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Dissipation of seabird-derived nutrients in a terrestrial insular trophic web

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Abstract Highly mobile organisms can transport nutrients and energy among distinct ecosystems, such as between oceanic foraging areas and terrestrial breeding sites. Seabirds are great nutrient carriers and potentially play a key role in the maintenance of trophic webs on islands. In this study, we assessed three dimensions of marine nutrient dissipation—horizontal, temporal and vertical—on the tropical Meio Island of Fernando de Noronha Archipelago, Brazil. For this, C_3 and C_4 plants, ants and spiders found in a 100 m long transect between colonies of masked (*Sula dactylatra*) and red-footed boobies (*Sula sula*) were sampled during the rainy (the masked booby breeding period) and dry seasons (the red-footed booby breeding period). The marine contribution to the terrestrial trophic web was analysed using Bayesian mixing models from a carbon and nitrogen stable isotope data set. The main findings indicate that marine nutrients in the terrestrial trophic web dissipated horizontally as the distance from the colony increased, which was more marked during the rainy season. On the vertical axis, the relative contribution of marine nutrients in terrestrial consumers was strongly related to food habits but not necessarily to the trophic level, dissipating rather than increasing, due to variable omnivory and the use of terrestrial food sources. The breeding strategy of the masked booby (i.e. incubating eggs on the ground), in addition to a larger body size and larger colony, could produce a more concentrated pulse of nutrients in comparison to seabirds nesting sparsely on trees, contributing more efficiently to the enrichment of marine nutrients on land. The importance of seabirds for the maintenance of interconnected ecosystems has been demonstrated, and the role of marine-derived nutrients in the enrichment of nutrient-poor tropical islands.

Key words: allochthonous nutrient, ecosystem functioning, marine subsidies, oceanic islands, tropical seabirds.

INTRODUCTION

Highly mobile organisms (e.g. seabirds and sea turtles) can transport nutrients and energy among distinct ecosystems, such as between oceanic foraging areas and terrestrial breeding sites (Moss 2017). In terrestrial environments with low primary productivity (biomass), as is typical of tropical oceanic islands, marine nutrients can be the main source of energy available, and spatiotemporal variations in resource availability can make terrestrial communities dependent on these nutrient pulses (Stapp *et al.* 1999). Thus, deposited marine nutrients from mobile organisms can modify the community composition of plants (Zwolicki *et al.* 2016), belowground invertebrates (Wright *et al.* 2010), above-ground invertebrates (Korobushkin 2014), and vertebrates (Stapp & Polis 2003), which changes the dynamic between consumers and resources (Bauer & Hoye 2014) and connects marine and terrestrial trophic webs (McLoughlin *et al.* 2016).

Seabirds are potential nutrient carriers and can play a key role as carriers in broad-scale nutrient cycling (Doughty *et al.* 2016). For instance, nutrients carried by seabirds are related to coral reef productivity (Savage 2019), bioengineering (Zwolicki *et al.* 2016; Duda *et al.* 2020), algal abundance and fish biomass enhancement (Benkwitt *et al.* 2019). On islands, they can assist in the maintenance of trophic webs, as seabird-derived guano increases the availability of nitrogen in environments by up to 100 times (Mulder *et al.* 2011) and provides ^{15}N enrichment to producers and consumers (Stapp & Polis 2003; Korobushkin 2014; Savage 2019).

Seabird colonies on oceanic islands are an ideal model for lateral transport studies because they represent a well-defined marine source for terrestrial environments. In these systems, low isotopic values of carbon, associated with high isotopic values of nitrogen in terrestrial consumers, suggest ^{15}N enrichment from marine sources (Tabak *et al.* 2016). Thus,

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stable isotope analysis of plants and invertebrates can be used to track the uptake of marine nutrients along with terrestrial food webs (Goncharov *et al.* 2011). Understanding patterns of energy and nutrient flows is key to the proper understanding of connected ecosystems, and for developing measures for the conservation of both marine and terrestrial species around oceanic islands.

Seabirds can perform long displacements looking for food (Young *et al.* 2015) and carry nutrients and trace elements to soils around their nests (Zwolicki *et al.* 2013; Mallory *et al.* 2015; Cipro *et al.* 2019). In seabird colonies, nutrients are directly introduced into terrestrial ecosystems through eggshells, chicks and carcasses, which are used as food and nutrient resources by terrestrial organisms (Sánchez-Piñero & Polis 2000), fertilizing the soil and providing energy for different trophic levels (Caut *et al.* 2012). Then, nutrients flow by pathways along different trophic levels (i.e. vertically), spatially along distances through biological carriers or abiotic factors, and temporally, for example through seasonal nutrient pulses (Spiller *et al.* 2010; Caut *et al.* 2012; Korobushkin 2014).

Sulidae seabirds (boobies and gannets) perform foraging trips 100 km or more away from their nests and feed in areas up to 300 km^2, staying at sea for some hours or up to approximately 2–4 days (Young *et al.* 2015; Lerma *et al.* 2020a; Roy *et al.* 2021). In the Fernando de Noronha Archipelago, tropical Atlantic Ocean, two central place foragers breed on a small islet during distinct periods. The masked booby (*Sula dactylatra*) resides on the island over the entire annual cycle (Roy *et al.* 2021) but breeds only during part of the rainy season (March–June) by establishing a colony with approximately 400 individuals nesting on the ground. The red-footed booby (*Sula sula*) colony holds ~1500 individuals on trees during part of the dry season (August–November), making sparse nests when the branches are leafless, and most individuals leave the island after the breeding season (authors' unpubl. data). Additionally, masked boobies present body masses heavier than red-footed boobies (1500–1700 g *vs.* 750–1050 g, respectively; Weimerskirch *et al.* 2006; Weimerskirch *et al.* 2009), which affects the amount of marine nutrients transported by each species to the terrestrial environment.

Based on the three dimensions of nutrient dissipation, we aimed to verify patterns of marine nutrient dissipation on land, mediated by seabirds and incorporated into terrestrial organisms. In the breeding sites of the masked and red-footed boobies, we assessed (i) the horizontal dimension, the magnitude of the spatial dissipation of marine nutrients along a terrestrial transect; (ii) the vertical dimension, the relative contribution of marine sources to the tissue synthesis of terrestrial organisms and ^{15}N dissipation upwards in the trophic chain, rather than enrichment, due to the variable omnivory of consumers and the use of terrestrial food sources; and (iii) the temporal dimension, the ^{15}N enrichment in producers and consumer tissues compared between the rainy and dry seasons.

In general, we expected to find a terrestrial trophic chain receiving a high influence of marine nutrients transported by seabirds near the colonies. Thus, we predicted a ^{15}N enrichment decrease spatially as the distance from the source increases; upper trophic levels presenting lower ^{15}N enrichment than lower levels due to upwards dissipation; and plants, ants and spiders with higher δ^{15}N values during the rainy season than during the dry season due to the breeding season of masked boobies being coupled with the growing season of plants.

METHODS

Study area

Fieldwork was carried out on Meio Island in Fernando de Noronha Archipelago (3°52′S; 32°26′W), which is located 360 km offshore the Brazilian mainland, in the tropical southwestern Atlantic Ocean (Appendix S1). Fernando de Noronha is an archipelago with 21 volcanic islands totalling 18.2 km^2 (Dias *et al.* 2017), covered by deciduous vegetation comprised of trees, shrubs and herbs (Mello & Oliveira 2016). The archipelago presents a well-marked dry season from August to January and a rainy season from February to July, with a mean annual rainfall of 1400 mm (Teixeira *et al.* 2003).

At the northern end of the archipelago, Meio Island is the model island used to assess the nutrient dispersion, chosen due to its small size and limited species diversity. This islet holds the masked boobies and the red-footed boobies, where the red-footed boobies breed in the only area with trees on the northwest of the island, while the masked boobies nest on the ground (Appendix S2). Shrubs and herbaceous vegetation cover most of the island, with patches of exposed soils and rock outcrops on the borders (Appendices S1 and S2). Meio Island also hosts the endemic Noronha skink (*Trachylepis atlantica*), yellow land crabs (*Johngarthia lagostoma*), wolf spiders (Lycosidae) and introduced black rats (*Rattus rattus*), which were eradicated some months after our fieldwork.

Sampling

Samples were collected in October 2016 and April 2017 during the dry and rainy seasons, respectively. Organisms were sampled along a 100 m long transect adapted from Korobushkin (2014) to assess the horizontal dimension of marine nutrient dissipation. This transect had two sections, both starting from colonies of masked and red-footed boobies (Appendix S1). Sampling of plants and arthropods was carried out at nine points along both sections: 0 (inside the

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colony), 5, 10, 20 and 50 m from the nitrogen input areas (i.e. colonies). Thus, the midpoint of the whole transect was 50 m from both colonies (Fig. 1).

To build a trophic chain model to assess the vertical dimension, producers and consumers at different levels were collected based on abundance, mobility and food behaviours. We consider that consumers could transition between different levels and nutrient assimilation methods (i.e. directly or indirectly), but with no variation in food items consumed due to limited species diversity on the island. Plant leaves of the C_3 (*Ipomoea piurensis* and *Ipomoea alba*) and C_4 (*Paspalum pleostachyum* and *Cyperus atlanticus*) photosynthetic pathways were collected manually at each distance from the colony, sun-dried to prevent decomposition and stored in plastic bags. Wolf spiders (Lycosidae) were collected manually, and three pitfall traps were installed at each distance to capture fire ants (*Solenopsis* sp.). We were unable to obtain ants inside the red-footed booby colony during the dry season. Other invertebrate species were not abundant or frequent in the trap, as there is a limited number of species available on this remote island; thus, we focused on ants and spiders for our study. Muscle samples of yellow crabs were obtained through nonlethal sampling by removing a pereiopod after manual collection, and black rats were trapped with a handnet and Tomahawk traps (50 × 21.5 × 20 cm), euthanized and dissected to obtain liver samples. We used liver samples to assess the diet of black rats because it is a metabolically active tissue with a shorter time-window than muscle or hair due to rapid turnover rates and could represent recent assimilated food (Tieszen *et al.* 1983). The tissue was chosen to ensure that the signatures represented wet or dry seasons rather than extending for periods long before the sampling time.

Yellow crabs and black rats present higher mobility, which allows them to consume food items from different transect distances rather than from the sampling point only. Therefore, both were randomly collected and were not used to assess the horizontal dimension, for which plants, ants and spiders were used. Due to logistic constraints during fieldwork, all samples were stored in 70% ethanol, as it does not influence $\delta^{15}N$ and $\delta^{13}C$ values (Hobson *et al.* 1997).

Stable isotope analysis

Plants were dried again in an oven for 48 h at 60°C, macerated with a mortar and pestle, weighed (3 mg) and stored in tin capsules. Due to the limited number of organisms and small body sizes of most invertebrates, samples were pooled to reach the minimum amount for stable isotope analysis. This procedure integrates values and variations potentially found in several individuals and samples but

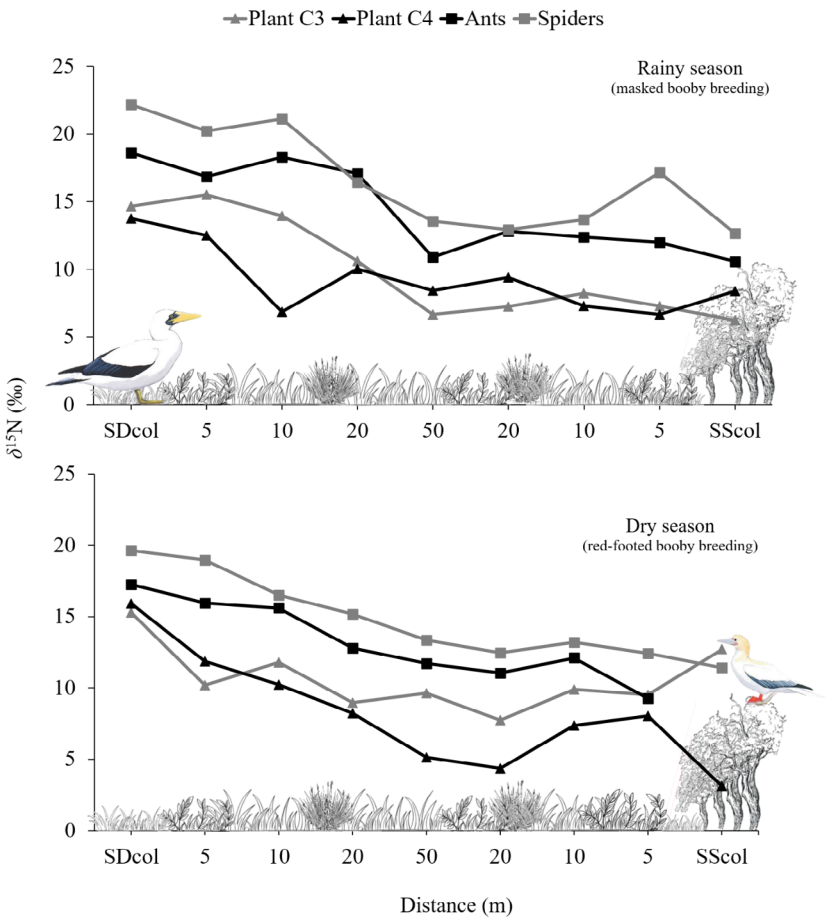

Fig. 1. Horizontal dissipation of nitrogen on Meio Island, Fernando de Noronha Archipelago, for C_3 and C_4 plants, ants and spiders. The rainy season is the breeding season of masked boobies nesting on the ground, while the dry season is the red-footed booby breeding season nesting in trees. Both sections, departing from the masked booby, *Sula dactylatra* colony (SDcol), and from the red-footed booby, *Sula sula* colony (SScol), were sampled for plants and invertebrates and are potential sources of allochthonous nutrients.

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precludes the calculation of variations among samples (Linán *et al.* 2011; Graves *et al.* 2018) of each taxon at each distance along transects. Lipids from the muscle of yellow crabs (n = 11) and liver from black rat (n = 9) samples were extracted using a Soxhlet apparatus with petroleum ether as the solvent for a 6 h cycle (Mancini & Bugoni 2014). Then, the animal samples were lyophilized, homogenized, weighed (1 mg) and stored in tin capsules.

All samples were sent to the Center for Stable Isotopes at the University of New Mexico (UNM-CSI) and analysed in an isotope ratio mass spectrometer (IRMS) coupled with an elemental analyser. The international standards used for carbon and nitrogen were Vienna PeeDee belemnite and atmospheric air, respectively. The results had an accuracy of 0.08‰ for δ^{13}C and 0.03‰ for δ^{15}N based on internal laboratory standards with known isotopic values of soy, casein, whey protein and tuna.

Data analysis

The horizontal dimension of marine nutrient dissipation from the two nitrogen sources (i.e. masked booby and red-footed booby colonies) were graphically analysed separately in each section (hereafter SDcol and SScol, respectively). We observed the variation in δ^{15}N values among C_3 plants, C_4 plants, ants and spiders along each transect.

To assess the differences in ^{15}N enrichment between the dry and rainy seasons, that is the temporal dimension, δ^{15}N values of each group (i.e. C_3 plants, C_4 plants, ants and spiders) were graphically analysed, and their mean values were compared among the dry and rainy seasons through Student's t-test with the 'lm' function in the R environment (R Core Team 2021). Significant differences were defined when $P < 0.05$. We considered all δ^{15}N values obtained at each point along the transect within each season.

Bayesian mixing models were performed through the SIAR package (Stable Isotope Analysis in R, Parnell *et al.* 2010) in the R environment (R Core Team 2021) to assess the vertical dimension of dissipation/diffusion and the contribution of marine and terrestrial sources to the tissues of terrestrial consumers. The range of δ^{13}C and δ^{15}N values obtained on the transects, and their standard deviation, were used to model assimilation by consumers, that is ants, spiders, yellow crabs and black rat tissues, and sources, that is marine and terrestrial (Table 1). The end-point values for terrestrial and marine nutrients were the isotopic values in the leaves of C_3 plants due to well-defined δ^{13}C values and the blood of masked boobies, respectively, and thus, this clearly characterized the marine and terrestrial isotopic signatures (Table 1).

Trophic discrimination factors (TDFs), ΔN and ΔC, were applied according to the consumer tissue, that is the muscle of yellow crabs and the liver of black rats. Values used for the whole body of ants and the muscle of yellow crabs were based on the estimated averages for generalist consumers obtained through invertebrates fed with plants and protein grains (McCutchan *et al.* 2003). The values used for wolf spiders were based on the values of individuals fed with fruitflies *Drosophila melanogaster* (Oelbermann & Scheu 2002). Finally, for the liver samples of black rats, we used diet-dependent trophic discrimination factor values, where the values were applied to each source, that is marine and terrestrial, obtained from experimental analysis of the species fed with fish meal, corn flour, alfalfa meal and casein (Caut *et al.* 2008).

To properly check whether marine nutrients were incorporated by terrestrial organisms derived from seabird colonies, we used isotopic values in the blood of red-footed boobies (Mancini & Bugoni 2014) and the muscle of flying fish (Exocoetidae, Waterbirds and Sea Turtles Laboratory at Federal University of Rio Grande – FURG, unpubl. data) regurgitated by masked boobies, obtained in Fernando de Noronha archipelago, for the mixing model analysis (Table 1).

RESULTS

Horizontal dissipation

Values of δ^{15}N on the SDcol section for all groups, that is spiders, ants, and C_3 and C_4 plants, decreased in tissues as the distance from the masked booby colony increased until the middle point at 50 m (Fig. 1). In contrast, the pattern of decreased δ^{15}N values from SScol towards the 50 m point was less clear, with lower variation as the distance from the red-footed booby colony increased. Exceptions were observed for C_3 and C_4 plants during the dry season, which presented the expected decrease in δ^{15}N in leaves as the distance from SScol increased towards the midpoint of the transect (Fig. 1).

Vertical dissipation

Bayesian mixing models showed that all consumers had marine carbon and nitrogen isotopic values assimilated into tissues. The contribution of the sources to tissue synthesis in consumers was estimated at a 95% credibility interval ($CI_{95\%}$), which presented a balance between terrestrial and marine contributions for spiders and ants. Yellow crabs had higher terrestrial than marine contributions, in contrast to black rats, which were highly dependent on marine nutrients in their diets, with a lower contribution of terrestrial sources. Analysis based on isotopic values from seabirds and flying fish also demonstrated marine input (Table 2; Fig. 2).

Temporal dissipation

Comparisons on the masked booby section (SDcol) were not statistically significant ($P < 0.05$) among all groups assessed, although the graphical result shows higher δ^{15}N values during the rainy season, mainly for ants (Fig. 3). C_3 plants had more variable values

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Table 1. Trophic discrimination factors (TDFs), range of isotopic values and standard deviation to each tissue of consumers and sources used in the Bayesian mixing models to estimate the contribution of marine and terrestrial sources to the terrestrial consumers in Meio Island, Fernando de Noronha Archipelago, Brazil

	Tissue	n	Stable Isotope Ratios (‰)		TDF (‰)	
			δ^{13}C ± SD	δ^{15}N ± SD	ΔC	ΔN
Source						
Marine[†]	Blood	11	−16.26 ± 0.18	10.78 ± 0.80		
Marine[‡]	Blood	10	−16.74 ± 0.23	9.31 ± 0.50		
Marine[§]	Muscle	7	−16.62 ± 0.44	10.37 ± 1.10		
Terrestrial	Leaf	9	−27.40 ± 0.60	10.63 ± 2.30		
Consumer						
Fire ants[¶]	Whole body	8	−21.86 ± 3.22	13.22 ± 2.8	0.50 ± 0.13	2.30 ± 0.18
Wolf spiders	Whole body	9	−23.36 ± 2.17	14.78 ± 3.0	0.44 ± 0.10	2.16 ± 0.10
Yellow-crabs	Muscle	11	−24.00 ± 0.61	13.60 ± 0.9	0.50 ± 0.19	2.20 ± 0.30
Black rats	Liver	9	−20.08 ± 3.42	13.16 ± 0.9	−2.78 ± 0.10[††]	2.09 ± 0.10[††]
					−0.84 ± 0.10[‡‡]	1.49 ± 0.10[‡‡]

[†]Marine source from blood samples of masked boobies.
[‡]Marine source from blood samples of red-footed boobies (Mancini & Bugoni 2014).
[§]Marine source from muscle of flying fish (Waterbirds and Sea Turtles Laboratory – LAATM-FURG, unpubl. data).
[¶]Sample is formed by pooling the whole body of ants.
[††]Value applied to terrestrial sources of black rat tissue synthesis.
[‡‡]Values applied to marine sources of black rat tissue synthesis.

in rainy than dry seasons (Figs. 1,3), while spiders and C_4 plants maintained similar values in both seasons (Fig. 3). In the red-footed booby section (SScol), plants had significant differences between seasons for δ^{15}N; C_3 plants had higher values during the dry season ($t = 3.171$; $P = 0.013$; d.f. = 8; Fig. 3), and the opposite was true for C_4 plants ($t = 2.365$; $P = 0.045$; d.f. = 8; Fig. 3). Finally, spiders and ants had similar values between the rainy and dry seasons.

DISCUSSION

Seabirds contribute strongly to marine nutrient input in terrestrial food webs, and these nutrients are dissipated as the distance from the colony increases. The input of marine nutrients in terrestrial ecosystems varies by species, and mobile terrestrial organisms exploit terrestrial and marine nutrients in different ways, independent of their trophic level. The breeding strategy of masked boobies, incubating eggs on the ground (Carboneras 1992), in addition to their heavier body mass and colony size, enhances the marine nutrient pool in the terrestrial ecosystem, contributing to more efficient enrichment of the terrestrial food web. Marine δ^{15}N values were detected up to the third trophic level, and the relative contribution of marine nutrients in terrestrial organisms is strongly related to food habits but not necessarily to the trophic level. Seasonal variation was important to plants located on SScol, which receive nutrients from red-footed booby colonies during the dry season, either carried from masked booby colonies through mobile consumers such as rats and crabs or physical carriers such as rain.

Horizontal and temporal dimensions

The decrease in δ^{15}N values on SDcol as the distance from the masked booby colony increases, in contrast to the low δ^{15}N values on the SScol transect detected in most groups during both seasons, suggests that marine nutrients are derived mainly from the masked booby colony in the study area, even reaching the SScol transect >50 m away. We suggest that the nitrogen added by red-footed boobies into the ecosystem is limited due to the small amount during the dry season, when plants are not synthesizing tissues and without the carrier effect of rainwater, and from being retained on branches and leaves before reaching the soil. In contrast, the nitrogen input on SDcol dissipates beyond the midpoint of the whole transect at 50 m, reaching 0 m of SScol, that is at 100 m from the masked booby colony and inside the red-footed booby colony. Therefore, the increased contribution from SDcol could be a consequence of ecological and biological factors, such as the distinct configuration of nests, their high density and being on the ground for masked boobies versus arboreal and sparser nests for red-footed boobies (Carboneras 1992), in addition to the interspecific differences in body mass, as masked boobies can be

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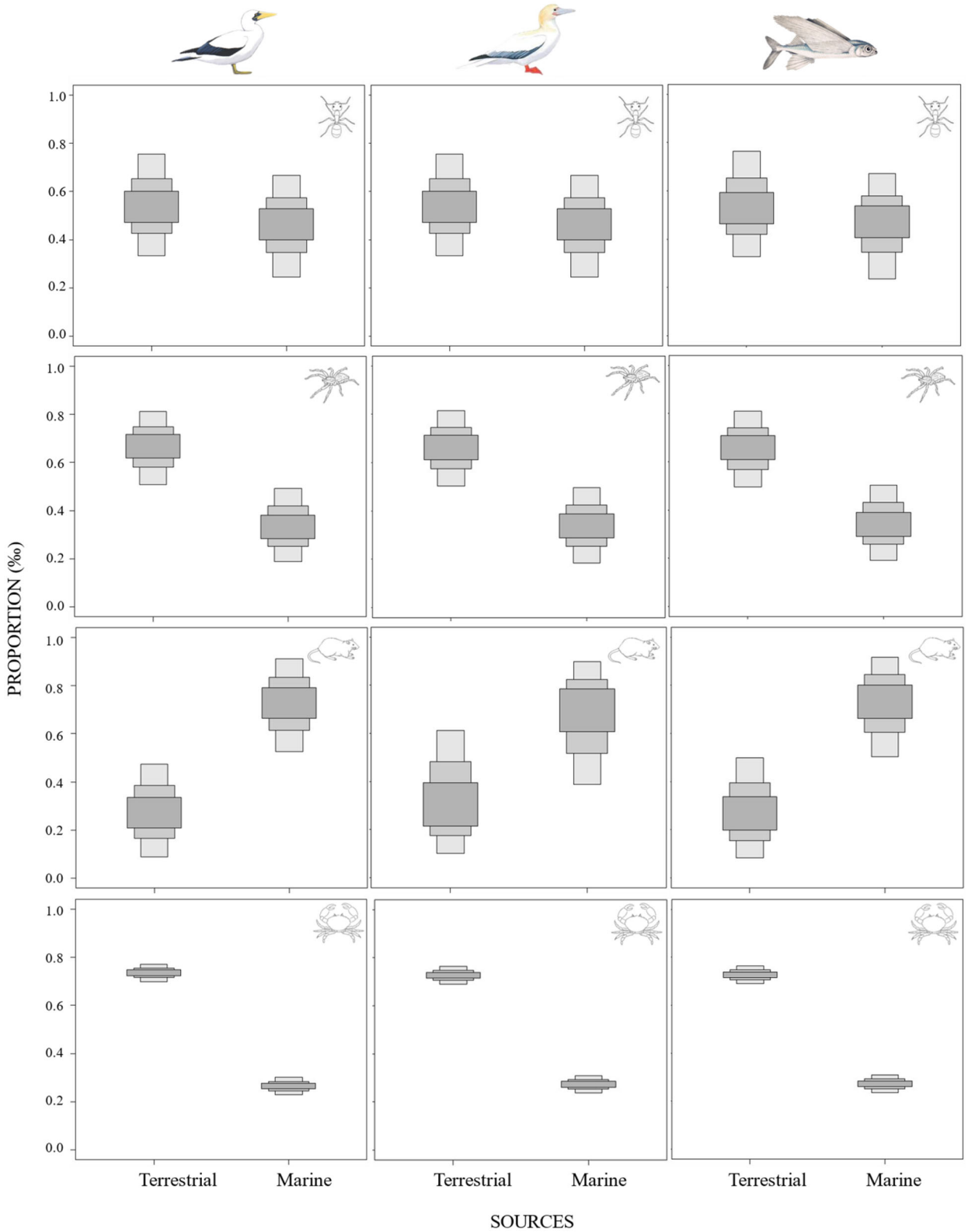

Fig. 2. Bayesian mixing models to assess the relative contribution of marine and terrestrial sources to the diets of spiders, ants, yellow crabs and black rats on Meio Island, Fernando de Noronha Archipelago. The first value applied for marine sources was isotopic values in the blood of masked boobies, followed by values from the literature for the blood of red-footed boobies and the muscle of flying fish. For terrestrial sources, C_3 plant leaves were applied in all analyses. The credibility interval was 95%.

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Table 2. Relative contribution of marine and terrestrial sources assessed through Bayesian isotopic mixing models to the diet of terrestrial consumers collected on Meio Island, Fernando de Noronha Archipelago

	Food items contribution (CI 95%)					
Consumers	Marine[†]	Terrestrial	Marine[‡]	Terrestrial	Marine[§]	Terrestrial
Fire ants	24–66	33–75	23–66	33–76	24–67	32–75
Wolf spiders	19–49	50–81	18–49	50–81	18–50	49–81
Yellow-crabs	23–30	70–77	23–31	68–76	23–31	68–76
Black rats	52–91	9–47	37–88	11–62	49–91	8–50

Models were always performed with C_3 plants as terrestrial sources, whereas marine sources were obtained from masked boobies, red-footed boobies and flying fish and calculated separately.

[†]Marine source from blood samples of masked boobies.

[‡]Marine source from blood samples of red-footed boobies.

[§]Marine source from muscle samples of flying fish.

approximately 30–50% heavier than red-footed bobbies (Nelson 2005).

Areas of allochthonous input are important sources of nutrient distribution, and higher nitrogen concentrations are expected in nearby areas (Doughty *et al.* 2016). However, nutrients deposited on land need carriers to reach sessile organisms and distant areas. Ants, spiders, crabs and rats are known to mediate nutrient distribution through foraging and transport of food (Stapp & Polis 2003; Frouz & Jilková 2008; Harada & Lee 2016; Griffiths *et al.* 2018). Thus, these groups could have contributed to the transport of marine nutrients towards the SScol transect. Furthermore, the masked booby remains on Fernando de Noronha in both the rainy and dry seasons, moving to foraging grounds eastward but returning regularly (Roy *et al.* 2021). This behaviour provides year-round nutrient input, mainly for soil and primary producers (Caut *et al.* 2012; Mallory *et al.* 2015), which explains the lack of a difference between dry and rainy seasons for groups assessed on the SDcol transect.

Abiotic factors, such as rain, can also contribute to energy transfer among organisms in an ecosystem (Caut *et al.* 2012; Rowe *et al.* 2017), as shown by higher δ^{15}N values during the rainy season in C_4 plants in comparison with the dry season on SScol. This is also the growing season for plants, which can assimilate nutrients more rapidly and efficiently. In contrast, higher δ^{15}N values of C_3 plants were recorded during the dry season, but both groups had decreasing values from SScol towards the midpoint where both transects converged during the dry season. We suggest that marine nutrients from red-footed booby colonies contribute to higher δ^{15}N values in plants only during the dry season, when marine input from SDcol is lower and dependent only on carriers to reach distant areas. Furthermore, biologging data indicate that most red-footed boobies on Meio Island leave the colony after the breeding season (authors' unpublished data), which makes their contribution during the nonbreeding period on SScol less influential than the year-round resident masked booby. In addition, due to the high density of trees and shrubs (C_3) in the SScol area, guano could remain on branches and leaves for a longer period before reaching soil and grasses (C_4), which could explain the different δ^{15}N values in plants during the dry season.

Seabirds increase available nitrogen on terrestrial or adjacent freshwater trophic webs through guano deposition (Anderson & Polis 1998, 1999), and the effects of seabird guano are usually higher than the inputs mediated by other animals, such as sea turtles on nesting beaches (Bouchard & Bjorndal 2000). Moreover, we suggest that different breeding and nonbreeding strategies, as well as the body features of seabirds, affect the deposition of marine nutrients on land (Smith *et al.* 2011) and consequently the horizontal dissipation and temporal variation in plants. High densities of nests placed on the ground could also contribute more to increasing the input of marine nutrients in trophic island ecosystems when compared with sparse nests (or night roosting) on trees. It is known that seabirds nesting in trees also contribute to soil properties (Wright *et al.* 2010; Korobushkin & Saifutdinov 2019); thus, our results suggest that this occurred in our study case but could not be generalized to other systems elsewhere. In addition, masked boobies have larger colonies and are almost twice as heavy as red-footed boobies (Weimerskirch *et al.* 2006, 2009), which could allow greater guano deposition as large animals and groups move a greater amount of biomass between ecosystems (Doughty *et al.* 2016).

During the rainy season, which corresponds to the breeding season of masked boobies, adults perform short foraging trips and spend more time in the colony, defending the territory and incubating and rearing chicks (Young *et al.* 2015; Lerma *et al.* 2020b).

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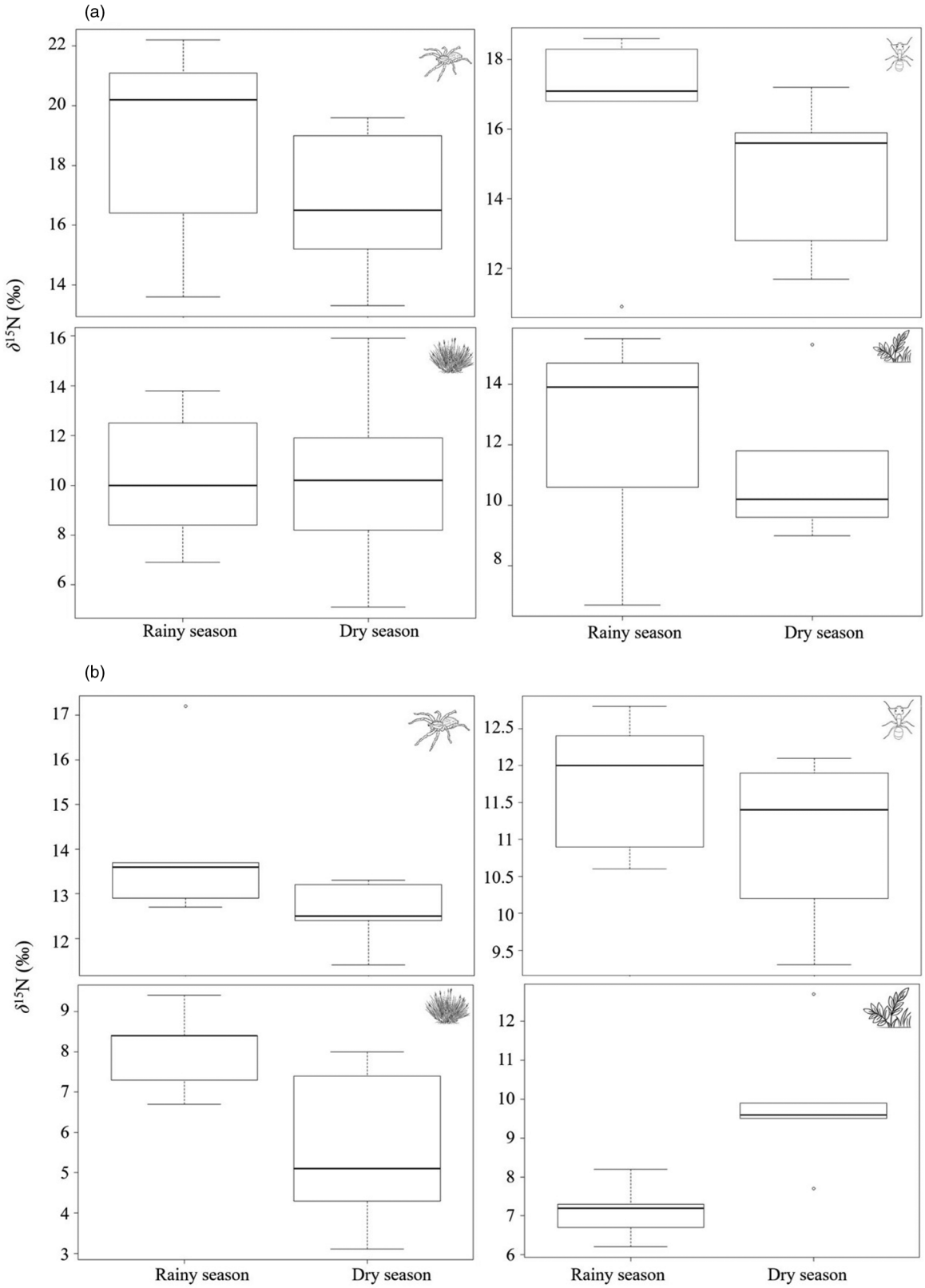

Fig. 3. Variation in δ^{15}N values among rainy and dry seasons on Meio Island for spiders, ants, C_3 (shrubs) and C_4 (grass) plants. (a) Groups from SDcol section. (b) Groups from SScol section. Outliers are represented by white dots; black lines are the median values; the boxes represent dispersion data; the whiskers represent the minimum and maximum values with no outliers.

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Thus, more time on land represents more time for guano deposition in space-restricted areas. On the other hand, during the dry season, masked boobies spend more time on foraging trips but eventually return to rest on breeding grounds (Kohno *et al.* 2019). However, during the dry season, when red-footed boobies breed in trees, a high marine nutrient input in this area was expected. Even so, nutrients from SDcol seemed to remain dissipating towards distant areas, whereas red-footed booby colonies contribute little to the ^{15}N enrichment of the terrestrial trophic web. These findings confirm that nests on trees have a lower contribution to ^{15}N enrichment over the environment and consumers, as the guano, eggs and carcasses remain sparsely distributed and do not reach the soil easily to be assimilated by producers.

The importance of seabirds as sources of nutrients for terrestrial food webs may vary according to the intrinsic features of breeding areas, such as seabird assemblage composition, weather, trophic structure and soil type. The main findings of the present study could be mirrored in other tropical regions with ground-nesting seabirds in open areas, which exposes the nutrients to abiotic and biotic carriers. The marked rainy season in tropical areas influenced by the Intertropical Convergence Zone seems to play a crucial role in spreading nutrients, since rain can carry out avian materials from seabird aggregations and allow them to reach organisms adjacent to nesting areas (Caut *et al.* 2012; Rowe *et al.* 2017). However, even in rainy seasons in tropical regions, nutrient transport may not occur or occur less efficiently if the area is used by seabirds nesting in burrows or trees, for example, which also makes the nesting strategy an important factor for nutrient dissipation.

The type of soil could also influence the enrichment from avian material because guano deposited on the rocks loses more of its nitrogen by volatilization than when deposited on sediments or vegetation (Lindeboom 1984; Blackall *et al.* 2008). In addition, the presence of historical depositions, such as ornithogenic soils (Oliveira *et al.* 2014; Silveira *et al.* 2020), could make nitrogen and phosphorous available to the terrestrial food web even during seasons and years with no or limited breeding activity. Finally, areas free of nutrient-carrying animals (e.g. ants, crabs, and rats) could be less enriched by the materials left by seabirds, which are able to transport nutrients over different spatial scales (Stapp & Polis 2003; Frouz & Jilková 2008; Harada & Lee 2016). Therefore, a combination of abiotic and biotic factors seems to be a determinant of the efficiency of seabird-derived nutrient dissipation in breeding areas and thus should be considered in studies in terms of sampling design and interpretation of the findings.

Vertical dimension

Food habits are important aspects for marine nutrient dissipation among trophic levels. The omnivorous trophic niche of ants that feed on plants, fungi and animal tissues (Lach *et al.* 2010) makes the proportion of each source (marine *vs.* terrestrial) vary according to food availability. On the other hand, spiders are predators (Oelbermann & Scheu 2002) but receive energetic inputs similar to their prey sources (DeNiro & Epstein 1978), such as ants and other insects. Yellow crabs have an omnivorous diet, ingesting skinks and bird eggs occasionally (López-Victoria & Werding 2008; Oliveira 2021), but their main diet is vegetarian, including leaves, fruits, flowers (Etchian *et al.* 2016), and organic matter during decomposition (JV Gaiotto, pers. obs., 2017). This could explain the substantial contribution of terrestrial nutrients observed in the muscle of yellow crabs and found for the same crab species on Trindade Island off the Brazilian coast (Oliveira 2021).

We suggest that marine contributions in ant, spider and crab tissues are dissipated indirectly through the enrichment of soil and primary producers. Then, marine nutrients are only available after passing through lower trophic levels and decomposition along the trophic chain pathway (Anderson & Polis 1999; Caut *et al.* 2012) and are thus less detectable upwards in the trophic chain. In contrast, rats are known for predating eggs and chicks (Hobson *et al.* 1999; Stapp 2002; Tabak *et al.* 2016), and the marine contribution assimilated in their tissues was clearly marked in our study, which confirms previous studies elsewhere (Polis & Hurd 1995) and on Fernando de Noronha (Gaiotto *et al.* 2020) that rats directly explore marine nutrients by feeding at high trophic levels, such as seabird carcasses, chicks, eggs, and regurgitated fish. Thus, a high trophic level can result in high $\delta^{15}N$ values when marine nutrients are directly obtained.

On the other hand, there is a limitation of the mixing models to distinguish between marine signals and highly ^{15}N-enriched C_4 plants, potentially caused by nitrogen saturation and temporal persistence in soil. However, these conclusions were maintained even when other marine sources were used as references for mixing models (i.e. blood of red-footed booby and muscle of flying fish), which reinforces our findings. Currently, rats have been eradicated from Meio Island, which could affect the dissipation of nutrients far from colonies at an initial instance but benefit the whole ecosystem by increasing the probability of seabird nesting in larger colonies or establishing other seabird species as nesters, and by not ingesting invertebrates, seeds and plants (Le Corre *et al.* 2015; Bell *et al.* 2019).

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In terrestrial ecosystems with marine inputs, isotopic values at different trophic levels are altered as the food source of seabirds changes (Caut *et al.* 2012; Zwolicki *et al.* 2016). In addition to marine nutrients carried by seabirds being relevant for soil enrichment and for primary producers (McLoughlin *et al.* 2016), our results suggest that nutrients can also be accessed directly (e.g. through carcasses) and promote fertilization and assimilation by nitrogen and other nutrients (e.g. phosphorous) by plants and consumers, respectively. In this context, our results could be observed on other islands around the world where piscivorous seabirds nest. However, islands and coastal regions with planktivorous species or with other food habits could present more nutrient contributions from guano than prey carcasses, that is, fertilization indirectly. Thus, terrestrial consumers can change their food sources and habitat use according to nutrient inputs by moving to inland areas (McCaulley *et al.* 2012; McCaffery & Eby 2016; McLoughlin *et al.* 2016). Therefore, the food habits of seabirds could change the way nutrients are transferred and reach high trophic levels, as we detected marine contributions at least up to the third trophic level.

CONCLUSION

The current study has demonstrated that seabirds are important carriers of marine nutrients into terrestrial ecosystems, which increase the nitrogen available through three dimensions of dissipation and could support the trophic web during breeding and non-breeding periods. Our findings indicate that marine nutrients dissipate horizontally as the colony distance increases. The marine nutrient contribution by terrestrial consumers is more related to food habits and their pathways to obtain marine nutrients than the trophic level that consumers occupy. We highlight the importance of protecting breeding areas and non-breeding sites of seabirds, which contribute to the maintenance of interdependent ecosystems, such as oceanic islands.

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AUTHOR CONTRIBUTIONS

Juliana Vallim Gaiotto: Conceptualization (equal); data curation (lead); formal analysis (lead); investigation (lead); methodology (equal); writing – original draft (lead); writing – review and editing (equal). **Guilherme Tavares Nunes:** Formal analysis (supporting); investigation (equal); supervision (equal); writing – review and editing (equal). **Leandro Bugoni:** Conceptualization (lead); investigation (equal); methodology (equal); project administration (lead); resources (lead); supervision (equal); writing – review and editing (equal).

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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SUPPORTING INFORMATION

Additional supporting information may/can be found online in the supporting information tab for this article.

Appendix S1. Study area in Fernando de Noronha Archipelago, tropical Atlantic Ocean, off north-eastern Brazil.

Appendix S2. Images of colony and nonbreeding areas on Meio Island, Fernando de Noronha Archipelago, Brazil.

Appendix S3. Raw isotopic data.

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