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ORIGINAL RESEARCH

Colonial waterbirds provide persistent subsidies to swamp forests along an estuarine island food chain

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Abstract

Birds are excellent vectors of allochthonous matter and energy due to their high mobility, with more intense flow when waterbirds congregate in breeding colonies, feeding in surrounding aquatic and terrestrial areas, and promoting nutritional pulses to nutrient-poor environments. In southern Brazil, a swamp forest on an estuarine island is used by waterbirds for breeding, providing an opportunity to investigate the potential effects of transport of matter between nutrient-rich environments. Soil, plants, invertebrates, and blood from terrestrial birds were collected and stable isotopes compared to similar organisms in a control site without heronries. Values of δ^{15}N and δ^{13}C from waterbirds were higher in the colony in comparison to the control site (spatial effect). The enrichment of ^{15}N and ^{13}C provided during the active colony period persisted after the breeding period, especially for δ^{15}N, which was higher in all compartments (temporal effect). Moreover, the enrichment of ^{15}N occurred along the entire trophic chain (vertical effect) in the colony environment, including different guilds of invertebrates and land birds. The enrichment in ^{13}C seems to lose strength and was mostly explained by factors such as trophic guild rather than site, especially in birds. Bayesian mixture models with terrestrial vs. estuarine endpoints demonstrated that all organisms from both colony and control environments had assimilated estuarine matter. Finally, detritivorous invertebrates showed greater assimilation when compared to other guilds. This study demonstrates that adjacent nutrient-rich environments, such as palustrine forests and estuaries, are nutritionally enriched in several dimensions from nearby autochthonous subsidies that are maintained throughout the year.

Keywords Allochthonous matter · Biological vectors · Lateral transport · Stable isotopes · Trophic guilds

Introduction

Mobile and migratory animals are good vectors of matter and energy between environments (Polis et al. 1997; Sanzone et al. 2003; Korobushkin 2014) because mobility is associated with transport capacity (Fariña et al. 2003). In addition to mobility, body size is an important factor for ecosystem functioning, because larger individuals tend to play a more substantial contribution for nutrient cycling (Vanni 2002; Norkko et al. 2013). Classic examples of flows between aquatic and terrestrial ecosystems are those promoted by bears, which transport salmon to forested riparian environments during migration from sea to rivers (Hilderbrand et al. 1999). Birds can also transport matter from their foraging areas in the sea, rivers, and lakes, moving part of the ingested or assimilated matter to colonies on land (Polis et al. 1997; Keatley et al. 2009; Gaiotto et al. 2022).

Waterbirds group together in colonies to increase protection from predators in specific locations where they can obtain food for themselves and their offspring in nearby areas (Frederick 2002; Keatley et al. 2009; Britto and Bugoni 2015). Pelecaniformes (herons, spoonbills, and ibises) depend on shallow aquatic environments for feeding and breeding (Frederick 2002). Foraging in areas adjacent to colonies results in a flow from the aquatic to the terrestrial environment mediated by waterbirds (Green and Elmberg 2014; Faria et al. 2016), with temporal and intense matter inputs, generating a nutritional pulse.

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The intensity of matter and energy input, as well as spatial and temporal variation (Polis et al. 1997), can influence the receiving biological communities, as well as the water and soil (Polis et al. 1997; Keatley et al. 2009). The flow occurs primarily through guano deposition, which can have a positive and rapid impact on primary productivity and site diversity (Green and Elmberg 2014), both terrestrial and aquatic. This occurs because guano is rich in essential nutrients for producers, such as nitrogen and phosphorus, and can impact primary productivity and subsequently dissipate along the trophic chain (Polis et al. 1997; Kolb et al. 2010). In this way, this generates an increase in the nutritional quality of primary producers, which is transferred vertically along the trophic chain (Caut et al. 2012; Savage 2019; Gaiotto et al. 2022; Linhares and Bugoni 2023). In addition to guano, waterbirds also transfer matter and energy through nest-building material, feathers, eggs, regurgitated food, and carcasses (Polis et al. 1997; Caut et al. 2012). Thus, bird colonies alter the dynamics of the local trophic web, influencing the populations of animals feeding on allochthonous sources directly or indirectly (Sánchez-Piñero and Polis 2000; Caut et al. 2012). In this scenario, the transport of aquatic resources carried out by birds is a key process for the trophic webs of islands, and they are often able to maintain the biodiversity of these environments (Sánchez-Piñero and Polis 2000; Green and Elmberg 2014).

Analysis of fluxes of matter between environments elucidates questions about how organisms cope with the nutritional pulses (Correa and Winemiller 2014). In this context, stable isotope analysis (SIA) is a useful tool to track transported matter and provide information about its effects on the environment (Horn et al. 2019). Carbon isotopes (δ^{13}C) allow for the tracking of the flow due to different values between C_3 and C_4 plants, remaining relatively similar along the trophic chain, while δ^{15}N values increase predictably along the trophic chain, 2‰–5‰ per trophic level (Peterson and Fry 1987; Fry 2006). Therefore, it is possible to infer the horizontal flow or dissipation of matter through δ^{13}C analysis whenever there are isotopic differences in the composition of primary producers and a vertical flow or dissipation of matter along the trophic chain. Several studies of plants, birds, rodents, arthropods, and lizards on marine islands occupied by bird colonies have demonstrated increased δ^{15}N values from these groups compared to resident organisms from islands without colonies (e.g., Stapp et al. 1999; Stapp and Polis 2003; Caut et al. 2012).

In addition, strategies such as grouping organisms into trophic guilds, that is, groups that exploit the same class of resources (Root 1967), associated with isotopic analyses, allow verification of the use of resources according to the food preferences of consumer groups (Layman et al. 2012; Hamer et al. 2015; Navarro et al. 2021; Villegas et al. 2021). These studies have shown that transported allochthonous matter can be accessed by organisms living in the receiving environment (Savage 2019). Trophic subsidies are especially important when there is asymmetry in the productivity of environments, i.e., from nutrient-rich to nutrient-poor (Polis et al. 2004). There have been several studies on matter flux from marine islands to arid environments, which are typically poor environments and thus dependent on allochthonous subsidies of energy and matter from the sea (e.g., Stapp et al. 1999; Sánchez-Piñero and Polis 2000; Kolb et al. 2010; Savage 2019). However, studies on the subsides between environments with high productivity, such as swamp forest regions and estuarine aquatic environments are still lacking.

In this context, the present study aims to analyze patterns of matter dissipation, vertically and horizontally, mediated by waterbirds in a large colony and incorporated by organisms in the terrestrial environment on an estuarine island. Specifically, we hope to demonstrate that (i) colony-mediated transport of matter generates isotopic enrichment in resident organisms of the swamp environment due to inputs of nutrients from the estuary in the resident organisms of the swamp environment; (ii) soil, plants, invertebrates, and resident land birds of the colony environment will be enriched in ^{15}N compared to the control environment; (iii) terrestrial enrichment mediated by colonial birds during the breeding period will be present in the colony environment even during the nonbreeding period; (iv) dissipation of estuarine matter obtained from foraging areas will reach higher trophic levels in the colony environment; and (v) assimilation of estuarine matter will occur only in the colony environment.

Materials and methods

Study area

Marinheiros Island, Lagoa dos Patos estuary, southern Brazil (Fig. 1), is the largest island in the estuary and is composed of wetlands, shallow lakes, dunes, and swamp forests (Quintela et al. 2009). The climate is temperate subtropical, with minimum and maximum temperatures ranging from 9.5 to 27 °C, respectively (Vieira 1983). The highest precipitation occurs between July and September, with an annual average of 1522 mm (Vieira 1983). The colony of Pelecaniformes on Marinheiros Island is occupied by seven species of herons and egrets (Ardeidae): great egret *Ardea alba*, cocoi heron *Ardea cocoi*, cattle egret *Bubulcus ibis*, little blue egret *Egretta caerulea*, snowy egret *Egretta thula*, black-crowned night heron *Nycticorax nycticorax*, and yellow-crowned night heron *Nyctanassa violacea*, as well as by roseate spoonbill *Platalea ajaja* (Threskiornithidae) (Gianuca 2010). The occupation of the colony, except for *A. cocoi* that uses the site year-round, is seasonal, from late August to March

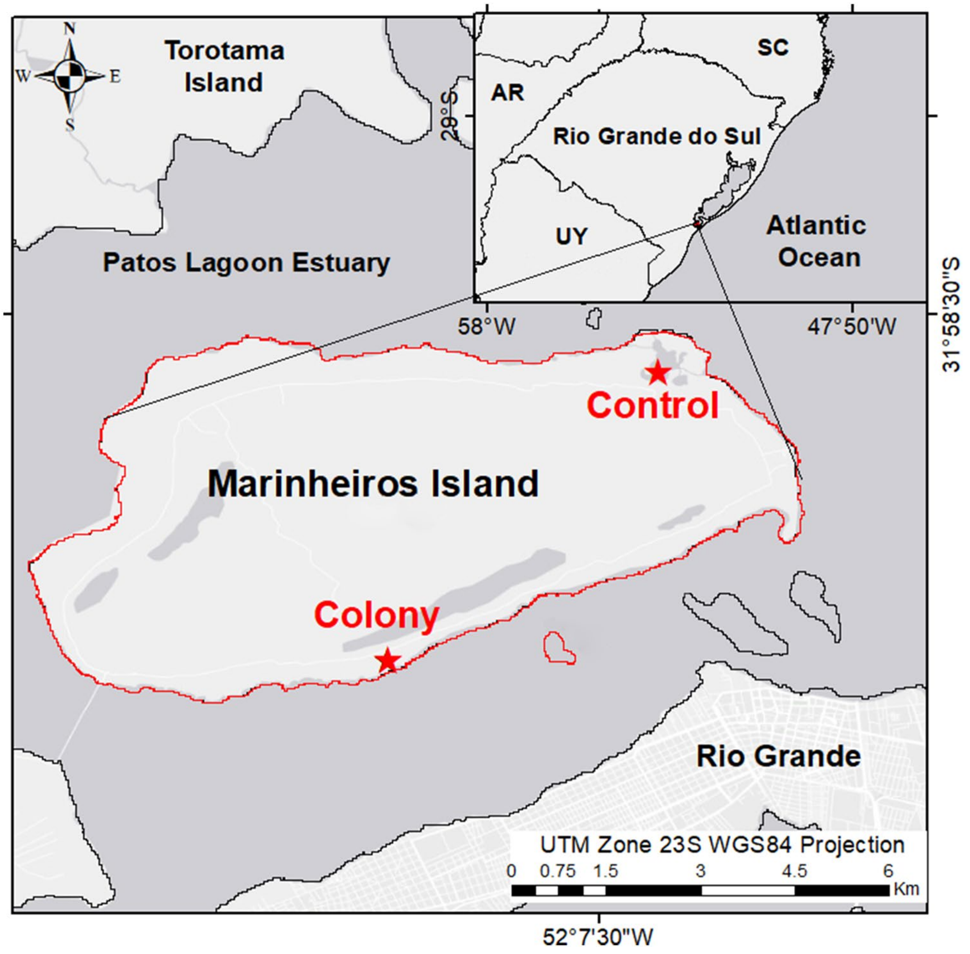


Fig. 1 Map of the study site on Marinheiros Island, Rio Grande do Sul state, Brazil, showing the colony and control sites. AR - Argentina; UY - Uruguay; SC - Santa Catarina state

(Gianuca 2010). The area is approximately 150 × 100 m, separated from the estuarine environment by an approximately 70 m wide strip of *Scirpus giganteus* (Gianuca 2010). The colony site is predominantly composed of tree species with a C_3 photosynthetic cycle (Faria et al. 2016), such as the cockspur coral tree (*Erythrina crista-galli*), Brazilian pepper tree (*Schinus terebinthifolius*), and fig tree (*Ficus cestrifolia*).

Approximately 5 km northeast from the colony site, on the opposite coast of the island, a swamp forest without colony or waterbird roosts was chosen as a control site (Fig. 1) due to its floristic characteristics and similar proximity to the estuarine shoreline. This area is 600 × 200 m, separated from the lagoon by a marsh with a predominance of ferns *Acrostichum danaeifolium* and *Cyperus* spp. It also presents a predominance of C_3 plant species, such as *S. terebinthifolius*, *E. crista-galli*, and large *Ficus* spp. The colony and control sites are isolated from each other, even for the most mobile organisms, such as land birds, as demonstrated by no recapture between sites during over 254 h of mist netting effort and individually tagged with metal rings provided by CEMAVE/ICMBio along 3 years.

Sampling

Sampling occurred in two summers and two winters in 2018 and 2019 at the end of each season, corresponding to periods with and without waterbird breeding, respectively (Supplementary Material Table S1). Soil collection occurred in triplicate in each of the study sites, randomly, during each sampling season. Soil samples were stored in plastic jars and frozen until preparation for isotopic analysis. Two to three buds of plants with a C_3 photosynthetic cycle (*A. danaeifolium*, *Crocosmia crocosmiiflora*, *Dioscorea* sp., *E. crista-galli*, *Heteranthera reniformis*, and *Hibiscus diversifolius*), predominant in both environments, were randomly collected during each sampling period, stored in plastic bags, and kept frozen until identification and preparation for isotopic analysis. Plants were identified using guides (Sobral 2006; Sobral et al. 2012) and with support from experts from the Floristics Laboratory at Universidade Federal do Rio Grande—FURG.

Abundant invertebrates at both sampling sites were randomly collected individually with tweezers through an active search in soil and vegetation. After collection, they were stored in plastic jars and frozen until preparation for analysis. The invertebrates were identified with support of experts and identification keys: *Armadillidium* sp., *Camponotus* sp. ants, *Lycosa* sp., Scolopendridae, and *Trichonephila clavipes* spiders.

Approximately 30 individuals of various land bird species (Table S1) were also captured in each sampling site (colony and control) per season. Captures occurred using six mist nets, 30 mm mesh, and 12 m long. Mist netting was distributed homogenously between seasons (summer and winter), years (2018 and 2019), and sites (colony and control). After capture, birds were identified (Narosky and Yzurieta 2011; Timm and Timm 2016) and a few drops of blood (approximately, 0.2 ml) were collected from the brachial vein using a hypodermic syringe.

Stable isotope analysis (SIA)

Soil samples were oven-dried at 60 °C, ground with pestle and mortar, acidified with 10% hydrochloric acid (HCl) to remove carbonates, washed in distilled water, oven-dried for about 12 h, and weighed (2 mg) for stable isotope analysis (Kennedy et al. 2005; Levin and Currin 2012). Plant tissues were washed with distilled water, dried for 24 h, ground as described above, and weighed (3 mg). Whole bodies of the collected invertebrates were prepared for isotopic analysis. Since lipid-rich tissues are depleted in ^{13}C, lipids were extracted from the samples in a Soxhlet apparatus for 6 h using petroleum ether as solvent (Bugoni et al. 2010). Samples were subsequently lyophilized for 24 h, homogenized, and weighed (1 mg) (Mancini and Bugoni 2014). Whole blood samples from land birds were also freeze-dried for 24 h and weighed (0.7 mg). In passerines, the estimated δ^{13}C half-life for whole blood is around 2.5 weeks (Hahn et al. 2012), reflecting the diet assimilated during this period. All samples were packed in tin capsules for analysis in an isotope ratio mass spectrometer (IRMS) coupled to an elemental analyzer at the Integrated Analysis Center, Federal University of Rio Grande—FURG (CIA-FURG, Brazil). The internal standards of the laboratory (glutamic acid and caffeine) had a standard deviation of 0.1‰ for δ^{13}C and 0.4‰ for δ^{15}N.

The determination of the values was expressed by the δ notation, in parts per thousand (‰). The standards used were VPDB (Vienna Pee Dee Belemnite limestone) for carbon and AIR for nitrogen.

Data analysis

Isotopic variation

To assess isotopic variation in soil, producers (C_3 plants), and consumers (invertebrates and land birds), we performed generalized linear models—GLMs (McCulloch and Searle 2000) with Gaussian distribution and identity family. We used values of δ^{15}N and δ^{13}C for all groups, except for plants, for which only δ^{15}N values were considered, as plants obtain their carbon from atmospheric air (Table 1).

The factors used in all models were sites (2 levels—colony and control); season (2 levels—winter and summer); and year (2 levels—2018 and 2019). For the models using plants, the species factor was included (6 levels—*A. danaeifolium*, *C. crocosmiiflora*, *Dioscorea* sp., *E. crista-galli*, *H. reniformis* and *H. diversifolius*). For invertebrates, the guild factor was included (3 levels—carnivorous, omnivorous, and omnivorous–detritivorous). The determination of trophic guilds for invertebrates followed Oelbermann and Scheu (2002), Ronque (2013), and Montesanto and Cividini (2017).

For models using land birds, the guild factor (5 levels—frugivorous, granivorous, insectivorous, nectarivorous, and omnivorous) was included. The guilds of the land birds followed the classifications found in the bibliography (Supplementary Material Table S2). The groups consisted in frugivorous (feeding predominantly on fruits); granivorous (predominantly seeds); insectivorous (predominantly insects); omnivorous (feeding on fruits, arthropods and small vertebrates); and nectarivorous (feeding on nectar). Bird's models also included feeding area, with four levels (factors): resident-restricted habitat (RRH); resident broad habitat (RBH); migrant-restricted habitat (MRH); and migrant broad area (MBH). For the categorization, we considered RRH as animals that live on the site throughout the year and are more restricted to the forest interior; RBH as animals that live on site throughout the year but are not restricted to the forest interior; MRH as animals that live only a period of the year on site (i.e., migratory) and are restricted to the forest interior; and MBH as animals that live a period of the year on site but are not restricted to the forest interior (i.e., migratory that also use open areas).

Several interactions among factors were tested, subsequently retaining the statistically significant interactions with the lowest AIC (Akaike information criterion) values of the model. The residuals of the GLMs were analyzed through an ANOVA to obtain the percentage of variation explained by each factor in the chosen model. Residuals were tested for normality, homoscedasticity, and independence, attending all assumptions for using a Gaussian distribution. The GLMs were carried out in R software version 4.1.2 (R Core Team 2022), using the packages "arm" version 1.11-2 (Gelman and Hill 2006), "lme4" version 1.1-27-2 (Bates et al. 2015), and "car" version 3.0-11 (Fox and Weisberg 2019). The *p* values were regarded as significant if < 0.05.

Table 1 Coefficient of the selected generalized linear models (GLM) of soil, vegetation, invertebrates, and land birds, at the colony and control sites, for δ^{15}N and δ^{13}C values

	Estimate	Standard error	*t* value	*p*
Soil δ^{15}N				
Intercept	1738.252	1698.466	1.019	0.320
Main effects				
Site (colony)	7.629	0.841	– 9.067	< 0.001
Season (winter)	– 0.742	0.841	– 0.882	0.388
Year	– 0.742	0.841	– 1.017	0.321
Plants δ^{15}N				
Intercept	4088.741	1887.153	2.162	0.033
Main effects				
Sp. (*C. crocosmiiflora*)	– 4.970	2.144	– 2.319	0.023
Sp. (*Dioscorea* sp.)	– 2.008	1.636	– 1.228	0.223
Sp. (*E. crista-galli*)	– 3.949	1.765	– 2.237	0.028
Sp. (*H. diversifolius*)	– 4.300	1.719	– 2.501	0.014
Sp. (*A. danaeifolium*)	– 0.622	1.737	– 0.358	0.721
Site (colony)	7.765	1.274	6.094	< 0.00
Season (winter)	1.106	0.951	1.163	0.248
Year	– 2.019	0.935	– 2.159	0.340
Invertebrates δ^{15}N				
Intercept	1442.575	1086.926	1.327	0.186
Main effects				
Site (colony)	7.568	0.825	9.176	< 0.001
Season (winter)	– 1.981	0.703	2.169	0.031
Year	– 0.711	0.538	– 1.320	0.189
Guild (omnivorous)	– 1.121	0.896	– 1.251	0.212
Guild (omnivorous–detritivorous)	– 1.094	0.886	– 1.234	0.219
Colony:winter	3.507	10.925	– 3.210	0.001
Land birds δ^{15}N				
Intercept	– 2053.000	1051.0	– 1.953	0.052
Main effects				
Site (colony)	3.528	0.513	6.872	< 0.001
Season (winter)	– 0.023	0.530	– 0.044	0.965
Year	1.021	0.520	1.961	0.051
Guild (granivorous)	– 0.920	2.175	– 0.423	0.672
Guild (insectivorous)	3.376	1.843	1.832	0.068
Guild (nectarivorous)	– 4.023	2.651	– 1.517	0.131
Guild (omnivorous)	2.561	1.823	1.405	0.161
Habitat (MBH)	– 4.827	1.735	– 2.783	0.005
Habitat (RRH)	– 2.038	1.439	– 1.416	0.158
Habitat (MRH)	– 3.444	2.033	– 1.694	0.091
Soil δ^{13}C				
Intercept	1252.908	626.415	1.999	0.059
Main effects				
Site (colony)	0.924	0.310	2.978	< 0.001
Season (winter)	0.034	0.310	0.110	0.913
Year	– 0.634	0.310	– 2.043	0.544
Invertebrates δ^{13}C				
Intercept	977.216	390.162	2.505	0.013
Main effects				
Guild (omnivorous–detritivorous)	1.522	0.323	4.705	< 0.001
Guild (omnivorous)	0.269	0.319	0.843	0.400
Site (colony)	– 0.410	0.204	2.011	0.045

Table 1 (continued)

	Estimate	Standard error	*t* value	*p*
Season (winter)	0.016	0.197	0.082	0.934
Year	– 0.496	0.193	– 2.57	0.011
Land birds δ^{13}C				
Intercept	– 382.608	653.712	– 0.585	0.559
Main effects				
Guild (granivorous)	2.336	1.350	1.730	0.085
Guild (insectivorous)	– 0.517	1.149	– 0.450	0.653
Guild (nectarivorous)	0.024	1.655	0.015	0.988
Guild (omnivorous)	0.605	1.132	0.534	0.593
Site (colony)	1.505	0.462	– 3.256	0.001
Season (winter)	– 2.170	0.452	– 4.794	<0.001
Year	0.178	0.324	0.551	0.582
Habitat (MBH)	– 2.217	1.087	– 2.039	0.042
Habitat (RRH)	– 1.514	0.904	– 1.674	0.095
Habitat (MRH)	– 0.252	1.264	– 0.200	0.842
Colony:winter	2.749	0.657	4.186	<0.001

Estimation of estuarine and terrestrial contribution to consumers

The δ^{15}N and δ^{13}C values were used to estimate the estuarine and terrestrial contribution in primary and secondary consumers of the colony, as well as to determine the assimilation of allochthone matter by each trophic guild of birds and terrestrial invertebrates. The vertical dissipation, i.e., along trophic levels, determined by nitrogen increased isotopic values, was determined through Bayesian isotopic mixing models generated in R software using the "simmr" package version 0.4.5 (Parnell 2021). The source for the terrestrial environment was represented by the isotopic mean of the C_3 photosynthetic pathway (leaf bud values) from the control environment for each season, due to the estuarine influence on the colony vegetation. As sources of nutrients mediated by colonial waterbirds and potentially representing estuarine baseline values, we used mean isotopic values from samples of particulate organic matter (POM) and sedimentary organic matter (SOM), which include photosynthesizing organisms such as phytoplankton and microphytobenthos, and green algae, through *Ulva* sp. and *Rhizoclonium* sp.

For the baseline for primary production determination, we used δ^{15}N of primary producers analyzed prior to our sampling season. We followed this approach based on results of a previous study conducted at the same estuary (Lagoa dos Patos), in which a set of models using δ^{15}N values along a period of 9 years indicated that the best temporal window to use when setting up a baseline for primary production is the season prior to the collection season (Possamai et al. 2021). Therefore, instead of using an interpolated approach, in which we would consider δ^{15}N from the previous and the sampling seasons for primary producers, we used a delayed approach, in which we just considered 2017 and 2018 values, as they were the years prior to this study and accounted for substantial environmental variability (see supplementary material for details and Possamai et al. 2021). The values used to build the baseline (Supplementary Material Table S3) were obtained from the Brazilian Long-Term Ecological Research program (PELD-ELPA; www.peld.furg.br and supplementary material S2), which has been carried out at the Lagoa dos Patos estuary since 1998.

The guilds of land birds used in the mixture models were defined as those used for the GLMs. However, we only used insectivorous and omnivorous trophic guilds for the mixture models, because these are the groups present in both sites with sufficient individuals for the analysis. Mixture models of each trophic guild of invertebrates followed the same classification as GLMs. Because source values in 2018 and 2019 did not differ between seasons and between sites, consumers from the 2018 and 2019 seasons were grouped into a single year. The source–consumer trophic discrimination factors (TDFs) used for ΔC and ΔN were selected according to the diet and tissues of the consumers (Supplementary Material Table S4).

Results

Spatial dissipation

For δ^{15}N values the input of matter into the colony environment from, or mediated by, waterbirds was demonstrated when compared to the control site for all ecosystem compartments, i.e., soil, plants, invertebrates, and land birds (Fig. 2). The variable "site" was significant, and explained 79%, 22%, 61%, and 15% of the data variation for models

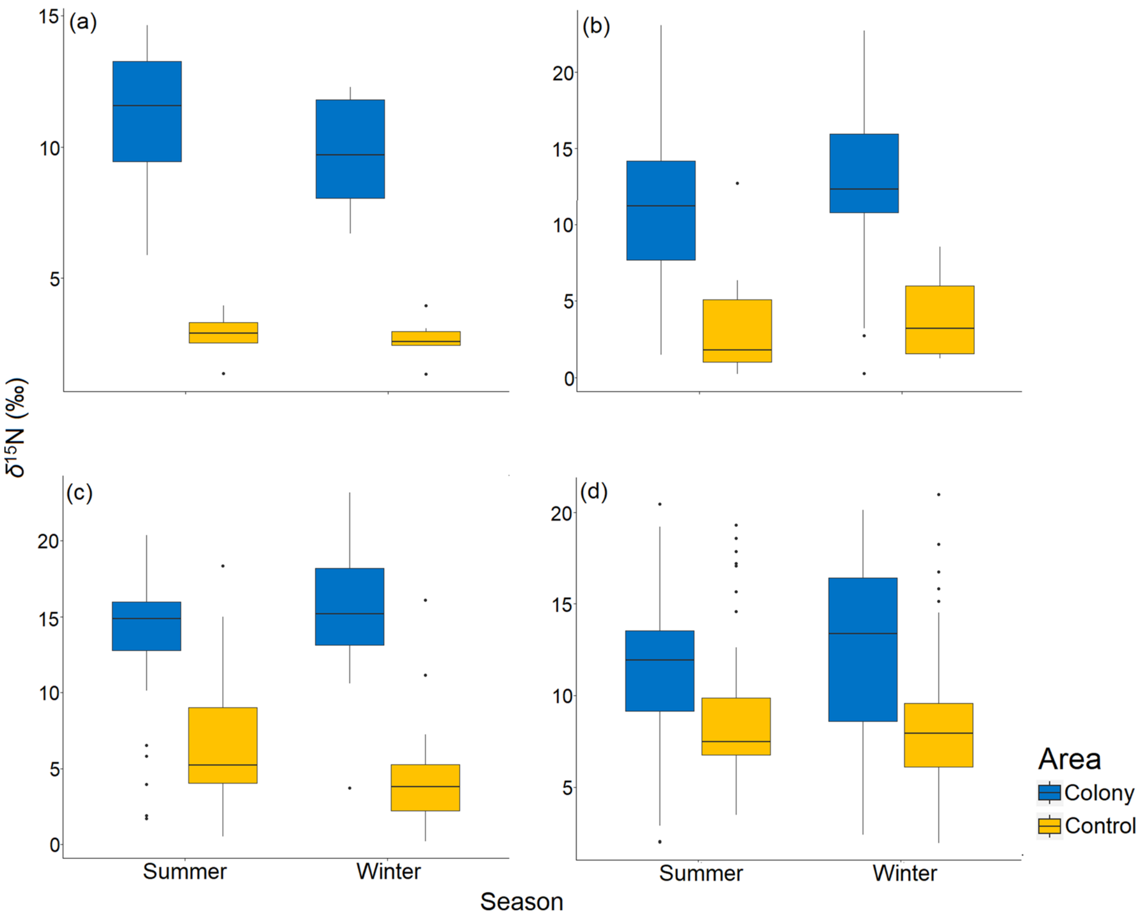


Fig. 2 Stable isotope values of δ^{15}N in soil (**a**), vegetation (**b**), invertebrates (**c**), and blood of land birds (**d**) from the colony and control environments during the summer and winter seasons. Values indicate the mean (central bars) and standard deviation (rectangles), with minimum and maximum values (outer lines)

developed for soil, plant, invertebrate, and land birds, respectively (Table 1).

For δ^{13}C values, the factor "site" showed positive effects in the soil and land bird models. Despite this, there were negative effects in invertebrates for δ^{13}C (Table 1). The ANOVA of these models indicated that the "colony" site explained the variation in δ^{13}C values by 26% for soil. For land birds, the effect of site lost the significance indicated by the GLMs when analyzed by ANOVA (Supplementary Material Table S5). For invertebrates, the effect was negative, and although significant, "site" explained only 2.4% of the data variation (Supplementary Material Table S5). The results showed a smaller difference in carbon when compared to nitrogen, but that could still be noticed in the soil samples compared to the control site (Fig. 3).

Temporal dissipation

Temporal variation in δ^{15}N values (with and without breeding waterbirds, i.e., summer vs. winter) occurred only for invertebrates, with the season factor "winter" indicating negative effects. The interaction between the factors "site" and "season" showed a positive effect on the colony in winter (Table 1). Despite this, the model showed no statistical significance for the seasonal effect and retained significance in the interaction, which explained only 2% of the variance in the data (Supplementary Material Table S5). This pattern was corroborated graphically (Fig. 4), as during winter the isotopic values of organisms in the colony environment maintained their positions at the top of the graph, thus indicating enrichment of ^{15}N compared to organisms from the control site (Fig. 4b, d).

For δ^{13}C values, the only group that showed a significant difference in GLMs was land birds, which showed negative effects for the factor "season" (Table 1). In addition, the interaction "site*season" showed positive effects: season explained 2.2% of the variation in the data, while the interaction site*season explained 6.1% (Supplementary Material Table S5), thus indicating the tendency of reducing δ^{13}C

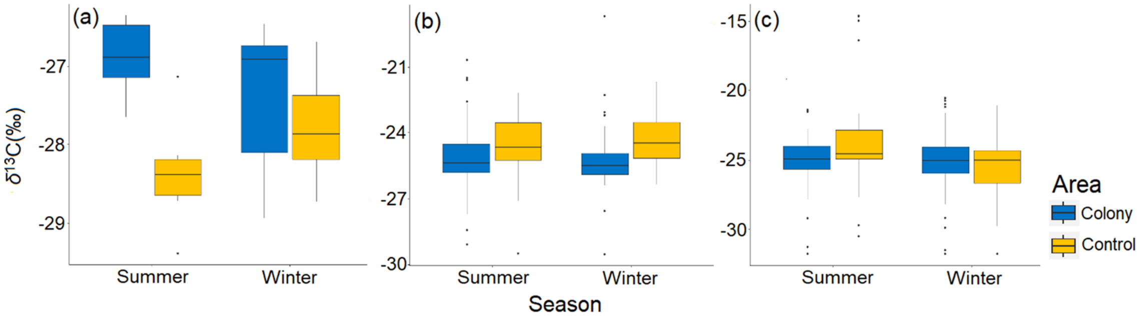


Fig. 3 Stable isotope values of δ^{13}C in soil (**a**), invertebrates (**b**), and blood of land birds (**c**) from the colony and control environments during the summer and winter seasons. Values indicate the mean (central bars) and standard deviation (rectangles), with minimum and maximum values (outer lines)

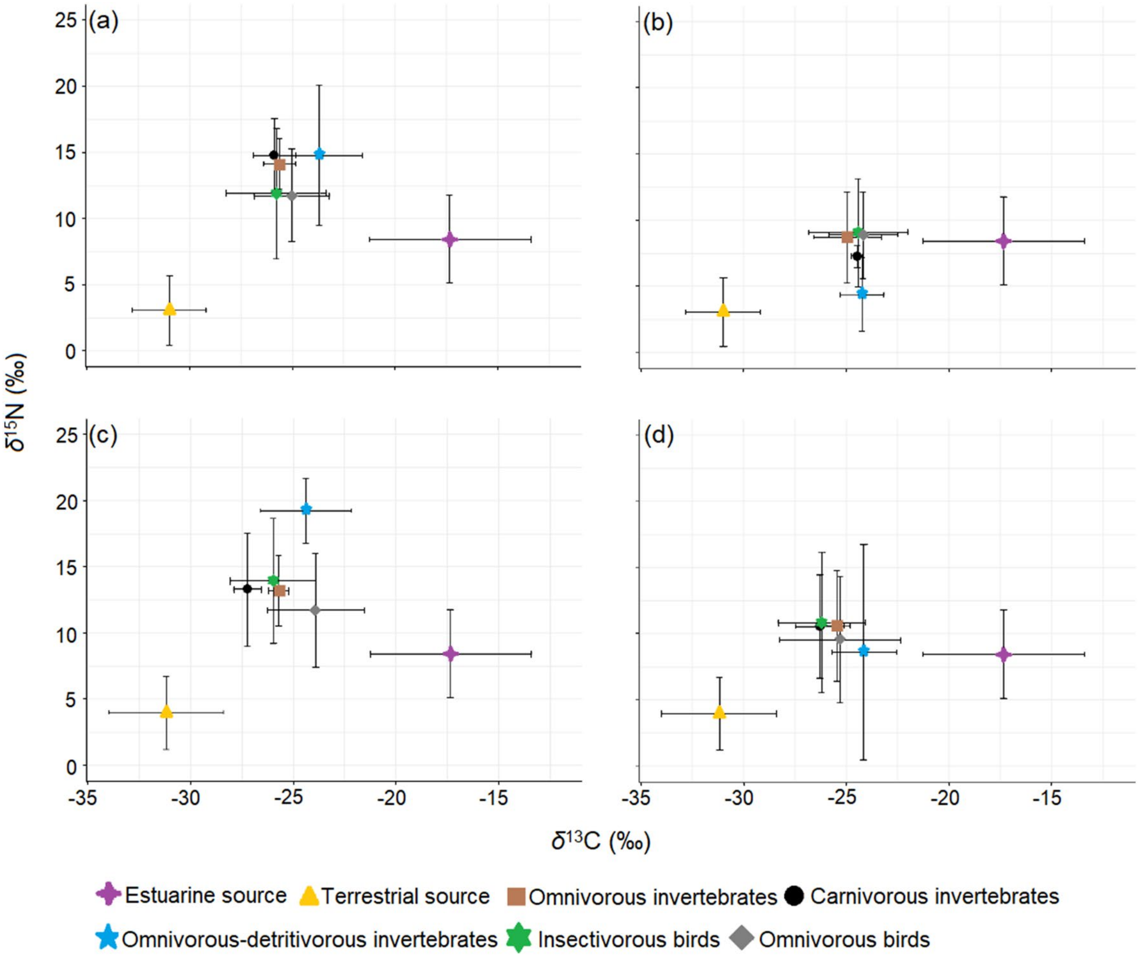


Fig. 4 Mean and standard deviation of δ^{15}N and δ^{13}C values of omnivorous, omnivorous–detritivorous, and carnivorous invertebrates and blood of omnivorous and insectivorous birds in the colony and control environment, respectively, during summer (**a**, **b**) and winter (**c**, **d**), and potential food sources

values in the blood of land birds during winter in the colony site (Fig. 3).

Dissipation along the trophic chain (vertical)

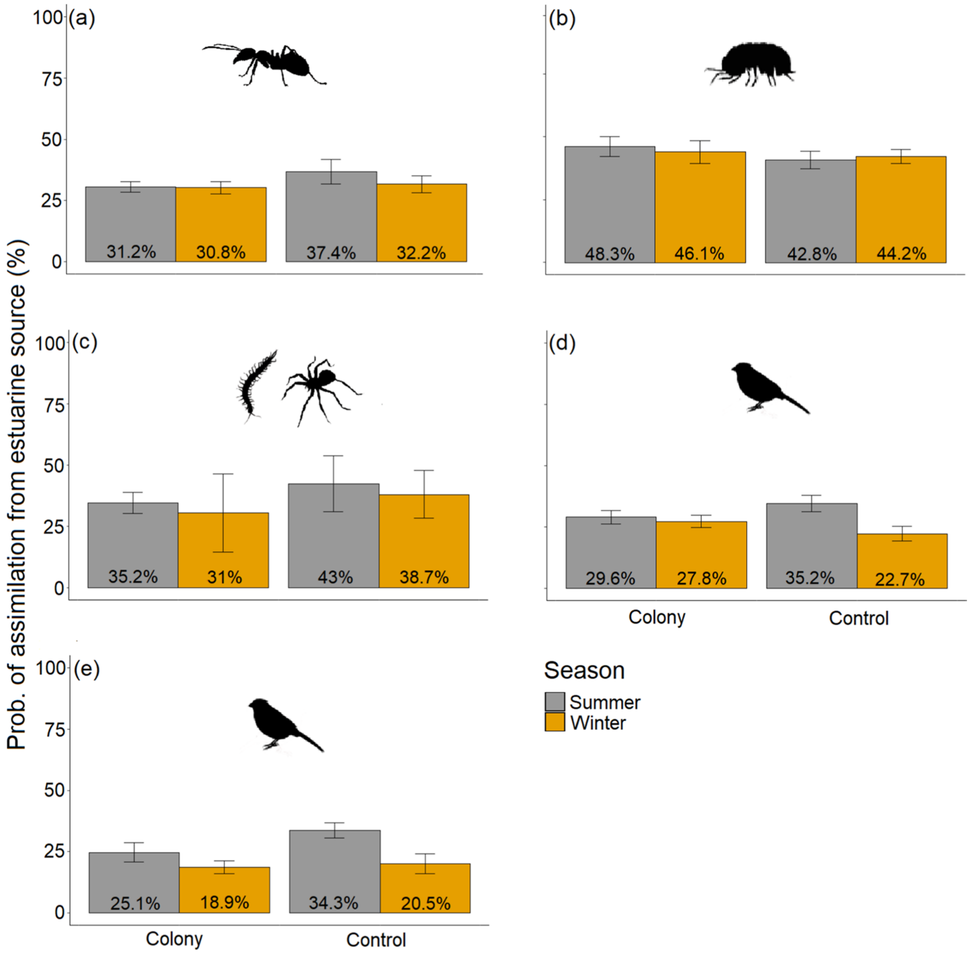
Soil, vegetation, and invertebrates showed positive effects on δ^{15}N values in the colony site (Table 1). The variance on the data for the vegetation model with δ^{15}N values was explicated by “species” (32.2%) and “site” (22.3%) factors (Supplementary Material Table S5). Land birds showed positive effects, but despite this, the group of migratory birds with a wide habitat (MBH) had negative effects on values. The data variance was explicated in 14.8% by “site” and in 3.3% by “habitat” used by birds (Supplementary Material Table S5). The positive effects on the vegetation occurred for both *Dioscorea* sp. and *C. crocosmiiflora*, indicating that both herbaceous plants and trees responded positively to nitrogen enrichment from allochthonous sources in the colony site.

For carbon isotopes, the colony site showed positive effects for soil values and negative effects for invertebrate values. The omnivorous–detritivorous invertebrate guild had positive effects on values (Table 1). Colony soil values explicated 26.8% of the variance in δ^{13}C values. For invertebrates, the factor “site” explicated 2.4% of the data variance, while “guild” explained 22% of the variations in δ^{13}C values (Table 1). Moreover, there was a positive effect on the mean δ^{13}C values for birds from the colony compared to the control site. However, similar to the results found for δ^{15}N, there was a negative effect on migratory birds that do not exclusively use the colony forest for feeding (MBH). The ANOVA indicated explicabilities of 3.2% and 8.1% for the factors “habitat” and “guild”, respectively (Supplementary Material Table S5). The factor “site” did not vary significantly.

Bayesian mixture models

Bayesian mixture models with two end points—terrestrial and estuarine—showed that all consumers, in both control and colony environments, had estuarine isotopic signatures in their tissues or from other sources with values similar to those found in the nearby estuarine waters (Fig. 5; Supplementary Material Table S6). The higher probability of assimilation of estuarine matter into the tissues of invertebrates in the colony and control environments, respectively, was 31.2% ± 2.2% and 37.4% ± 5.1% (omnivorous) (Fig. 5a), 48.3% ± 4.1% and 44.2% ± 2.8% (omnivorous–detritivorous) (Fig. 5b), and 35.2% ± 4.4% and 43% ± 11.5% (carnivorous) (Fig. 5c). For land birds, the higher probabilities of assimilation of estuarine matter in the colony and control environments were 29.6% ± 2.8% and 35.2% ± 3.4% (omnivorous) (Fig. 5d) and 25.1% ± 4.0% and

Fig. 5 Probability of assimilation (mean values) of estuarine sources in colony and control sites during summer and winter seasons by omnivorous invertebrates (**a**), omnivorous–detritivorous invertebrates (**b**), carnivorous invertebrates (**c**), omnivorous birds (**d**), and insectivorous birds (**e**)



34.3% ± 3.2% (insectivorous), respectively (Fig. 5e). Thus, the omnivorous–detritivorous invertebrate group showed a predominance of estuarine matter compared to the control environment in both seasons (Fig. 5b). Furthermore, during the summer season, omnivorous birds showed a higher probability of assimilating estuarine matter than the control (Fig. 5d). The other groups (omnivorous and carnivorous invertebrates and insectivorous birds) demonstrated a higher likelihood of assimilation of estuarine matter in the control environment than in the colony environment in both seasons (Fig. 5a, c, e).

Discussion

Nutrients transported by herons and spoonbills support the environment and the entire trophic web where they breed. This conclusion was based on analyses in several dimensions—spatial, temporal, and vertical—and in different compartments of the swamp forest ecosystems of the colony compared to a control non-colony site. This study demonstrates that the colony environment is enriched in ^{15}N and ^{13}C compared to the control environment, although this occurs to a lesser degree for ^{13}C (spatial dissipation). Resources remain in the environment even after the waterbird-breeding season, demonstrating that the nutrient load deposited during spring–summer is a key resource for the trophic web of the swamp forest long afterward (temporal dissipation). In addition, a vertical analysis (along the trophic chain) showed that estuarine subsidies reach higher trophic levels. However, there are other important factors, such as the influence of trophic guild and feeding habitat. Omnivorous–detritivorous invertebrates, for example, tended to assimilate estuarine matter more frequently than other invertebrate groups. These results may indicate that, because of their detritivorous habit of consuming matter available on the soil, they directly access the matter transported to the colony by waterbirds. This increases their assimilation of estuarine matter in comparison to other invertebrate guilds. Furthermore, migratory birds using broad habitats (MBH) showed lower isotopic values and lower assimilation of estuarine matter than other groups of land birds. This indicates that, because they are migratory and not limited to the colony forest, they use less enriched food resources. Therefore, their tissues were less isotopically enriched in comparison to other bird groups in the colony forest.

Spatial dissipation

The $\delta^{15}N$ and $\delta^{13}C$ values in the organisms and soil of the colony environment were higher than those of the control environment. This indicates that the presence of waterbirds isotopically enriches the colony forest. Furthermore, because predatory waterbirds occupy high trophic levels, they have excreta enriched in ^{15}N (Caut et al. 2012). Thus, guano and deposited nitrogen-enriched matter are accessed by organisms at low trophic levels in the terrestrial environment surrounding the colony (Gaiotto et al. 2022; Linhares and Bugoni 2023), generating an upward enrichment cascade across all higher trophic levels. The nitrogen isotope analysis showed that waterbird colony promoted ^{15}N enrichment, as demonstrated by the strong effect on the GLM with $\delta^{15}N$ values (Table 1; Supplementary Material Table S5). Similarly, $\delta^{15}N$ in soil, vegetation, invertebrates, and land birds in the colony environment showed higher values than those in the control site. Other studies conducted in oligotrophic receptor environments show that bird colonies, through the deposition of guano and matter, tend to enrich these environments (Polis et al. 1997; Kolb et al. 2010; Caut et al. 2012; Savage 2019). In the present study, it was shown that enrichment also occurs in a productive receptor environment, such as swamp forests. This is likely due to the intensity of loading, with recurrent breeding at the same site, mediated by large-sized and numerous waterbirds. Our results suggest enrichment by guano, tissues of waterbirds, and their prey, from estuarine areas, or nutrients with high $\delta^{15}N$ values, into the swamp forest, and from soil to land birds (Fig. 2). The isotopic nitrogen values of the organisms were higher in the colony when compared to the control environment, as shown in Fig. 4a, c, reinforcing the enrichment by ^{15}N in this environment. Despite this, our study indicates that this deposition is widely distributed throughout the colony area, as everything from soil to vertebrates appears enriched. This spatial distribution in the colony environment occurs through biotic and abiotic vectors (Green and Elmberg 2014; Schindler and Smits 2016; Griffiths et al. 2018; Gaiotto et al. 2020), with water-saturated soil likely playing a key role, similar to water runoff on oligotrophic tropical islands (e.g., Sánchez-Piñero and Polis 2000; Gaiotto et al. 2022).

Although the use of carbon isotopes as a marker of matter flux in complex environments, such as estuaries, can be inefficient (e.g., Spano et al. 2014), our results indicate that this is a useful tool for understanding the functioning of estuarine environments, confirming previous findings (e.g., Domingos and Lana 2017; Mont'Alverne et al. 2016). The constant input of terrestrial matter from C_3 plants that flows into the water may reduce $\delta^{13}C$ values (Spano et al. 2014). Moreover, in estuarine aquatic environments, the presence of C_4 plants (phanerogams, algae in tidal flats) contributes to the enrichment of ^{13}C, resulting in significantly higher mean values in the estuary (Garcia et al. 2007; Pereyra et al. 2016). Therefore, the significant differences in $\delta^{13}C$ values found in the colony soil in comparison to the control demonstrate the importance of carbon as a natural marker, complementary to the nitrogen isotope. The results also demonstrate that it is possible to detect ^{13}C enrichment generated by the transport of estuarine matter into terrestrial environments, even when the receiving environment is highly productive, as in swamp forests. Furthermore, regular heron breeding at the site, year after year, can lead to saturation of the environment, making it well marked isotopically.

Temporal dissipation

Soil, invertebrates, plants, and terrestrial birds maintained or increased values of $\delta^{15}N$ even during the winter without the presence of the colonial waterbirds. This indicates that the pulse is so intense that the enrichment of the environment persists in the soil and vegetation. Similar studies on marine islands also indicate that once the vegetation is isotopically enriched, the marine signature persists in terrestrial consumers, even during periods without the presence of the colonial seabirds (Stapp and Polis 2003; Caut et al. 2012; McLoughlin et al. 2016).

For $\delta^{13}C$ values, only land birds had a negative effect during the winter, although the effect shown was smaller than that shown for $\delta^{15}N$. It is expected that with the pause in the matter input pulse, the enrichment will not reach higher trophic level organisms, such as birds, due to the loss of trophic signal. In addition, other factors are involved in differences found between groups, such as the difference in tissue turnover related to each animal group, the guild, and the position in the trophic chain (Boecklen et al. 2011). However, for both isotopes, there is an indication that outside of reproductive periods, the soil and vegetation allow organisms in the environment to continue utilizing matter of allochthonous origin. Other studies have indicated that guano carried by birds has the ability to enrich producers in the environment (Shatova et al. 2017; Savage 2019). However, plants obtain their carbon from atmospheric air, and therefore ^{13}C enrichment does not affect producers but rather organisms that feed on the carcasses of herons that die in the colony and the food scraps transported from the estuary. The $\delta^{13}C$ values of these organisms are derived from their feeding and reflect the values at the base of the trophic chain (Craig 1953; DeNiro and Epstein 1981). Therefore, since vegetation carbon values are independent of allochthonous input, carbon enrichment ultimately has a limited influence on the trophic web. Even though, the colony shows higher isotopic carbon values in the winter compared to the control site at the same season, demonstrating the persistence of temporal enrichment by waterbirds.

Furthermore, our results demonstrated the depletion of ^{13}C in invertebrates in 2018 compared to 2019. This may indicate that matter dissipation during the winter of 2019 may have been influenced by El Niño, when longer and intense periods of precipitation occur (Odebrecht et al. 2017). Periods of inundation caused by rainfall may aid in the dispersal of colony-deposited matter, such as guano, leading to its dissipation further into the environment in rainy years. Other studies have also demonstrated that some of the nutrient distribution in the environment is driven during periods of flooding and precipitation (Caut et al. 2012; Schindler and Smits 2016; Li et al. 2017; Gaiotto et al. 2022). This may indicate that abiotic factors such as rainfall and inundation periods, in addition to transport by biotic vectors, also contribute to the temporal dissipation of transported nutrients, similar to oligotrophic environments (Gaiotto et al. 2022).

Vertical dissipation and trophic guilds

Estuarine-derived nutrients were detected in the soil and tissues of all groups of organisms analyzed in the colony, and ^{15}N enrichment was higher in the colony than in the control site. This indicates a link between the bird colony and the local trophic web, with the latter being dependent on allochthonous nutrient inputs mediated by waterbirds. Both herbaceous plants and trees were enriched by the input of estuarine matter, with no significant differences between them. Only the fern group showed no significant enrichment in the colony environment compared to the control. However, this group of plants was collected at the edges of the colony region, which may indicate that as the distance from the core region where a higher concentration of nests occurs, the enrichment loses intensity. Similarly, other studies have also shown that distance from the source of matter, whether rivers, ocean, or colonies, is important in regard to the dissipation of the isotopic signature (Caut et al. 2012; Korobushkin 2014; Gaiotto et al. 2022).

In primary consumers, the average enrichment was maintained compared to soil and vegetation. However, when separated into trophic guilds, we observed differences in the assimilation of estuarine matter. The omnivorous invertebrates (ants) of the genus *Camponotus*, which feed predominantly on plant matter, invertebrates, and fruits (Ronque 2013), showed lower levels of estuarine matter assimilation during winter (Fig. 5a). A similar pattern occurred with carnivorous invertebrates (Fig. 5c), which do not feed directly on producers but have isotopic signatures of their prey (DeNiro and Epstein 1981). In the guild of omnivorous–detritivorous (*Armadillidium*, common pill woodlouses), the pattern also emerged in the colony but not in the control environment, where there was an increased probability of assimilation during winter. Another difference found between invertebrate groups and the omnivorous–detritivorous guild was the higher probability of assimilation of estuarine matter in both seasons in the colony in comparison to the control (Fig. 5b). These results suggest that omnivorous–detritivorous common pill woodlice feed on sources other than matter from local producers, such as dead nestlings and food scraps carried by waterbirds (Markwell and Daugherty 2002).

Land birds at higher trophic levels in the colony environment had ^{15}N enrichment in their blood. Besides that, the results suggest that a dissipation of nitrogen upward in the trophic chain (vertical dissipation) is also occurring, which was observed in insects and resident birds. This is the same pattern of dissipation found in marine islands (e.g., Gaiotto et al. 2022), which indicates that the sources of nitrogen throughout the trophic web is likely due to the input of guano and other waterbirds-origin material.

Similar to results found for δ^{15}N values, the allochthonous carbon load seems to dissipate along the trophic web, but in the group of land birds, other factors seem to have a greater influence. Except for omnivorous birds during winter, the assimilation in insectivorous (both seasons) and omnivorous (summer) bird guilds had a higher probability and assimilation of estuarine matter in the control environment compared to the colony (Fig. 5d, e). These results can potentially be explained by the fact that the forest boundaries of the control environment are closer to the estuary than the colony environment. Previous studies have pointed out that emerging invertebrates in aquatic environments are important sources for terrestrial consumers (Nakano and Murakami 2001; Schindler and Smits 2016; Recalde et al. 2021). Therefore, we suggest that even in the control site not receiving any heron-mediated estuarine matter input, resident animal groups utilize external food resources associated with the estuarine environment found at the forest margins. Besides that, migratory birds, with a broad foraging habitat (MBH) and large movements, i.e., not feeding exclusively within the colony forest, tended to be less enriched than photophobic, forest-restricted bird groups. This group had lower ^{13}C and ^{15}N enrichment, suggesting that the length of time organisms had been present in the environment also influences the level of enrichment in tissues, due to the shorter exposure time to enriched foods from the colony site (DeNiro and Epstein 1978; Zupcic-Moore et al. 2017).

Conclusion

This study demonstrated that waterbird colonies located on estuarine islands are able to isotopically enrich the environment in which they are established, even though fluxes occur among two productive environments, i.e., estuarine waters and swamp forests. The ^{13}C and ^{15}N enrichment was substantial in the colony environment compared to the control, even long after the waterbird-breeding period. This pattern suggests that even in swamp forest environments, recognized as rich in organic matter and high primary productivity levels, the matter transported by birds and nutrient load is maintained throughout the year. However, further studies are necessary to understand the benefits of the estuarine matter assimilated to demographic parameters, physiology, and health of organisms in the environment. We conclude that the colony is an important source of nutrients, energy, and matter, and that it is able to support the environment throughout the year, contributing to ecological processes in swamp forests. Thus, environmental impacts that lead waterbirds to stop using the environment for breeding could cause a reduction in the availability of resources, generating impacts on the population of organisms that are already familiar with the pulses of nutrients from the estuary.

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Author contribution statement FCS and LB formulated the idea and developed the methodology. FAF and CTB provided methods adjustment advice. FCS, LB, FAF, CTB, and CNF carried out the fieldwork. FCS, LB, and FAF analyzed the data and CTB and CNF offered statistical advice. FCS wrote the manuscript. CTB, CNF, FAF, and LB reviewed and provided contributions to the content and offered editorial advice.

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Data availability All data produced from this study are provided in this manuscript.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable institutional and national guidelines for animal care and use were followed. Necessary licenses were obtained from the Ethical Committee on Animal Use (CEUA P020/2020) and biological sampling (SISBIO 50810-9) for this research.

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