al., 2016; Silva et al., 2021). Similarly, the seasonal production of diaspores, associated with migratory movements, may influence the species composition of dispersed diaspores (Green et al., 2002; Silva et al., 2021).

Information about bird displacement, population size and distribution of the studied waterbirds is scarce. However, as invertebrate propagules are typically retained in waterbird guts for at least 4-8 h, and given flight speeds of 50-78 km/h (Welhun, 1994; García-Álvarez et al., 2015; Lovas-Kiss et al., 2020), we can assume that the studied birds disperse invertebrates between wetlands, but at different spatial scales. Coscoroba swan and white-faced whistling duck are abundant migratory species in the region, and are able to disperse invertebrates during their movements of thousands of kilometres across the Pampa biome, in an east-west migratory route between wetlands from southern Brazil and Argentina, and from there along another route, north-south, reaching the Chaco/Pantanal and Patagonia (Blanco et al., 2020; Silva et al., 2021).

Ringed teal and silver teal are partially migratory and probably make regional north-south seasonal movements that have been little-studied, displacing hundreds of kilometres between our study area in southern Brazil and Uruguay (Somenzari et al., 2018; Silva et al., 2021). Brazilian teal and yellow-billed teal are resident species with high abundance, and are likely to mainly disperse invertebrates at a local scale, although the few data on their movements (Nascimento et al., 2010; Silva et al., 2021) means that we may be underestimating their dispersal capacity. Similarly, southern screamer (Anhimidae) and red-gartered coot (Rallidae) are considered resident, but few data are available to analyse their true distribution and movement pattern in the region, and their importance to dispersal.

Egrets and black-crowned night heron (Ardeidae) are residents, and their dispersal capacity is limited to local wetlands where they feed, and to their daily movements between feeding areas and roost sites. There is no information about the distance travelled by egrets and black-crowned night heron in the region, although personal observations indicate these species reach at least 20 km (probably much more) between feeding areas and the roosts. Plumbeous ibis and buff-necked ibis (Threskiornithidae) are also dispersers at a local scale, and their importance for invertebrate dispersal is probably low. Plumbeous ibis were residents and found in low numbers, usually in pairs, in wetlands or flooded fields. Buff-necked ibis also were found in low numbers and usually in dry fields surrounding wetlands, but also in flooded fields.

5. Conclusion

We demonstrated that 12 of the 14 waterfowl species studied have important potential to disperse a broad variety of invertebrates. The birds studied include resident and migratory species and have different ecologies and morphology, suggesting that endozoochory of invertebrates is an important process at different spatial scales, and promoted by a broad variety of waterbird species. The lack of regional studies on invertebrate ecology and bird movements limits our understanding of the magnitude of this dispersal, and studies addressing these themes combined with further studies of propagules carried by waterbirds can expand the knowledge and elucidate the patterns of endozoochory of invertebrates in the neotropical region.

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Supplementary Material

Supplementary material accompanies this paper.

Table S1. Total samples collected by waterbirds in cold (c) and warm (w) periods in five localities of the Coastal Plain of Southern Brazil. In the sample sites LP (National park of Lagoa do Peixe), TA (Taim Ecological Station) and SV (Santa Vitória do Palmar), the collection occurred in shallow freshwaters. In RG (Rio Grande) and IV (Ivoti) faecal samples were collected in bushes that were part of bird roost sites.

Figure S1. Study area in the coastal plain of southern Brazil showing the general location of the five sampling sites (black dots). Lagoa do Peixe, Taim and Santa Vitória do Palmar were shallower freshwater wetlands. In Ivoti, the site was a roost of black-crowned night-heron (Nycticorax nycticorax), while in Rio Grande it included roosts of roseate spoon-bill (Platalea ajaja) and herons (Egretta spp).

Figure S2. Non-identified morphotype I, found in a faecal sample of coscoroba swan collected in southern Brazil, seen wet soon after recovery from faeces (A), and dry (B).

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