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Seabirds subsidize terrestrial food webs and coral reefs in a tropical rat-invaded archipelago

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Abstract

Allochthonous resource fluxes mediated by organisms crossing ecosystem boundaries may be essential for supporting the structure and function of resource-limited environments, such as tropical islands and surrounding coral reefs. However, invasive species, such as black rats, thrive on tropical islands and disrupt the natural pathways of nutrient subsidies by reducing seabird colonies. Here, we used stable isotopes of nitrogen and carbon to examine the role of seabirds in subsidizing the terrestrial food webs and adjacent coral reefs in the Abrolhos Archipelago, Southwest Atlantic Ocean. By sampling invasive rats and multiple ecosystem compartments (soil, plants, grasshoppers, tarantulas, and lizards) within and outside seabird colonies, we showed that seabird subsidies led to an overall enrichment in ^{15}N across the food web on islands. However, contrary to other studies, $\delta^{15}N$ values were consistently lower within the seabird colonies, suggesting that a higher seabird presence might produce a localized depletion in ^{15}N in small islands influenced by seabirds. In contrast, the nitrogen content (%N) in plants and soils was higher inside the colonies, corresponding to a higher effect of seabirds at the base of the trophic web. Among consumers, lizards and invasive rats seemed to obtain allochthonous resources from subsidized terrestrial organisms outside the colony. Inside the colony, however, they showed a more direct consumption of marine matter, suggesting that subsidies benefit these native and invasive animals both directly and indirectly. Nonetheless, in coral reefs, scleractinian corals assimilated seabird-derived nitrogen only around the two smaller and lower-elevation islands, as demonstrated by the substantially higher $\delta^{15}N$ values in relation to the reference areas. This provides evidence that island morphology may influence the incorporation of seabird nutrients in coral reefs around rat-invaded islands, likely because guano lixiviation toward seawater is facilitated in small and low-elevation terrains. Overall, these results showed that seabirds affected small islands across all trophic levels within and outside colonies and that these effects spread outward to coral reefs, evidencing resiliency of seabird subsidies even within a rat-invaded archipelago. Because rats are consumers of seabird chicks and eggs, however, rat eradication could potentially benefit the terrestrial and nearshore ecosystems through increased subsides carried by seabirds.

KEYWORDS
allochthonous resources, coral reefs, cross-ecosystem subsidies, ecosystem function, invasive rats, island morphology, stable isotopes, terrestrial food web, tropical archipelago

INTRODUCTION

Ecosystem functions rely on the flow of organic matter and nutrients across food webs (Skinner et al., 2021). Despite their apparent borders and singularities, ecosystems rarely function independently of other ecosystems in the landscape (Barrett et al., 2005). Over the last few decades, it has been demonstrated that even ecosystems with well-marked barriers may be interconnected by the spatial flow of matter and nutrients mediated by physical (e.g., winds, currents, tides) or biological vectors (Garcia et al., 2019; Graham et al., 2018; Pascoe et al., 2021; Rizzolo et al., 2017). Highly mobile organisms that travel across ecosystem boundaries during their life cycle transport large amounts of energy among different habitats globally (Michelutti et al., 2010; Wing et al., 2014). Allochthonous inputs can be important for resource-limited environments due to the potentially large increase in the availability of resources, which may overcome in situ productivity (Polis et al., 1997). Food web dynamics in nutrient-subsidized environments are then altered through potential bottom-up effects when the allochthonous nutrients benefit primary producers and through top-down forces when consumers directly incorporate incoming matter through predation or scavenging (Adams et al., 2010; McLoughlin et al., 2016; Sánchez-Piñero & Polis, 2000; Stapp, 2002).

The contrasting productivities and close relationships between terrestrial and adjacent marine habitats make coastal and insular areas interesting models for investigating trophic connections between ecosystems (Stapp & Polis, 2003), and they are among the most commonly studied systems worldwide. Given the low productivity inherent to tropical islands, the input of marine matter provides energy that the entire terrestrial food web may depend on (Barrett et al., 2005; Polis & Hurd, 1996; Richardson et al., 2019). This resource flux often relies on animals that feed upon energy-rich and patchily distributed marine prey and use islands as roosting and/or breeding habitats, such as pinnipeds, sea turtles and seabirds (Caut et al., 2012; Fariña et al., 2003; Hannan et al., 2007). These animals often breed in colonies on land, concentrating large amounts of marine matter by constantly depositing nutrient-rich excrement, carcasses, eggs and prey remains (Barrett et al., 2005; Polis et al., 1997).

Seabirds are important components in global nutrient cycling processes and in maintaining insular ecosystem functions by providing pulses of resources that may support terrestrial and nearshore food webs. They fertilize soils with guano, increasing the nutritional content and biomass of plants (Richardson et al., 2019; Szpak et al., 2012; Young et al., 2010), consequently benefiting consumers indirectly and also directly through predation or carrion consumption (Polis et al., 1997). Allochthonous inputs can drive changes in species composition, inducing higher densities and abundances of consumers (Barrett et al., 2005; Fukami et al., 2006; Sánchez-Piñero & Polis, 2000), altering animal ecology and evolution on islands with breeding seabirds (Briggs et al., 2012; Richardson et al., 2019; Sánchez-Piñero & Polis, 2000). Remarkably, nutrients are not retained on land but return to the ocean through surface runoff and percolation, fertilizing adjacent seawaters (Honig & Mahoney, 2016; Kolb et al., 2010; Lorrain et al., 2017). Seabird-associated nutrients were found to be assimilated by macroalgae, filter-feeding sponges, corals, and fish, promoting species diversity in macroalgal communities (Rankin & Jones, 2021), higher biomass, and faster growth rates for corals and fish (Graham et al., 2018; Savage, 2019) and supporting key ecosystem functions in coral reefs, such as grazing and bioerosion (Graham et al., 2018).

However, an inconvenient outcome of seabird efficiency in supporting island food webs is that invasive predators may be directly benefited, increasing in numbers and disrupting the natural pathways of allochthonous subsidies. Invasive rats (*Rattus* spp.) are generalist consumers that are widely distributed on islands worldwide and pose a major threat to seabirds because they prey upon eggs, chicks, and even adults (Caut et al., 2008; Dias et al., 2019). Rats have been responsible for population declines or extinctions of several seabird species (Jones et al., 2016), mainly because most seabirds nest on the ground and their chicks lack effective antipredatory behaviors. In a cascade effect, seabird trophic subsidies are reduced due to decreasing seabird numbers and consumption of matter that would otherwise be incorporated into the local trophic chain (Fukami et al., 2006; Graham et al., 2018). Rat-invaded islands have fewer seabirds and guano inputs, poorer soils, lower biomasses of producers and consumers, lower fish biomasses, and lower diversity of macroalgal communities in the nearshore waters (Benkwitt et al., 2021; Graham et al., 2018; Rankin & Jones, 2021).

Trophic interactions and the incorporation of allochthonous subsidies from seabirds can be assessed through carbon and nitrogen stable isotope analysis

(Anderson & Polis, 1998; Fry, 2006). The nitrogen isotope ratio ^{15}N:^{14}N (expressed as $\delta^{15}N$) increases from 2‰ to 5‰ at each trophic level (DeNiro & Epstein, 1981), and seabird guano has high $\delta^{15}N$ values, partly due to the top-level predator position of seabirds in the marine environment and the preferential volatilization of ^{14}N during guano mineralization (Croll et al., 2005; Lorrain et al., 2017). Thus, a high $\delta^{15}N$ value in recipient ecosystems is used as a proxy for the incorporation of seabird-derived matter into terrestrial and nearshore food webs, as demonstrated in several studies, for a broad range of organisms (Benkwitt et al., 2021; Briggs et al., 2012; Caut et al., 2012; Lorrain et al., 2017; Richardson et al., 2019). Moreover, the carbon isotope ratio ^{13}C:^{12}C ($\delta^{13}C$) tends to closely reflect the values of the primary producers, thereby providing additional information on the origin of the matter incorporated by consumers (e.g., marine vs. terrestrial environments) (Mellbrand et al., 2011).

Studies that target the spatial variation in seabird-derived subsidies through the terrestrial food web and in adjacent marine environments are key to understanding the dynamics and roles of allochthonous inputs to ecosystems, especially on rat-invaded islands. For instance, it is often assumed that small islands with breeding seabirds are affected by seabirds across the entire area (Stapp et al., 1999). However, Caut et al. (2012) have shown notable differences in the $\delta^{15}N$ of plants, arthropods, and rats in areas a few meters from seabird colonies, and Sánchez-Piñero and Polis (2000) and Barrett et al. (2005) reported lower consumer abundances outside colonies. Additionally, responses to spatial variation may vary across trophic levels because sessile ecosystem components, such as soil and plants, incorporate matter passively, whereas mobile animals, such as rats, may be capable of transporting allochthonous matter (Mellbrand et al., 2011; Paetzold et al., 2008). Moreover, recent studies have shown that islands invaded by rats have lower $\delta^{15}N$ values on land and in nearshore waters (Benkwitt et al., 2021; Fukami et al., 2006; Graham et al., 2018; Pascoe et al., 2021), but it remains unclear whether the subsidies are completely disrupted or whether coral reefs are still affected by the seabird presence near rat-invaded islands. It is also unclear whether some island-specific environmental parameters, such as island size and elevation, play a role in allochthonous nutrients reaching nearshore waters. These topics are especially important to address on tropical islands in developing countries, where rat eradication programs are in their incipient stages at best and where these investigations may provide essential information for stakeholders to help plan management measures.

Here, we used stable isotope analysis to investigate the role and extent of marine subsidies from seabird colonies in the Abrolhos Archipelago, ~70 km off the coast of northeast Brazil. This tropical area holds five rat-invaded islands with breeding seabirds and is part of the largest and most diverse coral reef complexes in the Southwestern Atlantic Ocean (Leão & Kikuchi, 2001), enabling us to assess both the land and nearshore effects of seabirds. Specifically, we aimed to (1) reveal whether the incorporation of seabird-derived nutrients vary spatially and across multiple trophic levels in the terrestrial food webs of two small islands, targeting a range of organisms from plants to lizards, as well as the invasive rats, and (2) assess whether the influence of seabird guano in coral reefs near islands could be distinguished from areas without seabirds and whether island-specific environmental and biological parameters influence the incorporation of guano nutrients into coral reefs. We hypothesized that (i) seabirds exert a greater influence on the terrestrial food web inside their colonies in comparison to outside areas, which can be demonstrated by higher $\delta^{15}N$ values within the colonies, as well as by higher nitrogen contents (%N) in soils and plants; (ii) the spatial variation in the influence of seabirds is larger for sessile ecosystem components (i.e., soil and plants) than for mobile consumers; (iii) omnivorous and predatory consumers rely on marine-derived matter from seabirds, especially the invasive rats that prey on seabirds directly; and (iv) $\delta^{15}N$ values will be higher in corals around seabird colonies in comparison to nonsubsidized areas, with a greater influence detected around smaller islands where guano runoff may be facilitated.

METHODS

Study area

This study was conducted in the Abrolhos Archipelago in the Southwestern Atlantic Ocean. The climate is tropical warm and semiarid, with a rainfall of ~700 mm annually. The rainy and colder season is from May to August, and the driest and hottest months are January and February (Kemenes, 2003). The archipelago is composed of five small islands, with the largest (Santa Bárbara, ~1.5 km in length) governed by the Brazilian Navy and the remaining areas by the Abrolhos Marine National Park, which also protects ~90 ha of marine environments. The marine area protects a portion of an important and diverse coral reef complex in the Southwestern Atlantic Ocean (Leão & Kikuchi, 2001). Coral reefs in the region grow in a unique mushroom-like form locally called "*chapeirões*," and fringing reefs occur near islands.

Seven species of seabirds breed in the archipelago: masked boobies *Sula dactylatra*, brown boobies

S. leucogaster, brown noddies *Anous stolidus*, sooty terns *Onychoprion fuscatus*, magnificent frigatebirds *Fregata magnificens*, red-billed tropicbirds *Phaethon aethereus*, and white-tailed tropicbirds *P. lepturus* (Mancini et al., 2016). Invasive rats (*Rattus rattus*) are present on all the islands, where they are known to prey upon the eggs and chicks of boobies, frigatebirds, and tropicbirds, threatening population viability, especially for the nationally threatened *P. aethereus* (IBAMA, 1991; Sarmento et al., 2014). Approximately 50–80 goats also roam freely on Santa Bárbara Island, where they may trample eggs and destroy the vegetation used by seabirds for nesting (Mancini et al., 2016).

Sampling design and laboratory procedures

Sample collection for stable isotope analysis was conducted during two dry seasons in February 2020 and 2021. The terrestrial areas were set on Santa Bárbara and Siriba Islands to include both areas inside the colonies of masked boobies and control sites without breeding seabirds, supposedly not or less influenced by them (Figure 1). Control sites were dominated by tall sedge vegetation (*Cyperus* sp.) and were separated from colonies by at least ~65 m on Santa Bárbara and by ~5 m on Siriba. In Siriba, breeding seabirds surround the control site, which is located in a lower elevation than the densest nesting area. Censuses in the colonies during fieldwork indicated that masked boobies were in their final breeding stage, given the high proportions of postfledged juveniles.

Inside each colony and control area, the surface soil and the leaves of plants following the C3 (*Sida cordifolia* and *Ipomea pes-caprae*) and C4 (*Cyperus* sp.) photosynthetic pathways were collected manually and stored frozen. Grasshoppers (order Orthoptera) were collected manually (whole body). Tarantulas (hairy spiders; family Theraphosidae) were sampled at night only on Santa Bárbara in 2020 by removing a leg from each individual

FIGURE 1 The Abrolhos Archipelago in northeastern Brazil showing (a) coral sampling stations in the nearshore environment around the islands and in reference sites far from the archipelago (controls) and terrestrial sampling areas in (b) Santa Bárbara and (c) Siriba Islands, including seabird colonies (*Sula dactylatra*) and terrestrial controls.

with scissors and obtaining a muscle sample, which must not affect survival (e.g., Brueseke et al., 2001). Lizards *Tropidurus torquatus* were captured by hand or with nooses, and the tail tips (~10 mm), the terminal section usually lost by autotomy, was removed with sterilized scissors before the individuals were released (Delibes et al., 2015). The rats were trapped in 2021 with Tomahawk traps, euthanized, stored frozen, and then necropsied to obtain liver samples. All other animal samples (grasshoppers, tarantulas, and lizards) were stored in 70% ethanol until laboratory analysis, assuming a negligible effect on isotopic ratios (Hobson et al., 1997). With these samples, an ecosystem model was developed that included the soils and the different trophic levels in the food web, that is, primary producers (plants), herbivores (grasshoppers), omnivorous reptiles (*T. torquatus*) and mammals (*R. rattus*), and a carnivore (tarantulas). In addition, feces from goats, rats, and masked boobies were also collected over the islands to investigate the potential role of invasive species in dispersing seabird-derived nitrogen on islands and to establish the guano $\delta^{15}N$ baseline values entering the food web.

In the marine environment, sampling occurred in February 2021 at five sampling stations located in the nearshore environment around the islands with breeding seabirds and at two reference stations (i.e., controls) in *chapeirões*, ~1700 m from the nearest island and assumed to be unaffected by seabirds (Figure 1). Stations were set as close as possible to the islands, but distances varied due to different spatial settings and availability of the species sampled (20–158 m). Given that biological and environmental parameters can influence the assimilation of guano-derived nitrogen in coral reefs (Graham et al., 2018; Rankin & Jones, 2021), the nearshore stations were distributed around four islands to account for potential variability in $\delta^{15}N$ derived from island attributes, such as the size, elevation, and seabird numbers (Table 1). Although variation in seabird density and nutrient inputs—usually related to the impact of rats on seabird demography—have been shown to drive effects in nearshore communities (e.g., Benkwitt et al., 2021; Graham et al., 2018), guano runoff and percolation may also be facilitated in low-elevation and smaller islands due to their lower positioning and higher shoreline to area ratios. Similar soil types and vegetation structure suggest similar conditions on the islands besides those considered in our analysis. At each station, at water depths of 2–8 m, five fragments (~10 cm) of the scleractinian coral *Siderastrea stellata* were collected by free diving using a hammer and chisel. The fragments were stored frozen, and in the laboratory the entire coral tissue (holobiont) was removed from the skeleton using an airpick.

Samples were prepared according to the type of material being analyzed. The soil and coral samples were acid-washed with HCl 10% to remove carbonates that might have contaminated the samples (Graham et al., 2018) and then dried in an oven at 60°C. The leaves were washed with distilled water and then dried. The guano and feces

TABLE 1 Island size and seabird parameters on islands of Abrolhos Archipelago, Brazil.

Island	Area (ha)	Maximum elevation (m)	Nest density (nests m^2)	Seabird biomass (kg ha^{-1})	Nitrogen input per year (kg $year^{-1}$)	Nitrogen input per hectare per year (kg ha^{-1} $year^{-1}$)	Main breeding species (peak no. nests recorded)
Guarita	0.45	13	0.334	1201.60	877.71	1950.47	*Anous stolidus* (1502)
Santa Bárbara	31.31	35	0.003	99.64	1503.62	48.02	*Sula dactylatra* (797); *Sula leucogaster* (30); *Phaethon aethereus* (107); *Anous stolidus* (23)
Redonda	7.11	36	0.013	359.50	1236.32	173.89	*Fregata magnificens* (820); *Sula dactylatra* (20); *Sula leucogaster* (83); *Phaethon aethereus* (34)
Siriba	3.36	16	0.013	453.09	742.84	221.08	*Sula dactylatra* (410); *Sula leucogaster* (5); *Phaethon aethereus* (17)

Note: The number of nests was recorded between 2018 and 2019 by the seabird monitoring program of the Abrolhos Marine National Park in annual censuses (ICMBio, 2020). For details on the calculations of nitrogen inputs, see Appendix S1: Section S1.

of rats and goats were also dried. The lipids from the terrestrial animal samples (grasshoppers, muscle of tarantulas, lizard tail tips, and liver of black rats) were removed using a Soxhlet apparatus in three 6-h cycles with a 2:1 chloroform:methanol solution, assuring all samples were lipid free. The terrestrial animal samples were then freeze-dried, assuming no influence of drying methods on isotopic ratios, as demonstrated for benthic macroinvertebrates (Akamatsu et al., 2016). All samples were ground, homogenized, weighed, and placed in tin capsules for analysis using an isotope ratio mass spectrometer coupled to an elemental analyzer at the Centro Integrado de Análises of the Universidade Federal do Rio Grande (CIA-FURG, Brazil), which also provided %N values used here for the plant and soil samples. Measurements of laboratory standards (glutamic acid, caffeine, and acetazolamide) yielded a measurement precision of 0.1‰ for $\delta^{13}C$ and 0.5‰ for $\delta^{15}N$. Differences between the sample ratios and the international reference standards (Vienna Pee Dee Belemnite limestone for carbon and atmospheric air for nitrogen) were expressed in δ notation as parts per thousand (‰) (Bond & Hobson, 2012):

$$\delta^{13}C \text{ or } \delta^{15}N\,(‰) = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}}\right) - 1$$

where $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$.

Data analysis

The effects of explanatory variables on the $\delta^{15}N$ values of terrestrial ecosystem compartments and corals and on the %N in soils and plants were analyzed with generalized linear models (GLMs) implemented in an R environment (R Core Team, 2021). The models were fit with a Gaussian distribution and identity link, and assumptions for normality and homoscedasticity were checked by standard residual plots. The performances of the selected models and each of the explanatory variables were assessed by computing the percentage of the total deviance explained through ANOVA tables.

For the terrestrial ecosystem, the analysis focused on testing the influence of the variables "area" (control vs. colony sites) and "island" (Santa Bárbara vs. Siriba) and the interaction between area and island on the $\delta^{15}N$ values. Separately for each component of the terrestrial food web (i.e., soil and each organism), a stepwise procedure was used for model selection considering a basal model containing only "area" as the explanatory variable, and a global model that also included "island" and the interaction. We pooled samples collected in 2020 and 2021 for soil, plants, grasshoppers, and lizards for analysis, given that the fieldwork was carried out during the exact same period in successive dry seasons and because the difference in $\delta^{15}N$ between years, preliminarily tested with simple GLMs, was not significant in all cases, except for C3 plants (Appendix S1: Table S1). When the interaction (area: island) was included in selected models, we used a contrast analysis from the emmeans R package to check whether the difference between control and colony sites averaged for islands was significant ($p < 0.05$) (Lenth, 2021). Because tarantulas were only collected in Santa Bárbara, a simple model was built only containing area as an explanatory variable for these organisms. In addition, a simple GLM was also used to compare nitrogen isotope values in the excrement of organisms (i.e., guano from seabirds and feces of invasive rats and goats) against each other, without discrimination between sampling locations, using contrast analysis for pairwise comparisons.

The contribution of marine and terrestrial sources to island consumers (i.e., grasshoppers, lizards, rats, and tarantulas) was estimated using $\delta^{15}N$ and $\delta^{13}C$ values to generate Bayesian mixing models with the simmr package in R (Parnell, 2021). Because we expected that the seabird influence on consumers would differ between the colony and control sites, we ran one model for each area and consumer, with consumer samples combined across the islands. In these models, three sources were considered to distinguish the origin of the assimilated matter: blood of seabirds (i.e., masked and brown boobies collected in Abrolhos, from the database of the Waterbird and Sea Turtles Laboratory–FURG) and leaves of C3 and C4 plants. We assumed that a large contribution from seabirds would reflect a more direct consumption of marine-derived matter, whereas C3 or C4 contributions would represent a higher reliance on terrestrial food web resources, although plants may also have been subsidized by seabirds and therefore be an indirect source of marine-derived matter to consumers. Although there was a similarity between the $\delta^{13}C$ values of the C4 plants and seabirds, C4 plants were retained in the mixing models since they are abundant in the Abrolhos Archipelago, and their removal could imply biologically meaningless seabird-biased results. The source values for each mixing model were corrected for consumer-diet trophic discrimination factors using data available in the literature (Appendix S1: Table S2).

For coral samples, comparisons of $\delta^{15}N$ values were performed between the nearshore stations against the pooled reference sites (controls) to test whether corals were ${}^{15}N$-enriched near islands with breeding seabirds. For this, samples from the two reference stations were pooled and the GLM was set with the reference site defined as the model intercept (Lorrain et al., 2017).

This allowed values from nearshore stations to be directly compared with those of the reference site to test for significant differences. We interpreted our results based on island biological and environmental parameters, considering island size (in hectares), elevation (meters), and seabird nitrogen inputs per hectare per year (kg ha^{-1} $year^{-1}$) (Table 1). The seabird nitrogen input on each island was estimated using previously established methods (Graham et al., 2018; Smith & Johnson, 1995; Young et al., 2010). For this, the best available species- and island-specific seabird count data were used (for details see Appendix S1: Section S1), in addition to describing island nest density and seabird biomass.

RESULTS

Stable isotopic nitrogen along the terrestrial food web

Contrary to our predictions, for all terrestrial food web compartments, the estimated mean $\delta^{15}N$ value within seabird colonies was lower than that in control sites, as shown in the GLM analysis (Figure 2; Appendix S1: Tables S3–S5). In general, differences in $\delta^{15}N$ between colonies and control sites seem to be larger for the most mobile vertebrate consumers (i.e., lizards and rats) than for arthropods and sessile ecosystem components. Indeed, the selected models had a strong explanatory performance for rats (58% deviance explained) and lizards (70%) and an intermediate explanatory performance for soils (35%) and C3 plants (32%), but they performed poorly (<10% explained) for C4 plants, grasshoppers, and tarantulas (Appendix S1: Table S3). Area was the strongest predictor for soils, lizards, and rats, whereas the island was the strongest predictor for C3 plants (Appendix S1: Table S3), and these models also included interactions, which indicated that the relationship between the colony and control sites differed among the islands (Figure 2; Appendix S1: Table S4). For instance, rats presented contrasting $\delta^{15}N$ values between areas in Siriba, but this difference was smaller in Santa Bárbara (Figure 2; Appendix S1: Table S6). Nonetheless, contrast analysis indicated that the averaged difference between areas was significant for soils, lizards, rats, and C3 plants (Appendix S1: Table S6). Differences between areas were not significant for C4 plants, grasshoppers, and tarantulas (Appendix S1: Table S4). Finally, values for the guano and feces from goats and rats were significantly different from each other, with guano having lower $\delta^{15}N$ values (9.5 ± 0.3‰), goat feces having higher $\delta^{15}N$ values (19.5 ± 1‰), and rat feces having intermediate $\delta^{15}N$ values (15 ± 3.2‰; Appendix S1: Tables S4 and S6).

In relation to the %N, the models explained 20.3%–70.1% of the deviance, with a substantially larger nitrogen content in colony areas, as expected, especially

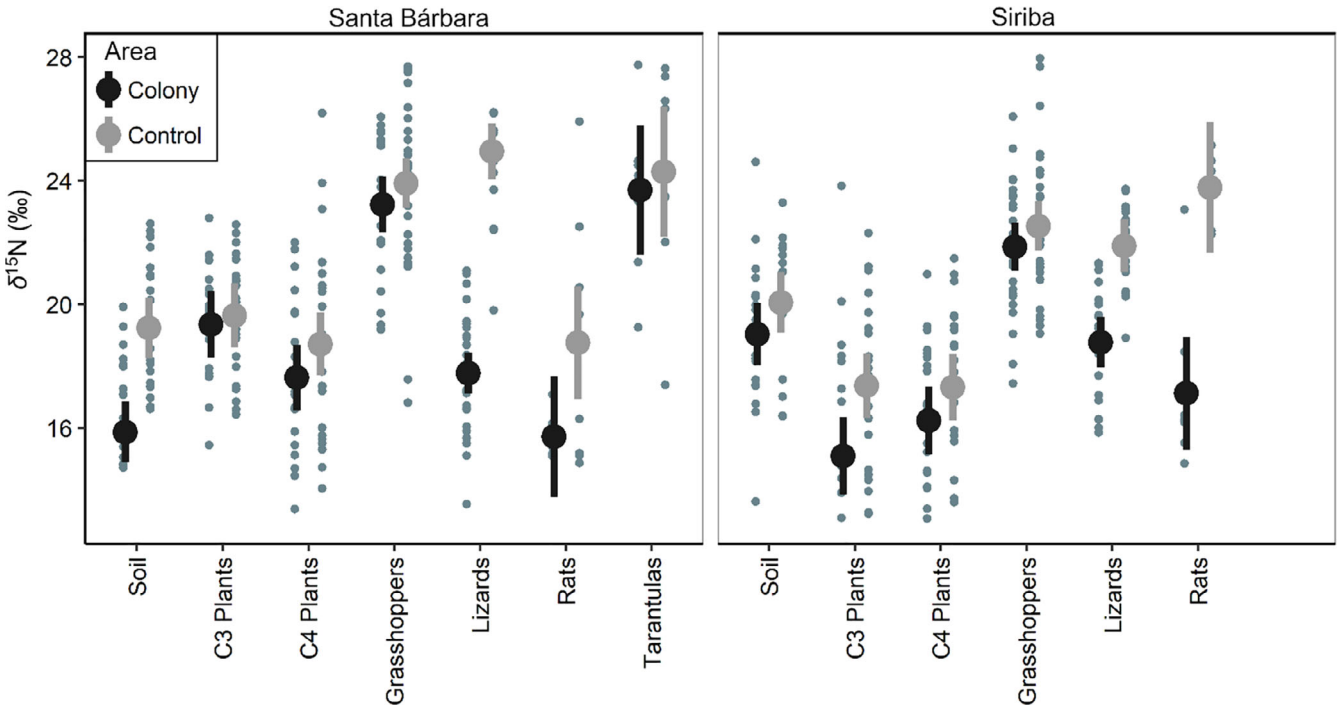

FIGURE 2 Generalized linear model predictions of $\delta^{15}N$ values across terrestrial food web in areas within and outside seabird colonies on two islands of Abrolhos Archipelago, Brazil. Black and grey points with error bars represent estimated means and 95% confidence intervals, while raw data points are presented in blue. A few outliers are omitted due to figure dimensions.

for C3 and C4 plants, but it also significantly differed for soils (Figure 3; Appendix S1: Tables S3, S4, and S6). Models of %N in plants included interactions, apparently because the differences in %N were more prominent in Siriba than Santa Bárbara, although it was statistically significant on both islands (Appendix S1: Table S6).

Contribution of marine matter to terrestrial consumers

All sample types from all areas in the terrestrial food web were ^{15}N-enriched in relation to values from seabirds and their guano, generally by more than 5‰ (Figure 4). Variations in the δ^{15}N values in consumer tissues among different areas were more prominent for lizards and rats, with lower values in the colony sites, similar to those of the C3 and C4 plants, and positioned in the isospace close to seabirds, whereas much higher values were measured in the control sites, although less prominently for the rats on Santa Bárbara Island (Figures 2 and 4). In relation to carbon sources, C3 plants were clearly ^{13}C-depleted, with the lowest δ^{13}C values (−27.3 ± 1.4‰), whereas C4 plants had the highest values (−12.9 ± 0.6‰), and seabirds had intermediate values (−16.6 ± 0.3‰). Soils and consumers, in general, had δ^{13}C values skewed toward those of seabirds and C4 plants (Figure 4).

The mixing models indicated different patterns in the assimilation of marine-derived nutrients by consumers in the Abrolhos Archipelago (Figure 5). Clear differences between the colony and control sites were evidenced for lizards and rats, with higher marine contributions within seabird colonies. Lizards had marine matter contributions of 2.3%–5.5% (50% credible interval) outside the colonies, which increased to 51.1%–57.0% inside the colonies (Figure 5c), whereas rats assimilated 7.1%–19.8% of marine matter in control sites, with an increase to 30.2%–42.0% in the seabird colonies (Figure 5b). For the other taxa, models for grasshoppers showed that, overall, they relied heavily on C4 plants, with minor contributions from C3 plants and seabirds (Figure 5a). Models for tarantulas showed a moderate contribution from seabird-derived matter (Figure 5d), with no marked differences among areas.

Assimilation of seabird-derived nitrogen by corals

The patterns for the assimilation of seabird-derived nutrients varied drastically among the nearshore sampling stations. The reference sites had a δ^{15}N value of 3.0 ± 0.7‰, and only stations around Guarita and Siriba showed clearly higher δ^{15}N values than the reference, with values

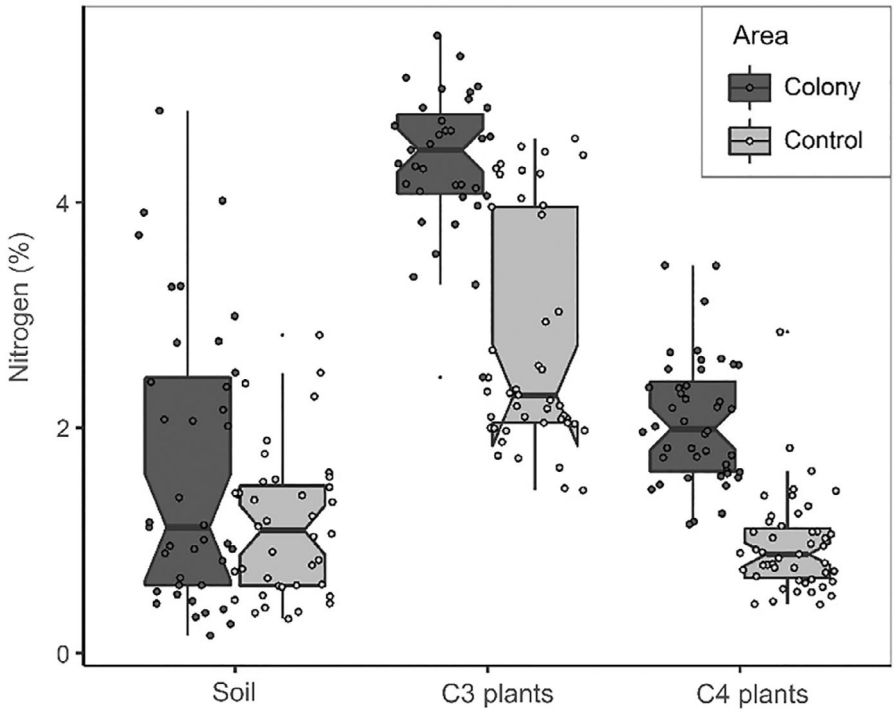

FIGURE 3 Nitrogen content (%N) in soils and in C3 and C4 plants collected inside and outside the seabird colonies on two islands in the Abrolhos Archipelago, Brazil. In the notched boxplots, the central line is the median, the box limits depict the interquartile range, the whiskers represent the 95% quantiles, and the notches (depression in the center of the box) approximately illustrate the 95% confidence intervals around the median.

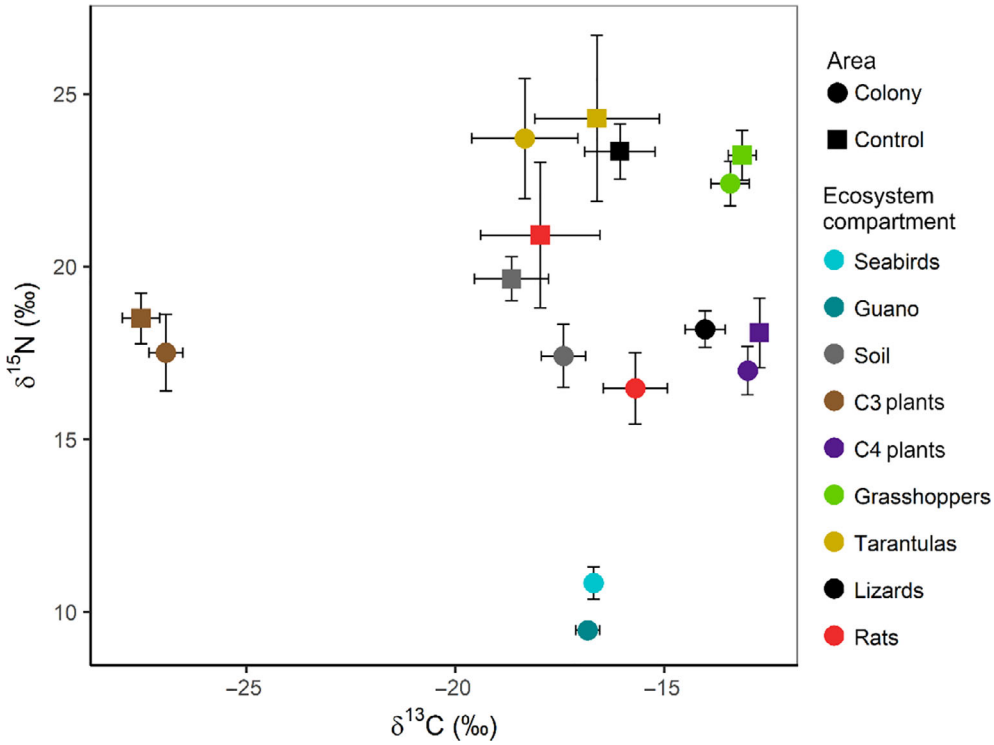

FIGURE 4 Isospace showing $\delta^{15}N$ and $\delta^{13}C$ values of seabirds, guano, and multiple components of terrestrial food web of islands in Abrolhos Archipelago, Brazil. Symbols and error bars represent the means and 95% confidence intervals, respectively. The results are provided separately for samples obtained within and outside (i.e., control) the seabird colonies.

of 6.6 ± 0.6‰ and 6.5 ± 0.9‰, respectively (Figure 6; Appendix S1: Tables S4 and S5). Guarita and Siriba were the two islands with smaller sizes and lower elevations, as well as with higher seabird biomass per hectare and higher concentration of guano inputs (Table 1). The stations around the Santa Bárbara and Redonda Islands presented $\delta^{15}N$ values of ~3‰, similar to the reference sites (Figure 6).

DISCUSSION

Through a multitrophic and ecosystem approach, we revealed the incorporation of marine subsidies mediated by seabirds on tropical islands and coral reefs in the Abrolhos Archipelago, Brazil. Main findings suggested that seabird-derived nutrients are assimilated either directly or indirectly by all trophic levels across the entire area of small islands, both inside and outside seabird colonies, and by coral reefs only adjacent to small islands with low elevation and high nitrogen input from seabirds. Native and invasive vertebrate consumers exhibited marked spatial differences in the way they use seabird-derived nutrients, relying on it directly inside seabird colonies, and indirectly when outside colonies, in areas where seabirds do not breed currently. These findings contribute to the elucidation of the ecological roles of seabirds in supporting island and coral-reef food webs even in rat-invaded archipelagos, and show that subsidies may affect all trophic levels over entire areas of small tropical islands.

Effects of seabirds on the terrestrial food web

All trophic levels in the terrestrial food web had $\delta^{15}N$ values ~5–15‰ higher than values in seabird guano and blood, both within and outside their colonies, likely indicating the isotopic influence of seabird-derived nutrients, elevating the baseline $\delta^{15}N$ over the entire island ecosystem. We assume that $\delta^{15}N$ values of this magnitude on all areas and organisms, higher than those in seabird tissues, may only be caused by seabird presence and the direct and indirect assimilation of their nutrients, because seabirds are ^{15}N-enriched in relation to terrestrial environments, as they are top predators in the marine ecosystem. This finding is consistent with a large body of evidence showing that food webs on islands with breeding seabirds are substantially ^{15}N-enriched in relation to islands without their influence (Anderson & Polis, 1999; Richardson et al., 2019; Stapp et al., 1999),

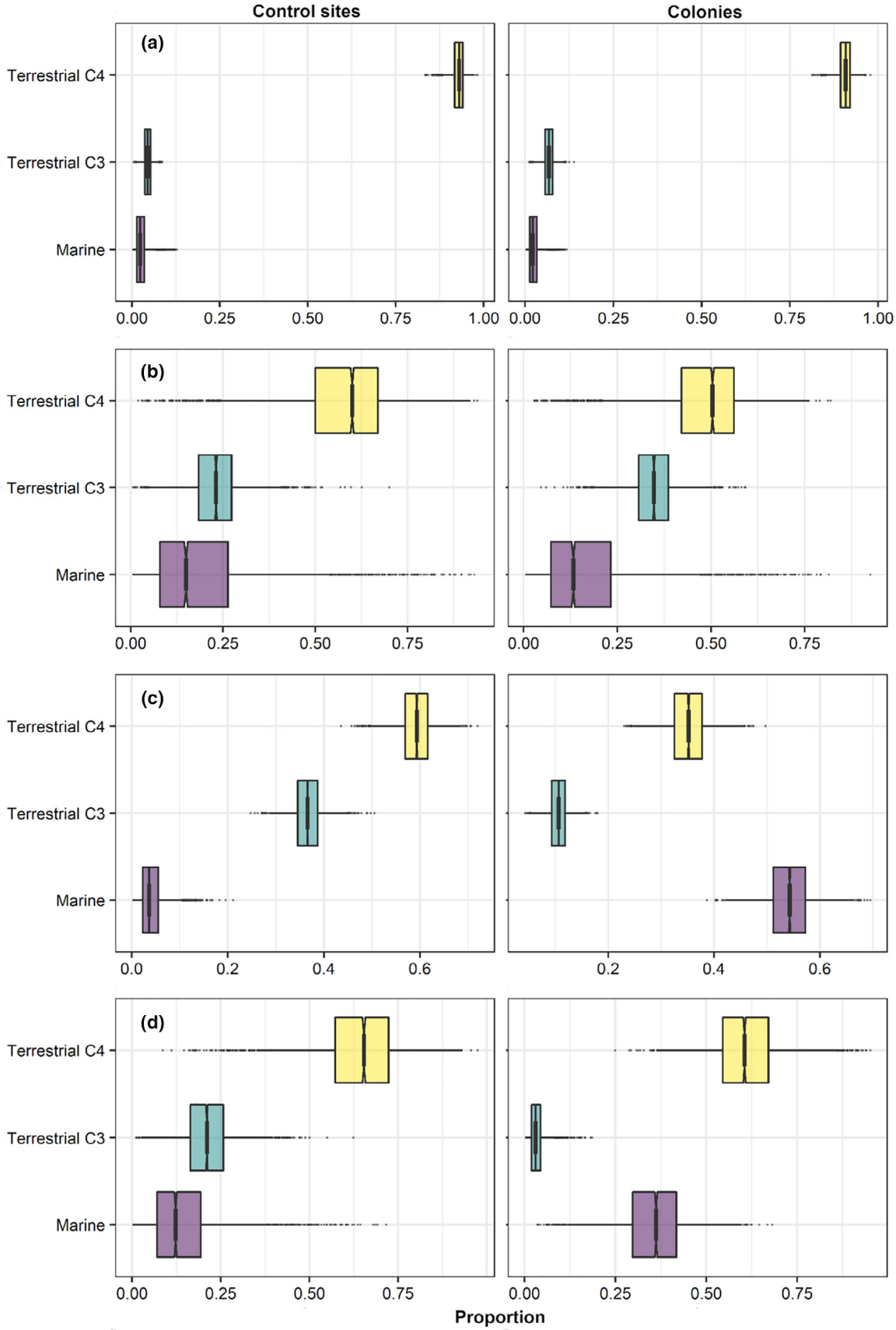

FIGURE 5 Output of Bayesian stable isotope mixing models, showing estimated contributions of terrestrial (C3 and C4 plants, green and yellow symbols, respectively) and marine (seabird blood, purple symbol) sources to the diet of consumers collected inside and outside seabird colonies in the Abrolhos Archipelago, Brazil. The graphics show the estimated mean, the symbols show the 50% credible intervals, and the lines show the 95% credible intervals. (a) Grasshoppers; (b) tarantulas; (c) lizards; (d) black rats.

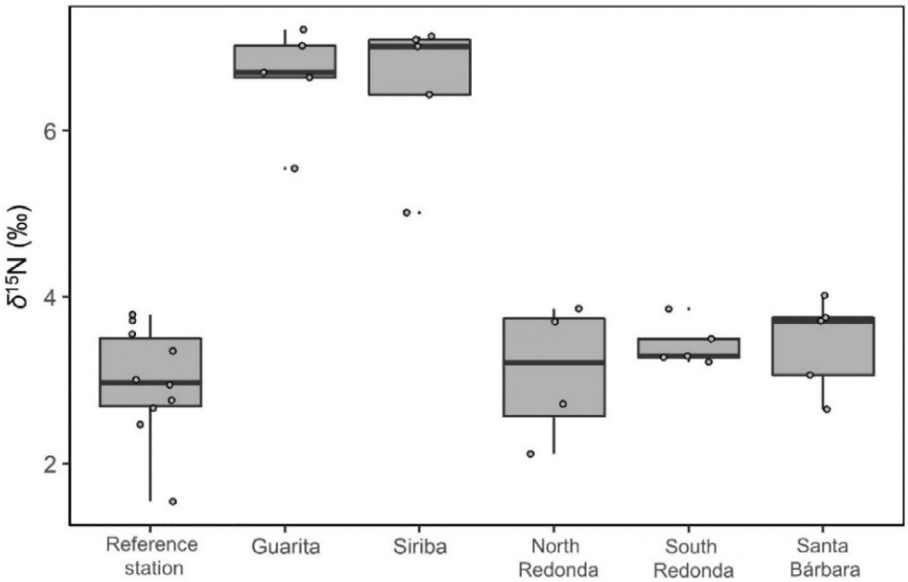

FIGURE 6 Variation in $\delta^{15}N$ values in tissues of scleractinian coral *Siderastrea stellata* collected near four islands with breeding seabirds in Abrolhos Archipelago and in reference stations (two sites pooled) ~1700 m from nearest island. The islands appear from smallest to largest in size (Table 1). The boxplots depict the median and 25% and 75% percentiles. Only the results from the Guarita and Siriba Islands were significantly distinct from the reference station.

although Abrolhos lacked islands without breeding seabirds for comparison. Within the space of each island, however, such differences between areas would be expected to occur between colony sites and nearby colony-free areas (e.g., see Caut et al., 2012; González-Bergonzoni et al., 2017; Pascoe et al., 2021), but we observed the opposite spatial trend in Abrolhos. Higher $\delta^{15}N$ values were consistently detected in control sites for all trophic levels, suggesting that the direct influence of seabirds inside the colony may have, in fact, caused a local depletion in ^{15}N, as we discuss below. This finding suggests a more complex spatial pattern of the seabird isotopic influence on small islands than generally assumed, and could induce the misleading interpretation that seabirds had a larger ecological influence in areas outside their colonies, since high $\delta^{15}N$ is a signal of guano incorporated into the ecosystem (Barrett et al., 2005; Ellis et al., 2006; González-Bergonzoni et al., 2017; Szpak et al., 2012).

However, in our study system, a more plausible explanation could be related to the intense nitrogen fractionation process occurring after guano is deposited in soils due to the microbial decomposition process that converts uric acid into ammonia (Mizutani et al., 1985). The isotopically lighter ^{14}N in ammonia is volatilized, resulting in the much higher $\delta^{15}N$ values we detected in the soils (18.5 ± 2.7‰) than in guano (9.5 ± 0.3‰; Mizutani & Wada, 1988), thereby inducing high $\delta^{15}N$ along the entire terrestrial trophic chain that feeds on autochthonous terrestrial resources (Briggs et al., 2012; Caut et al., 2012; Stapp et al., 1999). Sampling soils within the seabird colony resulted in soil samples mixed with dry guano that had apparently not yet been mineralized, which therefore could explain the lower $\delta^{15}N$ in soils observed in colony sites, especially on Santa Bárbara Island. This must have had a larger impact on our results because none of the control areas were truly free of seabird influence, whereas it seems that, in some other studies (e.g., Caut et al., 2012; Gaiotto et al., 2022), sampling conditions allowed a clearer distinction of areas with and without seabird influence.

Similarly, the lower $\delta^{15}N$ values in C3 and C4 plants in the colonies suggests uptake of guano-derived nitrogen in leaf tissues before complete fractionation, despite spatial differences were subtle and model performance for C4 plants was low. Corroborating this explanation, the higher %N in plants within the colony areas indicates that the influence of guano is, indeed, higher where seabirds are breeding (Anderson & Polis, 1998; Fukami et al., 2006; Richardson et al., 2019; Szpak et al., 2012; Young et al., 2010). The enhanced nutritional content in plants may have important ecological consequences on islands because it provides higher-quality resources for consumers, potentially leading to increased consumer abundance (Sánchez-Piñero & Polis, 2000) and, in the long term, was even attributed to driving evolutionary shifts, such as gigantism in iguanas at a seabird island in the Bahamas (Richardson et al., 2019). Although these

results may be somewhat conflicting at first glance, they suggest that a larger seabird influence within the colony may not always result in higher $\delta^{15}N$ in comparison with adjacent areas. In fact, the opposite may be true, especially on small islands where the seabird isotopic influence is blurred across the system. In these cases, stable isotope analysis should be interpreted cautiously or complemented by other methods, such as quantifying the nitrogen content in soils and plants. Nonetheless, we observed this pattern in a semiarid environment during the dry season when biological activity in the soils, and thus guano fractionation, is severely reduced due to high temperatures and lack of water (Hadas & Rosenberg, 1992; Loder-III et al., 1996); thus, it is possible that seasonal differences in isotopic patterns occur due to changes in climatic conditions.

Nonetheless, for consumers, the differences in $\delta^{15}N$ values between the colony and control areas were more substantial for lizards and rats, but they were small for grasshoppers and tarantulas. The marked differences for these vertebrate consumers in relation to other ecosystem components suggests that ecological preferences are more important than the mobile capacity to drive spatial variations in the incorporation of cross-ecosystem subsides. Furthermore, the high values found for rats and lizards in the control areas and over all areas for grasshoppers and tarantulas suggest consumption of ^{15}N-enriched terrestrial resources, probably benefiting from bottom-up seabird nutrients entering the food web through soil and plants (Sánchez-Piñero & Polis, 2000). However, in the colony areas, the rats and lizards were substantially ^{15}N-depleted, with $\delta^{15}N$ values similar to those of soils and plants or even lower, suggesting terrestrial sources were of limited importance. Thus, given the lower $\delta^{15}N$ in seabird tissues and the enrichment of isotopic nitrogen across the trophic levels (generally 3‰–5‰; Fry, 2006; Schoeninger et al., 1983), this finding suggests a more direct consumption of marine-derived matter by these animals within the colonies (Stapp, 2002). A similar pattern was previously reported by Stapp et al. (1999) for rodents in the Gulf of California, where *Peromyscus maniculatus* consuming ^{15}N-enriched plants during the wet season had much higher $\delta^{15}N$ values than during the dry season, when the species shifted its diet to marine intertidal invertebrates.

Indeed, the mixing models estimated a shift in the foraging ecology of lizards and rats between sampling areas, with a higher contribution of marine-derived matter detected inside seabird colonies. This finding highlights the foraging plasticity of these animals that explore different resources across island habitats and suggests a top-down seabird influence that benefits consumers within the colonies more directly (Gaiotto et al., 2020; Ruffino et al., 2011; Sánchez-Piñero & Polis, 2000). It also indicates spatial segregation in the feeding habits of these animals, exploring site-specific resources even among adjacent areas, as previously demonstrated for rats elsewhere (Hobson et al., 1999; Russell & Ruffino, 2012). For invasive rats inside colonies, this finding may suggest predation on seabirds, especially on seabird eggs and chicks, which could result in reduced breeding success, thereby becoming a threat to seabird populations in Abrolhos (Sarmento et al., 2014). Although predation was not directly evidenced by our methods, it had been verified previously in Abrolhos (B. A. Linhares and L. Bugoni, personal observation). During the dry season, when other terrestrial resources are scarce, seabirds may constitute a high proportion of the rats' diet in the archipelago because seabirds provide a large and predictable pulse of resources on the islands (Caut et al., 2008; Yang et al., 2008).

Nonetheless, given that lizards are unable to consume seabirds through predation, the high marine contribution for these consumers suggests other food sources not sampled in this study, such as seabird prey, egg remains, seabird ectoparasites, or scavenging arthropods relying on seabird carrion (Barrett et al., 2005), which are commonly abundant in seabird colonies (Polis & Hurd, 1996). Indeed, Gaiotto et al. (2020) found a high number of seabird ticks in the stomachs of black rats in the Fernando de Noronha Archipelago, Brazil. Similarly, a study on the diet of three lizard species in Abrolhos found that ~38% of the diet of *Mabuya agilis* was numerically composed of mites, which could be seabird parasites (Rocha et al., 2002), although this food source was not detected for *T. torquatus* sampled in the current study. Seabird-derived resources are potentially important for *T. torquatus* in Abrolhos because it is highly abundant on the rocks within seabird colonies (B. A. Linhares and L. Bugoni, personal observation), where other resources are apparently scarce. This is in line with findings for other lizard populations in insular areas (Barrett et al., 2005; Markwell & Daugherty, 2002).

In contrast, grasshoppers and tarantulas had limited variations in their marine matter consumption between the colony and control sites. Indeed, GLMs had a poor explanatory performance for these animals, showing that $\delta^{15}N$ differences were not clear between colony and control areas or islands. The mixing models confirmed that the diet of grasshoppers was composed mainly of C4 plants (*Cyperus* sp.) because they had similar $\delta^{13}C$, and the high $\delta^{15}N$ detected suggested that the trophic enrichment in relation to C4 plants should be at least 4‰. As grasshoppers are herbivores, the direct consumption of marine-derived matter is impossible; therefore, they rely exclusively on bottom-up subsidies, and the models responded accordingly. Notwithstanding, tarantulas showed a marginal, but detectable, contribution from marine matter in their diet, regardless of whether they were sampled within or outside

the seabird colony. Although tarantulas might be able to consume seabird carrion or eggs and prey remains occasionally, they likely do not depend on these resources because they seemed to occur mainly in the control area at Santa Bárbara, associated with patches of tall vegetation, and were only collected near the border of the seabird colony (B. A. Linhares and L. Bugoni, personal observations). Nonetheless, a larger sample size for tarantulas associated with other complementary methods (e.g., visual observations) would be desirable to better understand their use of marine-derived matter in Abrolhos.

The finding that sessile ecosystem compartments, such as soils and plants, in the control sites were substantially ^{15}N-enriched may have been influenced by a combination of factors. First, given that seabirds were subjected to several historical threats in Abrolhos (e.g., hunting, tourism, invasive rats, cats, and goats; Darwin, 1988; IBAMA, 1991; Mancini et al., 2016), it is likely that the control sites were occupied by seabird colonies in the past and that their ornithogenic soils are still present, as demonstrated by a previous study in the archipelago (Schaefer et al., 2010). Second, the distance between the sampled sites may not have been sufficient to find an ideal seabird-free area, especially on Siriba, where the control area is surrounded by breeding seabirds. However, previous studies suggested a spatially restricted seabird influence (Caut et al., 2012), whereas the control area on Santa Bárbara was clearly separated from the colony location, precluding the drainage of guano due to similar elevations. However, distances seemed to have a negligible effect on the results. Finally, island consumers, especially the goats and invasive rats, may act as vectors of marine-derived matter across habitats of the islands (Mellbrand et al., 2011; Paetzold et al., 2008) because they are large, numerous, and highly mobile organisms. Isotope analysis demonstrated that the excrement of these exotic species had higher δ^{15}N values than guano, which related to their feeding habits (i.e., consuming seabirds or ^{15}N-enriched terrestrial resources). If the goats and rats feed on seabird-affected resources in the colony sites, they can transport marine matter through their feces, potentially contributing to the high δ^{15}N values observed at the control sites. Rats, for instance, may feed on colonies at night, but build burrows in the highly vegetated control areas where they rest during the day, which could result in an intense daily movement of marine-derived matter toward control sites, whereas goats could dissipate large amounts of nutrients from colony plants throughout Santa Bárbara Island. This scenario might suggest that eradicating invasive species, such as rats and goats, could induce more spatially restricted seabird subsidies on islands, despite the well-known importance of such management to restore seabird ecological roles.

Effects on nearshore corals

By simultaneously sampling scleractinian corals close to four islands with varying environmental and biological characteristics in Abrolhos, we were able to demonstrate a pattern of seabird influence in the nearshore environment. We found that seabird-derived nitrogen reached coral reefs only around the two smaller, low-elevation islands, which had, in turn, higher seabird biomass and guano inputs. This finding suggests that island morphology might influence guano effects on nearshore environments by facilitating guano runoff and percolation toward adjacent waters around islands with lower elevations and smaller areas. In Guarita, brown noddies breed in high densities and roost in rocks by the water, so the island receives at least an eightfold higher concentration of nitrogen input from seabirds, with guano-derived nitrogen made quickly available to the coral reefs nearby. In contrast, Santa Bárbara and Redonda are larger islands with some surrounding sandy beaches, and most of the breeding seabirds are 30–36 m above sea level; thus, their guano inputs should be much larger than those at Guarita and Siriba in order to affect coral reefs. However, the concentration of seabirds and their inputs is usually lower on larger islands, since colonies occupy a larger proportion of smaller islands which tend to be perceived as safer for nesting (Polis & Hurd, 1996).

Nonetheless, a variety of environmental parameters could influence the assimilation of seabird-derived nitrogen by corals in the Abrolhos Archipelago. Rankin and Jones (2021) showed that the sampling season, depth, surface runoff, and wave actions were important predictors of δ^{15}N values in macroalgae near seabird colonies. They detected that macroalgae had substantially higher δ^{15}N during the wet season, given that rain is the main carrier of guano nutrients into adjacent waters. Our time-limited sampling during the peak of the dry season is a potential cause of the contrasting pattern observed in the results, as seabird nitrogen was virtually undetected around Santa Barbara and Redonda. During the dry season, guano nutrients are mainly retained on land, especially on larger, high-elevation islands in this arid archipelago. It is possible that during the wet season, the influence of seabirds on corals would reach the areas around the higher and larger islands, which deserves further investigation. In addition to the temporal aspects, a larger spatial coverage would be desirable to confirm whether the patterns observed in Abrolhos can be generalized across other islands and archipelagos.

Moreover, recent studies showed that seabird effects in nearshore communities were influenced by rat invasion history, with fewer nutrients reaching adjacent coral reefs around rat-invaded islands. Rats are known for their

devastating impact on seabirds globally, inducing population declines and consequently reducing the input of marine matter into the system (Benkwitt et al., 2021; Fukami et al., 2006; Graham et al., 2018). Overall, we showed that in Abrolhos, corals around some rat-invaded islands were still affected by seabirds, depending on the environmental context. Nonetheless, although our results were not designed to demonstrate the impacts of rats on seabird demography or on their ecological roles on islands, rats exhibited a high direct consumption of seabird-derived matter in Abrolhos, suggesting some level of interference on subsidies that would otherwise be incorporated into the island food web and adjacent coral reefs. Based on previous studies, this supports the necessity of managing invasive rats to protect seabirds and their cross-ecosystem subsidies. Worldwide, rat eradication is the most effective management strategy on islands to restore seabird populations and their effects on land and water (Benkwitt et al., 2021; Jones et al., 2016). Since the Abrolhos region protects one of the largest and most diverse coral reefs in the South Atlantic (Leão & Kikuchi, 2001) and it is under strong external pressures, such as contamination from mining (Nunes et al., 2022) and predatory fishing (Giglio et al., 2020; Previero & Gasalla, 2020), management actions within the archipelago to eradicate rats and goats can be important to guarantee the protection of seabirds and their ecosystem-wide ecological effects.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Linhares, 2022) are archived in IsoBank under Dataset ID 482.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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