



# Biogeographic variation on dietary aspects of a widely distributed seabird

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## Abstract

The diet of widely distributed species is influenced by the availability of food resources, which can vary according to local conditions. Thus, heterogeneity in diet patterns can help understand population structure and illustrate biogeographic boundaries. In this study, published and unpublished datasets of regurgitated material and stable isotopes of carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) from whole blood of brown boobies (*Sula leucogaster*) in the southwestern Atlantic Ocean (27°51'S to 0°55'N) were used to assess dietary spatial patterns. The variations in prey composition and isotopic niche breadth were associated with colony location (coastal/oceanic), genetic population structure, and marine biogeographic zonings—Large Marine Ecosystems, Longhurst's Biogeochemical Provinces, and Spalding's Provinces and Ecoregions. Boobies from coastal and southern colonies showed higher diversity in their diet compared with boobies from oceanic and northern colonies, given the presence of demersal taxa associated with bottom trawling discards. The variation in prey composition from regurgitates and stable isotopes was well framed with genetic structure and biogeographic boundaries, although less fitting with Spalding's zoning. The brown booby showed trophic plasticity throughout the study area, suggesting that their diet is shaped by food resources available around the colonies, including those from fishery discards. These results demonstrate that highly mobile vertebrates are potentially useful samplers of the marine environment, able to indicate the diversity of prey organisms available in the foraging area through diet, and support biogeographic zonings. Furthermore, diet composition associated with population structure sheds light on local adaptation as a potential mechanism for promoting/disrupting gene flow in seabirds.

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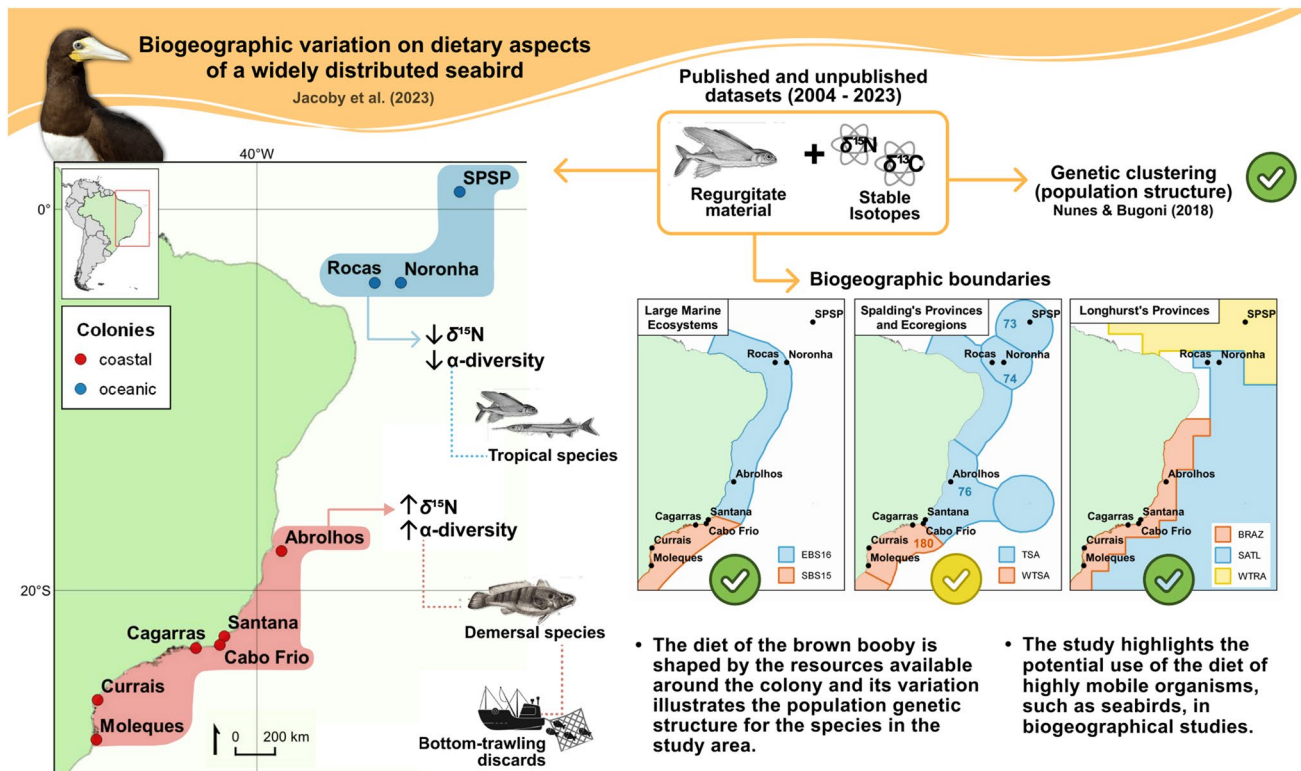
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## Graphical abstract



**Keywords** Brown booby · Local adaptation · Marine biogeography · Seabirds · Stable isotopes · Trophic plasticity

## Introduction

Trophic relationships of widely distributed species may not be homogeneous along their home range, as local conditions influence the availability of food resources (Garvey and Whiles 2017). This can allow the identification of dietary variations between groups, which can be used as tools to understand local adaptation (Sanford et al. 2003; Barnagaud et al. 2019). In addition, understanding prey composition could potentially illustrate and refine biogeographic boundaries at regional (Lozano et al. 2006; Piatt et al. 2018) or global scales (Duffy et al. 2017; Romano et al. 2020).

Trophic plasticity, i.e. the capacity of an organism to adapt its diet according to the variability of food resources available in time and space (Larkin 1956; Gerking 1994), is an advantageous strategy for organisms inhabiting places subject to seasonal fluctuations in environmental conditions (Gerking 1994; Abelha et al. 2001). For instance, seabirds are able to adjust their foraging behavior according to oceanic features, whether static (depth, slope) or ephemeral (chlorophyll, sea surface temperature, sea-ice distribution) (Widmann et al. 2015; Gilmour et al. 2018). Such plasticity can also be advantageous for organisms that depend on

resources with unequal and ephemeral distributions in space (Harding et al. 2007), especially for species with high mobility and wide geographic distribution such as sharks (Drymon et al. 2012), marine mammals (Spitz et al. 2006), and migratory birds (Parrish 2000; Bugoni and Vooren 2004). In the long term, intraspecific variation in diet could lead to local adaptation and even influence genetic structure (Pilot et al. 2012).

Diet heterogeneity can contribute to local adaptation, intensifying processes that lead to gene flow disruption. Isolation by Environment/Ecology (IBE) is a pattern in which population differentiation is increased according to environmental differences (Wang and Bradburd 2014), and is the most common model to explain population structure in animals (Sexton et al. 2014), including seabirds such as prions and petrels (Quillfeldt et al. 2015), and brown boobies *Sula leucogaster* (Nunes and Bugoni 2018). According to IBE, gene flow is higher between environmentally similar sites, while in distinct environments, local adaptation intensifies selection against immigrants, leading to isolation (Richardson et al. 2014; Sexton et al. 2014) and consequently genetic differentiation between subpopulations (i.e. population structure) (Hartl and Clark 1997). In this context,

variability in the diet of a widely distributed species may act as a complementary cause to population structure because variations in food availability and composition can contribute to the development of intraspecific genetic (Sanford et al. 2003), morphological (Grant and Grant 2002), physiological (Fohringer et al. 2021), and behavioral variations (Moseley et al. 2012).

Information on the distribution of organisms has been historically used to establish biogeographic zonings in the oceans (Forbes 1859; Briggs 1974) or to refine and illustrate patterns previously established (Floeter et al. 2007; Menni et al. 2010; Pereira et al. 2014). Alternatively, additional proposals used environmental parameters such as ocean currents, bathymetry, and primary productivity as input for marine zonings (Sherman 1994; Longhurst et al. 1995). Fish is the most common vertebrate group used to identify biogeographic boundaries in the marine realm, from sedentary species associated with coral reefs (Pinheiro et al. 2018) to highly mobile species such as tunas and swordfishes (Reygondeau et al. 2012). However, an inherent challenge in using these groups as indicators of marine life distribution is associated with the need to sample large areas in the ocean, whose sampling is hampered by logistical and methodological constraints (Robinette et al. 2007; Duffy et al. 2017; Piatt et al. 2018). Thus, assessing the prey composition of widely distributed marine organisms, such as seabirds, sampled along their distribution, can provide relevant information to refine biogeographic patterns without the biases of fish sampling methods applied to different locations.

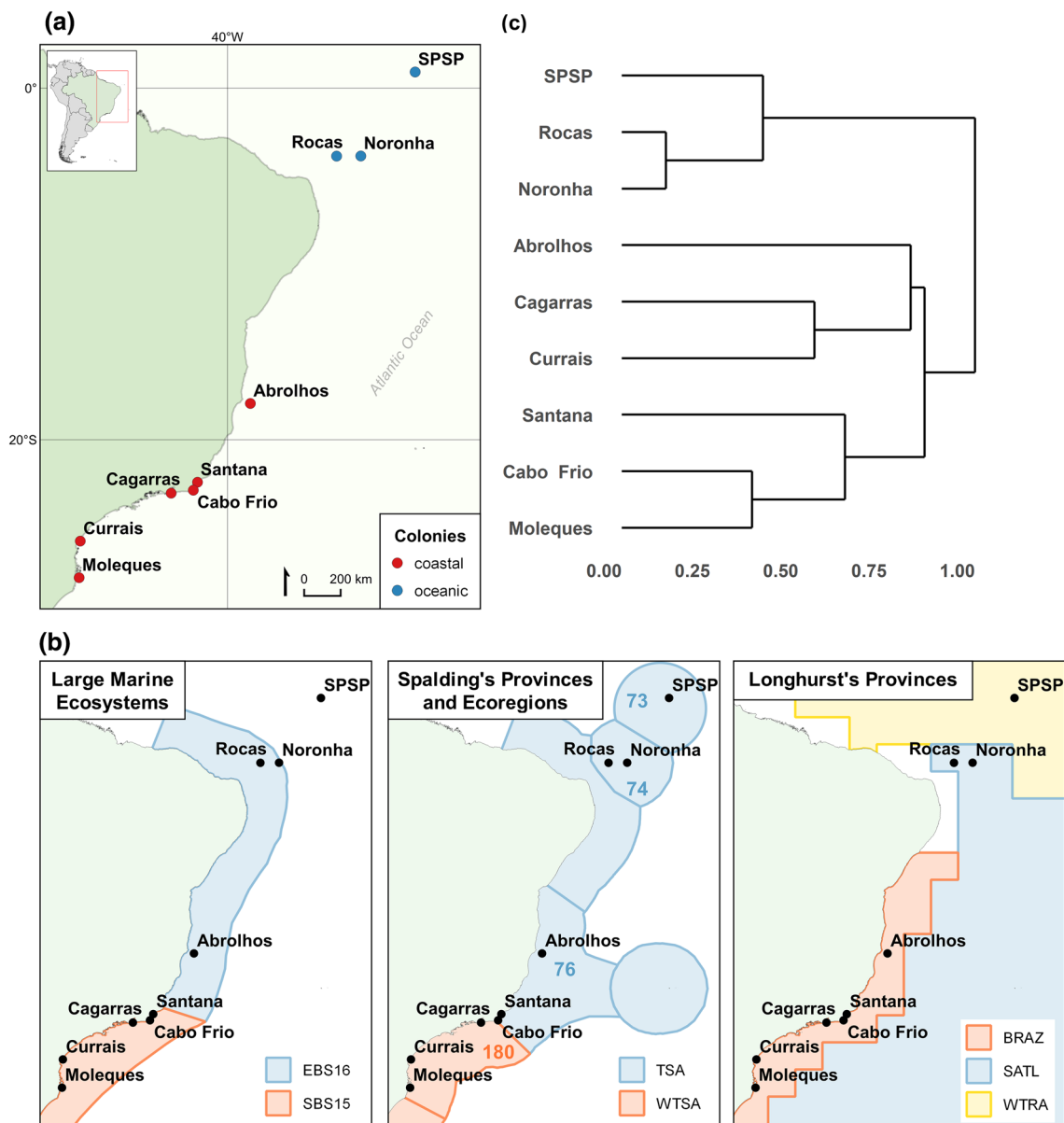
Seabirds depend on the marine environment for at least part of their lives (Votier and Sherley 2017) and present consistent philopatry (i.e. tendency to return to the natal site to breed), despite their high mobility (Schreiber and Burger 2002; Friesen 2015). Due to the adaptation and specialization to conditions around colonies, seabirds can present population differentiation even between nearby colonies (Nunes and Bugoni 2018; Danckwerts et al. 2021). Therefore, the use of food resources available around breeding areas makes local adaptation a potential mechanism of population differentiation in the group (Friesen et al. 2007; Friesen 2015), although historical aspects may also influence population structure (Lombal et al. 2020). Additionally, such processes make seabirds indicators of spatial and temporal variability of food resources, so that dietary information and its variations among colonies can contribute to understanding the distribution patterns of prey species (Montevecchi and Myers 1996; Piatt et al. 2018).

The brown booby is a strictly marine bird widely distributed in all ocean basins in tropical and subtropical regions (Nelson 1978). This is a piscivorous species that feed on prey around colonies (i.e. central-place foragers) in an opportunistic way (Castillo-Guerrero et al. 2016; Nunes et al. 2018) in addition to consuming discards from

fisheries (Schreiber and Norton 2020). Brown boobies hold a marked phylogeographic structure, so basal populations inhabit the northwest Pacific Ocean, from where dispersal historically occurred towards the Indian and Atlantic Oceans (Morris-Pocock et al. 2011). In the southwestern Atlantic Ocean, brown booby colonies are distributed under a heterogeneous seascape (Nunes et al. 2017) and colony landscapes (Nunes et al. 2018) which are suggested to influence population structure. Low-latitude colonies are located around the Equator in oceanic zones, while the southern breeding areas are on the continental shelf and close to the mainland, ranging from 27°50'S to 0°55'N, comprising 28° of latitude.

Differences in prey availability around brown booby colonies may expose them to distinct selective pressures associated with the use of food resources, which may represent a potential explanation or consequence for the population structure observed in the southwest Atlantic Ocean. In this region, colonies located on the continental shelf share similar environmental conditions, and individuals exhibit gene flow between them, while oceanic colonies maintain higher gene flow between each other (Nunes and Bugoni 2018). However, the colony located in São Pedro e São Paulo (hereafter 'SPSP'), a remote small oceanic archipelago, is genetically isolated from the remaining colonies, which has been associated with local adaptation promoted by intense intraspecific competition for nesting areas (Nunes et al. 2018). Considering that prey distribution may be associated with oceanographic variables such as chlorophyll- $\alpha$  and sea surface temperature, the spatial diet patterns associated with population structure can contribute to demonstrating that IBE is an important mechanism in seabird populations. Additionally, patterns of variation in the diet between breeding sites of the species may represent useful information for the refinement of biogeographic boundaries in the marine realm since it is a proxy of important biotic and environmental variables in the seascape. In this context, the use of complementary techniques to assess the diet of an organism provides accurate information on variations in the use of food resources in space and time (Garvey and Whiles 2017).

The acquisition of dietary information from seabirds is facilitated because they spontaneously regurgitate the ingested food in stressful situations (Mallet-Rodrigues 2010). From this, prey can be identified at the species level, even if partially digested. Nevertheless, this method is limited because of the short time window represented (i.e. last meal) (Schreiber and Burger 2002). Thus, the use of stable isotopes is complementary to the analysis of regurgitated material as they can act as natural markers of trophic position (i.e.  $\delta^{15}\text{N}$ ) and feeding environment (i.e.  $\delta^{13}\text{C}$ ) (Fry 2006), such as between coastal and oceanic zones (Magozzi et al. 2017). Isotopic measurements can be obtained from different tissues, which have distinct turnover rates and therefore provide information from wider temporal windows than information obtained from regurgitates



**Fig. 1** **a** Distribution of brown booby *Sula leucogaster* colonies sampled along the southwest Atlantic Ocean. SPSP=São Pedro e São Paulo. **b** Biogeographic boundaries of Large Marine Ecosystems, following Sherman (1994) (bottom left): EBS=East Brazilian Shelf, and SBS=South Brazilian Shelf; Spalding's Provinces (initials) and Ecoregions (numbers), following Spalding et al. (2007) (bottom middle): TSA=Tropical Southwestern Atlantic, WTSA=Warm Temperate Southwestern Atlantic; Longhurst's Provinces, following Lon-

ghurst et al. (1995) (bottom right): BRAZ=Brazil Current Coastal Province, SATL=South Atlantic Gyral Province, WTRA=Western Tropical Atlantic Province. **c** Dendrogram generated from the dissimilarity matrix of the beta-sim index ( $\beta_{sim}$ ) of the prey community consumed by brown boobies in the southwest Atlantic Ocean, based on data from regurgitated material. The x-axis values range from 0 (low dissimilarity, identical community) to 1 (high dissimilarity, no species in common)

(Dalerum and Angerbjörn 2005). Additionally, stable isotope values can also be used as coordinates to an area ( $\delta$ -space) defined as 'isotopic niche' (Newsome et al. 2007). Therefore, the use of complementary techniques makes it possible to understand the use of food resources more accurately, due to the greater representativeness of the diet in the combined datasets.

In the present study, we aimed to assess the variation in the brown booby diet in the southwest Atlantic Ocean and to test its association with pre-established biogeographic zonings and population structure, as well as their potential use as biological samplers of the fish communities. For this, we reviewed and compiled data on regurgitate material (hereafter 'regurgitates') and stable isotopes of carbon and nitrogen from

**Table 1** Data sources and their respective sample sizes obtained by non-systematic search that described the diet of *Sula leucogaster* from regurgitated material and stable isotopes in colonies along the southwestern Atlantic Ocean

Colony	Regurgitates			Stable isotopes		
	<i>n</i>	Data sources	Sampling years	<i>n</i>	Data sources	m/y
Moleques	257	Kohlrausch, AB (unpubl data*)	1997/2002	18	Nunes and Bugoni (2018)	Feb/2014
	46	Branco et al. (2005)	2002–2004			
Currais	43	Krul (2004)	1995–1996	0	–	–
Cagarras	25	Torres et al. (unpubl data*)	2012	27	Nunes and Bugoni (2018)	Dec/2014
Cabo Frio	81	Coelho et al. (2004)	1990	0	–	–
Santana	54	Mancini et al. (2023)	2017–2018	40	Bighetti et al. (2021)	Feb–Nov/2018
				62	Mancini et al. (2023)	Jun/2017 to May/2018
Abrolhos	17	Alves et al. (2004)	1990–91/1994–96	31	Mancini et al. (2014)	Feb/2011
	19	Mancini, PL (unpubl data*)	2011	12	Nunes et al. (2022)	Feb/2019
	5	Rede Rio Doce Mar (unpubl data*)	2018–2019			
Noronha	15	Mancini, PL (unpubl data*)	2011	27	Mancini et al. (2014)	Mar/2011
	5	Bertrand, SL (unpubl data*)	2019			
Rocas	92	Kohlrausch, AB (unpubl data*)	2000–2002	28	Mancini et al. (2014)	Sep/2010
	20	Mancini, PL (unpubl data*)	2010			
SPSP	93	Kohlrausch, AB (unpubl data*)	2000–2002	29	Mancini et al. (2014)	Aug/2010 and Aug/2011
	33	Mancini and Bugoni (2014)	2010–2011	98	Nunes et al. (2018)	Jul/2015
	72	Nunes et al. (2018)	2014–2015			

*n* = total samples by each study; m/y = month/year of sampling; years separated by bars indicate isolated years of sampling and years separated by a dash indicate continuous sampling over the years. SPSP = São Pedro e São Paulo

\*References of ‘unpubl data’ are in Table S1

previous publications and unpublished databases. We expect the diet to vary spatially according to environmental heterogeneity, fitting into biogeographic patterns and the population structure already described for the species in the southwestern Atlantic Ocean.

## Materials and methods

### Study area

The study area comprises the entire distribution of brown booby colonies in the southwestern Atlantic Ocean, from Moleques do Sul islands (hereafter ‘Moleques’; 27°50′42″S, 48°25′49″W) to SPSP (0°55′00″N, 29°20′45″W) (Sick 1997) (Fig. 1a). Coastal colonies (Moleques, Currais, Cagarras, Cabo Frio, Santana, and Abrolhos) are located on the continental shelf with distance from mainland ranging from less than 1 to a maximum of 70 km and are influenced by shelf waters, such as Tropical Water and Subtropical Shelf Water, in addition to river discharges (Piola et al. 2000) and upwelling processes (e.g. South Atlantic Central Water in Cabo Frio) (Valentin 2001). Offshore the continental shelf, the oceanic colonies are located at the Fernando de Noronha archipelago (‘Noronha’), Rocas atoll (‘Rocas’), and SPSP,

ranging from 200 to a maximum of 1000 km from the mainland and under the influence of the South Equatorial Current (Richardson and Walsh 1986). In addition, SPSP is also influenced by the Equatorial Undercurrent (Araujo and Cintra 2009).

## Data collection and analysis

### Regurgitates

We gathered data on regurgitates from an active and non-systematic search in articles, book chapters, technical reports, and conference abstracts. We obtained six sources of datasets published between 2004 and 2023, two Ph.D. theses, one conference abstract, one technical report, and one unpublished database from Noronha, totaling nine breeding sites from Moleques to SPSP (Table 1, and Table S1), which were classified into at least two distinct biogeographical zones (Fig. 1b). The prey taxonomy was updated according to Eschmeyer’s Catalog of Fishes (Fricke et al. 2022) for fish and the World Register of Marine Species (WoRMS 2022) for other *taxa* (e.g. squids). Then, we extracted information on the number of regurgitates (i.e. samples), and prey abundance at the family and species levels per colony from each data



source using the ‘vegan’ (Oksanen et al. 2020) and ‘plyr’ (Wickham 2011) packages in the R software (R Core Team 2021). For descriptive metrics of prey species and families, we calculated the frequency of occurrence (FO%), relative abundance (RA%), richness (R), and  $\alpha$ -diversity (Shannon Index) (Magurran 2003) from each data source separately. Prey items not identified at species and family levels were disregarded from species and family analysis, even if it was the only representative of a taxonomic lineage. Items derived from cannibalism were also removed from the analysis (as showed in A. Kohlrausch unpubl. data).

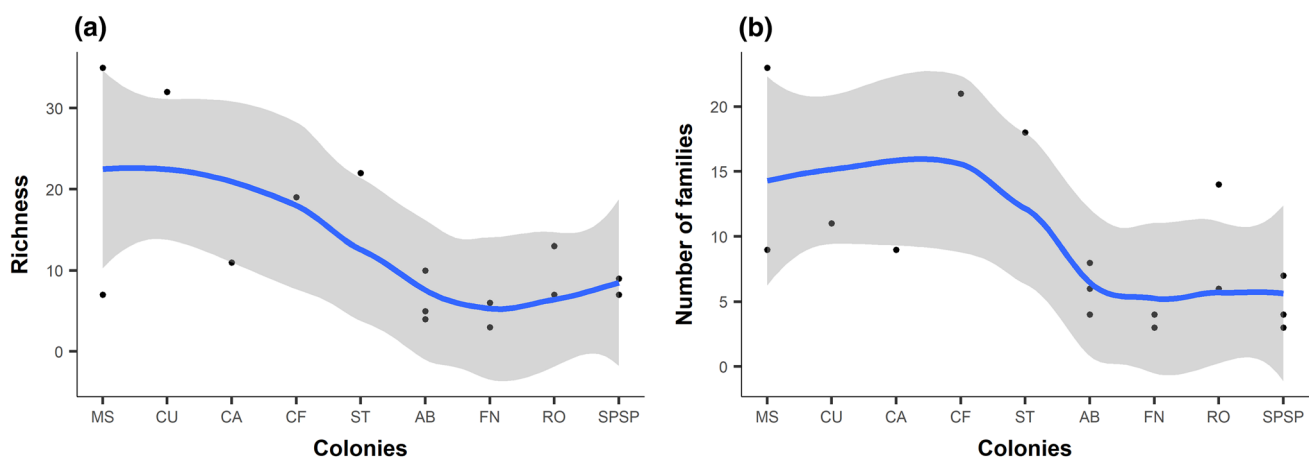
To assess differences between prey communities, we used complementary statistical approaches. Due to the differences in sampling efforts between studies and databases, the dataset was converted to a binary matrix of presence/absence. Paired distances between colonies were estimated with the beta-sim index ( $\beta_{sim}$ ) with subsequent generation of a dendrogram based on Euclidean distances using the ‘betapart’ (Baselga et al. 2021) and ‘ggdendro’ (Vries and Ripley 2020) packages. The  $\beta_{sim}$  was calculated according to the following equation (Kreft and Jetz 2010):

$$\beta_{sim} = 1 - \frac{a}{\min(b,c) + a},$$

where “a”=total number of shared species between colonies, and “b,c”=number of exclusive species of each colony.  $\beta_{sim}$  varies between 0 (low dissimilarity, identical *taxa* list) to 1 (high dissimilarity, no shared *taxa*). To visually identify similarities between colonies and location (Fig. 1a), genetic (as described below), and biogeographic criteria (Fig. 1b), we performed a non-metric multidimensional scaling (NMDS) with the Bray–Curtis index. Additionally, we ran

a permutational analysis of variance (PERMANOVA) with 999 permutations to test differences between the prey dataset and the criteria, assuming no dietary differences as the null hypothesis (Legendre and Legendre 2012). For graphing, we used the ‘ggplot2’ package (Wickham 2016).

The criteria used for the analyses were categorical and considered geographic, genetic, and biogeographical aspects. Colony location concerning the continental shelf was assigned as ‘coastal’ or ‘oceanic’ whether the colony was on or off the shelf, respectively. The genetic criteria followed the previously published clustering based on microsatellites (Nunes and Bugoni 2018), where the  $K=2$  arrangement splits the colonies into two groups (SPSP; and Others), and the  $K=3$  suggests isolation of SPSP, in addition to a weaker gene flow between “Coastal” (Moleques, Cagarras, and Abrolhos) and “FN-RO” (Noronha and Rocas) groups. For standardization purposes, we included the coastal colonies not studied by Nunes and Bugoni (2018) in the “Coastal” group. Finally, we considered distinct biogeographical classifications of the marine environment: the Biogeochemical Provinces of Longhurst (hereafter “Longhurst’s Provinces”) (Longhurst et al. 1995); the Large Marine Ecosystems, (hereafter “LME”) (Sherman 1994); and the Provinces and Ecoregions established by Spalding et al. (2007) (hereafter “Spalding’s Provinces” and “Spalding’s Ecoregions”, respectively). The Longhurst’s Provinces were outlined based on chlorophyll- $\alpha$  concentration, which is a proxy of primary productivity for coastal and oceanic regions. LME were delimited from the characterization of the margins of ocean basins based on bathymetric, hydrographic, and depth data; in addition to fish distributions (Sherman 1994). Spalding’s Provinces and Ecoregions were



**Fig. 2** **a** Species richness and **b** number of prey families consumed by *Sula leucogaster* in colonies along the southwest Atlantic Ocean. The colonies are ordered in a decreasing latitudinal gradient (from left

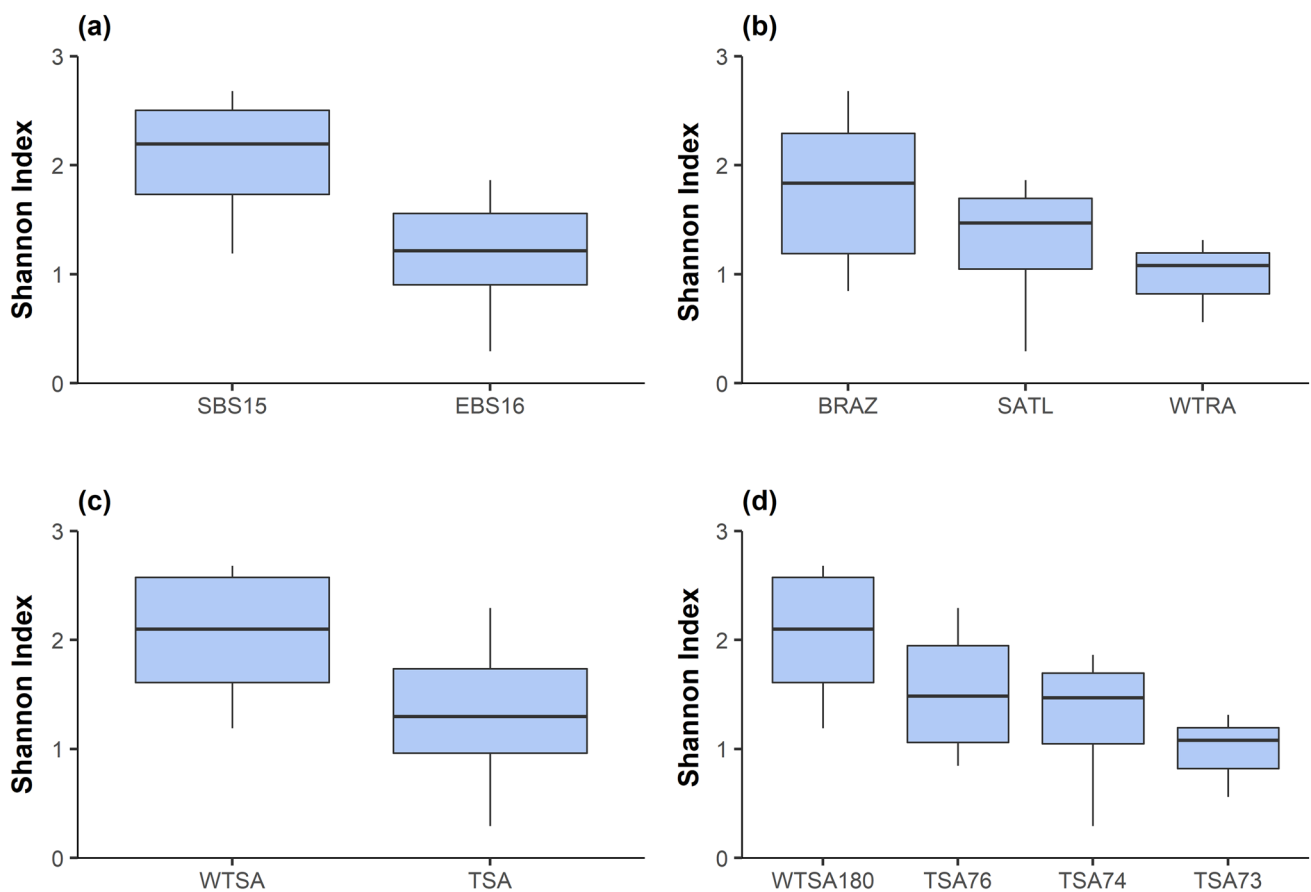
to right). MS=Moleques; CU=Currais; CA=Cagarras; CF=Cabo Frio; ST=Santana; AB=Abrolhos; FN=Noronha; RO=Rocas; SPSP=São Pedro e São Paulo

developed from a review of pre-existing classifications which combined benthic and pelagic *taxa* distribution with multiple oceanographic and geomorphologic factors (i.e. islands, current dynamics, upwellings, and salinity), in addition to adjustments according to geopolitical limits. In this classification, the provinces are identified by names and subdivided into ecoregions, represented by numbers (Spalding et al. 2007).

### Stable isotopes

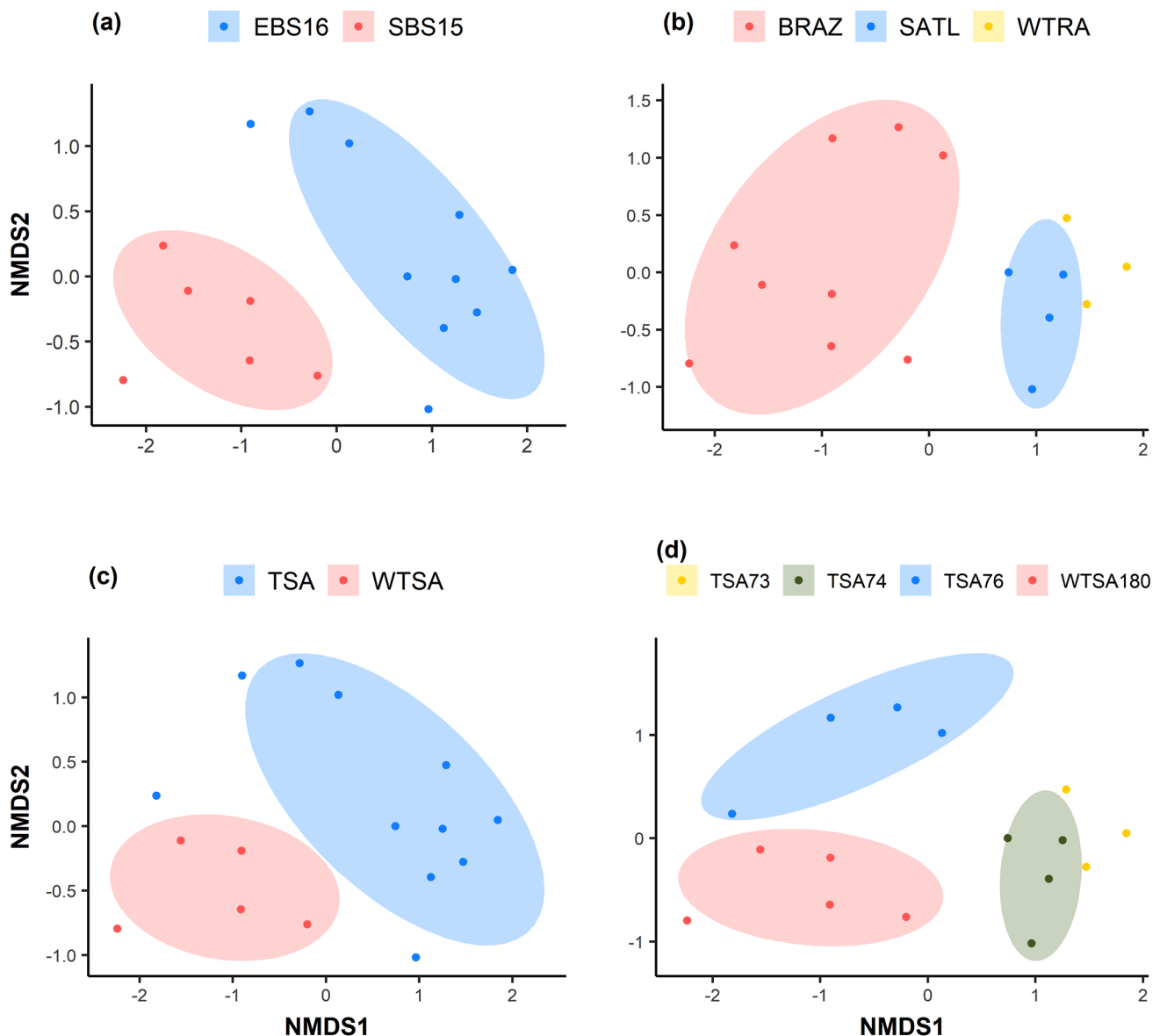
We used carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotopic ratios from brown booby whole blood samples obtained from scientific articles, technical reports, and unpublished datasets (Table 1). All data were collected from breeding individuals and without distinction between males and females. Sample processing of the unpublished datasets consisted in place a few drops of the whole blood on tubes, which were air-dried. Blood samples were freeze-dried, ground, and homogenized.

Subsamples of 1 mg were weighed into tin cups and analyzed in a mass spectrometer (Mancini et al. 2014; Nunes et al. 2018). Standards used were Vienna Pee Dee belemnite and atmospheric air for carbon and nitrogen, respectively. Measurement precision of both  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  is described in each reference as well as secondary isotopic reference materials used by each laboratory (Table 1). Lipids were not extracted from seabird blood due to their expected low concentration (Bearhop et al. 2000). We calculated the mean and standard deviation of each colony using the 'FSA' package (Ogle et al. 2021). Then, we tested univariate differences between colonies using the Kruskal–Wallis test, and Mann–Whitney *U* test as post-hoc, using False Discovery Rate for adjusting *P* values (Benjamini and Hochberg 1995). Additionally, we calculated the two-dimensional isotopic niche breadth based on Bayesian ellipses as implemented in the 'SIBER' package (Jackson et al. 2011).



**Fig. 3** Shannon diversity index of prey species consumed by *Sula leucogaster* in the southwest Atlantic Ocean considering colony location with **a** Large Marine Ecosystems (LME); **b** Longhurst's Provinces; **c** Spalding's Provinces; and **d** Spalding's Ecoregions. SBS15=South Brazilian Shelf; EBS16=East Brazilian Shelf;

BRAZ=Brazil Current Coastal Province; SATL=South America Atlantic Gyral Province; WTRA=Western Tropical Atlantic Province; WTSA=Warm Temperate Southwestern Atlantic; TSA=Tropical Southwestern Atlantic



**Fig. 4** Two-dimensional NMDS plots considering a binary matrix of the prey community consumed by *Sula leucogaster* in relation to the framework of each colony in the following biogeographic zonings: **a** Large Marine Ecosystems; **b** Longhurst's Provinces; **c** Spalding's Provinces; **d** Spalding's Ecoregions. *EBS16*=East Brazilian Shelf;

*SBS15*=South Brazilian Shelf; *BRAZ*=Brazil Current Coastal Province; *SATL*=South America Atlantic Gyral Province; *WTRA*=Western Tropical Atlantic Province; *TSA*=Tropical Southwestern Atlantic; *WTSA*=Warm Temperate Southwestern Atlantic

## Results

### Regurgitates

In total, 877 regurgitates composed the dataset, with 4270 prey belonging to at least 105 species, 43 families, and 17 orders (Table S2), showing an increasing accumulation curve of prey species relative to the number of datasets (Fig. S1). Different sample sizes were reported among studies, with Rocas ( $n=1128$ ) presenting the highest prey numbers and Noronha ( $n=85$ ) the lowest ones (Fig. S2).

For the analysis at the species-level only, we considered 3727 prey belonging to 99 species. Moleques exhibited the highest species richness ( $R=39$ ) and Noronha the lowest ( $R=8$ ) (Fig. 2a). Considering all colonies, the most frequent species were *Sardinella aurita* and *Harengula clupei* (FO=55.5%), followed by *Micropogonias furnieri*, *Ctenosciaena gracilicirrus*, *Pellona harroweri*, *Hirundichthys affinis*, *Cetengraulis edentulus* and *Opis-thonema oglinum* (FO=44.4%). Additionally, *C. edentulus* also showed the highest relative abundance in Moleques



(RA = 24.9%) and Cagarras (RA = 39.6%), and *S. aurita* in Currais (RA = 15.7%) (Table S3).

For the family-level analysis, 43 families and 4200 prey were included. The lowest number of families was recorded in Noronha ( $n = 4$ ) and the highest in Moleques ( $n = 24$ ) (Fig. 2b). The highest frequency of occurrence was observed for Clupeidae (FO = 88.9%) followed by Scombridae, Sciaenidae, Hemiramphidae, Engraulidae, and Carangidae (FO = 66.7%). Exocoetidae and Hemiramphidae occurred only in Abrolhos, among sites over the continental shelf, and in the oceanic colonies and together accounted for over 90% of the prey consumed by SPSP boobies. Among colonies south of Abrolhos, the most representative prey families were Sciaenidae, Engraulidae, and Clupeidae (Table S4 and Fig. S3).

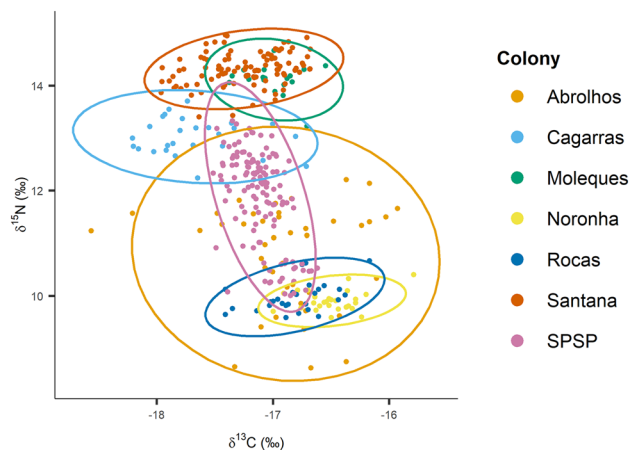
Diversity values ranged from 2.68 in Currais to 0.29 in Noronha (Fig. S4a) and oceanic colonies showed lower diversity in comparison to coastal colonies (Fig. S4b). Considering the genetic criteria, SPSP had lower diversity compared to the remaining colonies for  $K = 2$  (Fig. S4c); while for  $K = 3$ , the coastal group had higher diversity compared to the FN-RO group and SPSP (Fig. S4d). For the LME and Spalding's Provinces, the highest diversity was observed, respectively, in the South Brazilian Shelf (SBS) and Warm Temperate Southwestern Atlantic (WTSA) regions, which correspond to the southernmost portions of the boundaries established for these classifications (Fig. 3a, c). The Longhurst's Provinces showed decreasing diversity values from the Brazil Current Coastal Province (BRAZ) to the

Western Tropical Atlantic Province (WTRA) (Fig. 3b). Spalding's Ecoregions in the Tropical Southwestern Atlantic (TSA, named TSA74 and TSA73), which correspond to the FN-RO and SPSP colonies, respectively, had lower diversity (Fig. 3d).

Colonies were clustered into two large groups following the  $\beta_{sim}$  index: the oceanic Noronha, Rocas, and SPSP; and the colonies on the continental shelf (Fig. 1c, Table S5). PERMANOVA grouping the prey community with the pre-defined criteria generated significant results ( $P \leq 0.01$ ) for geographic, genetic, and biogeographic, except for the clustering  $K = 2$  ( $P = 0.02$ ). NMDS showed that colonies were grouped according to all criteria (Fig. 4 and Fig. S5), except for the delineation of Spalding's Provinces (Fig. 4c).

### Stable isotopes

The analyzed dataset comprised 194 blood samples from seven colonies (Table 1). The mean carbon and nitrogen isotopic ratios obtained from the data sources ranged from  $-17.7\text{‰}$  in Cagarras to  $-16.5\text{‰}$  in Noronha for  $\delta^{13}\text{C}$ , and from  $9.9\text{‰}$  in Noronha to  $14.3\text{‰}$  in Santana for  $\delta^{15}\text{N}$  (Table S6). Univariate differences between colonies were significant both for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values ( $P \leq 0.01$ ). Pairwise differences between colonies resulted in significant differences for  $\delta^{15}\text{N}$  between all colonies, except between Noronha and Rocas ( $P = 0.42$ ). For  $\delta^{13}\text{C}$ , significant pairwise differences were identified among all colonies, except between Moleques and Abrolhos ( $P = 0.27$ ), Moleques and Rocas ( $P = 0.03$ ), Moleques and SPSP ( $P = 0.03$ ), and Abrolhos and Rocas ( $P = 0.40$ ). Differences occurred between genetic and biogeographic criteria for  $\delta^{15}\text{N}$ , except between Spalding's Ecoregions WTS180 and TSA76 ( $P = 0.02$ ), which correspond to the Moleques-Cagarras and Santana-Abrolhos, respectively. Differences in  $\delta^{15}\text{N}$  between coastal and oceanic colonies were not significant ( $P = 0.86$ ). Considering the genetic criteria  $K = 3$ , paired significant differences were identified for  $\delta^{13}\text{C}$  between FN-RO and the coastal group, and also between FN-RO and SPSP ( $P \leq 0.01$ ). Additionally, the biogeographic criteria for  $\delta^{13}\text{C}$  resulted in significant differences between Longhurst's Provinces, LME, Spalding's Provinces, and most Ecoregions ( $P \leq 0.01$ ), except between TSA73 and TSA76 ( $P = 0.66$ ), which corresponds to SPSP and Santana-Abrolhos, respectively. Finally, we also observed similarities between ellipse areas among the brown booby colonies, with Noronha and Rocas holding similar areas, with lower  $\delta^{15}\text{N}$  values and Cagarras, Santana, and Moleques showing higher  $\delta^{15}\text{N}$  values and sharing similar  $\delta^{13}\text{C}$  ranges. Population from Abrolhos showed the widest ellipses among the colonies (ellipse area = 9.58) (Fig. 5).



**Fig. 5** Bayesian ellipses generated from carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotopic ratios from blood samples of *Sula leucogaster* obtained in colonies along the southwest Atlantic Ocean. Ellipses comprise 95% of the data and resulted in the following areas: Abrolhos = 9.58; Cagarras = 2.69; SPSP = 2.68; Santana = 1.94; Rocas = 1.5; Moleques = 1.28; Noronha = 0.89. SPSP = São Pedro e São Paulo

## Discussion

In the present study, we evidenced the diversity and spatial patterns in the diet of brown boobies, which forage over a hundred prey species in the southwest Atlantic Ocean. Diet variation was associated with colony location, genetic clustering, and biogeographical zonings. Findings suggest that the diet of brown boobies can be directly influenced by the prey available around breeding sites, considering the number of demersal prey species associated with trawling in coastal colonies and tropical prey species in oceanic colonies. These results reinforce the role of local adaptation in shaping population structure, considering the association of the diet (i.e. prey community and pairwise differences of  $\delta^{15}\text{N}$  between colonies) with the known brown booby population structure in the southwest Atlantic Ocean (Nunes and Bugoni 2018), especially between colonies on and off the continental shelf. Additionally, the results demonstrate the usefulness of dietary aspects of widely distributed seabirds in informing biogeographic boundaries, considering that these species can be used as samplers of local biodiversity.

The diet of the brown booby varies according to the prey availability around the colonies throughout its global distribution, which can even make such interactions predictable. For example, differences in foraging behavior and diet can be identified according to variations in the abundance of their main prey (Mellink et al. 2001), to oceanographic dynamics in the Gulf of California (Castillo-Guerrero et al. 2016), and to the risk of kleptoparasitism in Australia (Miller et al. 2018). Similarly, brown boobies breeding in the north (Harrison et al. 1983) and south (Harrison et al. 1984) of the Pacific Ocean take advantage of any prey available around the colonies. Over a hundred prey species were reported in the diet of brown booby in the southwest Atlantic Ocean compiled here, with marked differences associated with previously proposed biogeographic patterns, which in turn are based on oceanographic parameters (i.e. biological, physical, and chemical). Therefore, the analysis of environmental covariates around the colonies and their temporal variations can predict aspects of the brown booby diet, which may represent an interesting model to predict potential impacts of climate change scenarios in trophic interactions of seabirds (Barbraud et al. 2012; Ramírez et al. 2021; Watanuki et al. 2022).

Isotopic niche variation among the colonies may be associated with behavioral aspects driven by food availability, but also with differences in isotopic baselines. Nitrogen values could be influenced by the feeding ecology of the main prey species at each colony. In southern sites, there is a substantial contribution of carnivorous species, such as sciaenids (Lucena et al. 2000; Sedrez et al. 2021), whereas the predominant prey in Noronha and Rocas are

planktivorous, such as clupeids (Whitehead 1985) and flying fish (Van Noord et al. 2013). Boobies from Abrolhos forage on both planktivorous and carnivorous species (e.g. Carangidae), the latter being usually a bycatch of shrimp trawling in this region (Santos et al. 2008). Considering all colonies, Abrolhos showed the widest and largest isotopic niche, which may be associated with the variety of prey consumed at this site, both pelagic and demersal. This wider isotopic niche in Abrolhos could indicate that seabirds are feeding on a greater variety of prey, while a narrow niche, as observed in Noronha, would suggest a lower variety of prey ingested (Mancini et al. 2014), as corroborated by regurgitates. Different isotopic values may also be associated with spatiotemporal variations in isotopic baselines among colonies, which may be influenced by fluctuations of environmental conditions in foraging areas (Bond and Jones 2009), such as the influence of the upwelling in Cabo Frio (Soares et al. 2014) that can impact northern areas, e.g. Santana (Bauer et al. 2017). However, the variations in isotopic niche breadth observed in the present study suggest this is closely associated with the resources available around the colonies, which represents additional evidence of adaptation to local conditions.

Because brown boobies use fishery discards as a food source, the variation in prey composition and predictability may also be associated with the spatial distribution of fisheries. Demersal prey (e.g. Sciaenidae and Batrachoididae) discarded from shrimp trawling were frequent in the diet of boobies from southern coastal colonies (Vianna and Almeida 2005; Branco and Verani 2006; Cattani et al. 2011; Silva et al. 2016) and absent in oceanic colonies, suggesting an influence of such fishery in the dietary composition of brown boobies. However, prey usually associated with discards were scarce in Cagarras, despite the occurrence of bottom trawling around the archipelago (Moraes et al. 2013; Amorim and Monteiro-Neto 2016). It is possible that the dataset from Cagarras is biased by insufficient sampling (i.e. one breeding season) (Torres et al. unpubl. data), but the availability of engraulids and clupeids around the colony (Jablonski et al. 2006; Silva-Jr. et al. 2016) may favor “natural prey” over discards from trawling, as observed in other Sulidae species (Votier et al. 2010; Moseley et al. 2012). Another possible influence may be from interspecific interactions such as kleptoparasitism of frigatebirds (Cunha et al. 2013). At oceanic colonies, fisheries targeting large pelagic fishes, such as tunas and sharks, are carried out by using live bait, such as clupeids in Noronha (Sazima and Sazima 2008) and flying fish in SPSP (Viana et al. 2015). Surplus baits are discarded after fishing and then used by brown boobies as a food source around Noronha and SPSP (pers. obs. GT Nunes), which could explain the high contribution of these prey to the diet of boobies, in addition to the ones that are naturally predated. In this context, the variety of fisheries

throughout the study area could play an important role in the prey composition of boobies and therefore decisions targeting the management of fisheries and fishery discards should consider their effects on the persistence of seabird populations.

Prey community and isotopic niche variations among colonies were associated with the population structure of brown boobies in the southwest Atlantic Ocean, reinforcing the idea of local adaptation as a relevant mechanism for the promotion/disruption of gene flow. Genetic clustering among coastal colonies, as well as between Noronha and Rocas (Nunes and Bugoni 2018) was mirrored in dietary aspects explored in this study, demonstrated by the clustering generated from the  $\beta_{\text{sim}}$  index and the associations between the genetic clusters and isotopic ratios. This suggests that population structure could be influenced by local adaptation in obtaining available food resources. Dispersal ability could be more likely among colonies with similar environmental conditions (e.g. sea surface temperature, chlorophyll- $\alpha$  concentration, fisheries), representing similar prey communities and selective pressures, as it was observed among coastal colonies. Additionally, Abrolhos could represent a stepping-stone for dispersal between coastal and oceanic colonies, due to the occurrence of prey species found both in the northern (i.e. Hemiramphidae and Exocoetidae) and southern colonies (i.e. fishery discards), which is supported in the genetic clustering model (Nunes and Bugoni 2018). Finally, SPSP is genetically isolated from the remaining colonies, which is suggested to be associated with selective pressures in the nesting area (Nunes et al. 2018). However, the high availability and consumption of flying fish in SPSP (RA ~63%) can also influence population differentiation through local adaptation, even when compared to adjacent colonies, such as Noronha and Rocas. Therefore, spatial patterns of diet variation associated with population structure provide support to the IBE model (Wang and Bradburd 2014) and local adaptation as an important mechanism of population structuring, even in highly mobile organisms such as seabirds.

Dietary aspects investigated from regurgitates and isotopic values (especially  $\delta^{15}\text{N}$ ) were demonstrated to be relevant tools to inform biogeographic patterns, even considering differences between boundaries of each zoning. Comparing the boundaries of Spalding's Provinces with LME, Santana is placed differently, grouped with the northern colonies in the first and with the southern colonies in the second one. Spalding et al. (2007) proposed delimitations based on the zoning of Sealey and Bustamante (1999) in South America, which assumes the northern limit of the Falkland Current as the boundary between WTSA and TSA provinces, in Cabo Frio. However, upwelling of the South Atlantic Central Water (SACW) in this same location can extend environmental conditions (e.g. lower sea surface temperature) northward, and make Santana more similar to the

southern colonies, regarding environmental conditions and species composition (Soares et al. 2014; Bauer et al. 2017). Therefore, the biogeographic models which place Santana in the same zoning as the southern colonies are better supported by dietary variation, given that primary productivity distribution is the criteria used by Longhurst et al. (1995), while LME are based on bathymetry, ocean currents, and fish community (Sherman 1994). Considering that diet composition may represent local biodiversity, these findings can contribute to the refinement of distinct marine zonings, helping to identify inconsistencies and adjust boundaries.

Finding spatial distribution patterns and associations with biogeographic models in highly mobile species of wide home range is challenging, but meta-analysis approaches can enable representative sampling in time and space, despite the limitations they may offer in analytical and interpretation terms. Publications and databases used in the present study comprised variable sampling efforts, periods, sex ratios, and researchers, which could make results biased regarding prey abundance and richness. In addition, the comparison of isotopic values requires caution, as the study covers colonies distributed over a 28° latitudinal gradient and therefore include potential differences in isotopic baselines. Temporal variation in sampling the colonies could lead to variations in isotopic information given the dynamics of primary productivity and prey availability around the colonies (Mancini et al. 2014). However, the heterogeneity of the sample for each colony also has an important positive aspect, since the representativeness of the dietary variations in the colony is greater compared to a point-in-time sampling. In this context, the framework applied in this study was successful in integrating information about the prey species consumed by the brown booby in a vast study area and was sufficient to detect spatial patterns of the brown booby diet along the southwest Atlantic Ocean. This allowed testing for fitting into pre-established marine biogeographic zonings and demonstrated the suitability of using top predators as samplers of fish fauna at large biogeographical scales. Additionally, as central-place foragers, seabirds use extensive areas around colonies to obtain food and breed in aggregations, which facilitates sampling. Spontaneous regurgitation increases the potential of seabirds as a source of information about the pelagic and demersal species community because regurgitates provide accurate taxonomic information about prey. Finally, the use of complementary approaches, such as regurgitates and stable isotopes, can take a more accurate picture of the dietary aspects and therefore of the prey community. Thus, studying the seabird diet is an important and useful tool to define and refine marine biogeographic zoning, especially from the perspective of widely distributed and hard-to-sample organisms, such as flying fish.

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**Author contributions** GTN and JJ conceptualized the idea and designed the study. GTN, PLM, SLB and LB collected and shared data. GTN and JJ analyzed the data and wrote the manuscript and PLM, SLB, MAE, and LB contributed critically to the final revision.

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**Data availability** All data and the R script are publicly available through the GitHub repository: <https://github.com/SeabirdEcology/URGS/DietBiogeography>

## Declarations

**Conflict of interest** The authors declare no conflict of interest.

**Ethical approval** The sampling of the unpublished datasets was approved by SISBIO 64234-6 and by the ethics committee at UFRGS.

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