



Niche segregation persists over years and during the breeding and non-breeding seasons in sympatric seabirds

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ABSTRACT: The coexistence of seabirds with similar ecological requirements relies on niche partitioning mechanisms to avoid interspecific competition, especially during the breeding season when energetic demands are high. In this study, we investigated interspecific and seasonal (breeding vs. non-breeding) trophic niche differences of masked boobies *Sula dactylatra* (MBs) and red-footed boobies *S. sula* (RFBs) in the Fernando de Noronha Archipelago, tropical Atlantic Ocean. Stable isotope ratios of carbon and nitrogen ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) were obtained from blood samples over 6 yr (2015–2022) in April ($n_{\text{MB}} = 97$, $n_{\text{RFB}} = 10$) and September ($n_{\text{MB}} = 57$, $n_{\text{RFB}} = 56$). These months capture contrasting breeding moments: April represents the peak breeding period for MBs and September the non-breeding period, while the pattern is reversed for RFBs. MBs exhibited significantly higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values than RFBs across all seasons and years, with low isotopic niche overlap, indicating marked niche partitioning. Additionally, MB niche width remained stable throughout the annual cycle, suggesting that chick-rearing constraints minimally influenced its foraging strategies. Conversely, the RFB had a narrower niche during its non-breeding season (April) than during the breeding season (September). This seasonal shift likely reflects the trophic plasticity of RFBs in response to seasonal variations in prey availability or a strategy to reduce competition with the larger-bodied MBs throughout the breeding cycle. Moreover, seasonal variations in $\delta^{15}\text{N}$ values were similar for both species, likely reflecting shifts in isotopic baselines. This study highlights how trophic niche partitioning and adjustments associated with breeding cycles can facilitate species coexistence in tropical environments.

KEY WORDS: Coexistence · Interspecific competition · Foraging · Stable isotopes · Sulidae · Trophic ecology

1. INTRODUCTION

The coexistence of species with similar ecological requirements increases the potential for intra- and interspecific competition, particularly when common resources are limited, affecting population persis-

tence (Gause 1932, Hardin 1960). Niche partitioning is a fundamental strategy for mitigating such competition, allowing species to coexist by adjusting one or more niche dimensions (Hutchinson 1957, Schoener 1974). In this context, seabirds serve as excellent models for investigating niche partitioning and coex-

istence, as many species occur in sympatry throughout their life cycle and exploit available resources around the colony for self-maintenance and chick provisioning (Jessopp et al. 2020, Petalas et al. 2024).

Seabirds have developed different strategies to avoid competition, such as spatial and trophic niche partitioning (Ashmole & Ashmole 1967, Petalas et al. 2024). These adaptations are closely linked to foraging behavior, such as exploring distinct areas at varying distances from the colony or diving at different depths, which may result in the consumption of different prey (Petalas et al. 2021, Fromant et al. 2022, Fayet et al. 2023). In such cases, differences in morphological traits among sympatric species, particularly body size and mass, may play an important role by influencing flight performance, diving depth, and size of consumed prey (Lewis et al. 2005, Catry et al. 2009, Mancini et al. 2014). However, the need for these adjustments may vary year-round, as competitive pressure tends to increase during breeding (Young et al. 2010a, Almeida et al. 2021, Fromant et al. 2022).

Breeding is a particularly demanding period, as the need to sustain both parents and offspring entails high energy expenditure and, consequently, intense resource exploitation (Barger et al. 2016, Fromant et al. 2022). As central-place foragers during this stage, seabirds return to the nest periodically between foraging trips, leading to repeated exploitation of resources near the colony to minimize provisioning costs (Schreiber & Burger 2001, Weber et al. 2021). This restriction often limits the spatial foraging range and potentially reduces the diversity of available resources (Tocker et al. 2023, Lerma et al. 2024). By contrast, during the non-breeding period, birds are freed from parental duties and frequently exhibit shifts in their foraging ecology, such as expanded foraging range and prey diversity (Lisnizer & Yorio 2019, Mills et al. 2021, Roy et al. 2021). Consequently, these distinct foraging strategies across the avian life cycle can lead to variations in ecological niche breadth, which is typically more constrained during the breeding season and wider during the non-breeding season (Cherel et al. 2007, Lisnizer & Yorio 2019, Tocker et al. 2023). However, these dynamics are further modulated by the presence of sympatric species, as intensive exploitation of limited resources by one species during its breeding period may increase competitive pressures on co-occurring species (Mancini et al. 2014, Almeida et al. 2021, Fromant et al. 2022). Therefore, year-round adjustments in niche dimensions are crucial for promoting and maintaining local diversity of species, especially in environments with limited food availability (Soanes et al. 2021, Lerma et al. 2024).

In oligotrophic tropical oceans, where resources are patchily distributed and scarce, niche partitioning is essential for species' coexistence (Hardin 1960, Longhurst & Pauly 1987, Young et al. 2010a). Boobies (Sulidae: *Sula* spp.) are seabirds that inhabit tropical and subtropical environments and often form multi-species colonies (Nelson 1978), where interspecific niche segregation is a common response to limited resources (Lerma et al. 2024). Studies on the more size-dimorphic species of the genus, the masked booby *Sula dactylatra* (MB) and the red-footed booby *S. sula* (RFB), have shown differences in foraging strategies in breeding and non-breeding periods. Generally, MBs tend to forage closer to the colony, feed mainly on flying fish, and occupy a higher trophic position than RFBs, which typically forage in more oceanic areas and consume a higher proportion of squid (Young et al. 2010b, Kappes et al. 2011, Lerma et al. 2024). These differences are usually attributed to the higher energetic requirements and larger body size of MBs (total length: 74–86 cm; 1200–2353 g; Grace et al. 2020), compared to RFBs (total length: 69–79 cm; 850–1100 g; Schreiber et al. 2020), which is suggested to confer competitive advantages (Kappes et al. 2011, Mancini et al. 2014).

In the Fernando de Noronha Archipelago, tropical western Atlantic Ocean, both species occur in sympatry alongside 9 other breeding seabird species (Mancini et al. 2016), including the brown booby *S. leucogaster*. The archipelago hosts the largest population of RFBs in the South Atlantic Ocean (>800 individuals; Santos et al. 2024), while the MB population is estimated at 400 individuals (Mancini et al. 2016). Although both species breed and remain in the area year-round, they exhibit asynchronous breeding peaks (abundance of nests with chicks) that coincide with different climatic seasons. For the MB, this breeding peak occurs between March and May during the rainy season (Castro 2009, ICMBio 2022). Conversely, for the RFB, the peak occurs between August and September (Santos et al. 2024), during the dry season, a time when MB nesting activity is decreasing (Castro 2009, ICMBio 2022). Tracking data indicate that MB individuals exhibit local foraging in Fernando de Noronha during their breeding and non-breeding periods, with a marked increase in foraging range and trip duration during the latter (Roy et al. 2021, Jacoby et al. 2025). This overlap in ecological requirements and the year-round presence in a tropical archipelago suggest that behavioral adjustments may facilitate resource partitioning to promote coexistence.

In this context, we aimed to test differences in the trophic niche of 2 sympatric booby species in the Fer-

nando de Noronha Archipelago across their breeding and non-breeding periods, using a stable isotope data set of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) systematically collected from 2015 to 2022. Given their year-round coexistence in the archipelago and prior knowledge on species-specific morphological and behavioral characteristics, we expected to observe (1) narrower niche width during the breeding compared to the non-breeding period in both species, reflecting the shifts in foraging strategies between seasons; (2) low isotopic niche overlap between species, identifying trophic segregation during all sampled periods, as a strategy to facilitate coexistence; and (3) higher $\delta^{15}\text{N}$ values (as a proxy for trophic level position) in MBs than in RFBs, as a result of morphological differences between species.

2. MATERIALS AND METHODS

2.1. Study area

Birds were sampled on Meio Island ($3^{\circ} 49' 12'' \text{ S}$, $32^{\circ} 23' 35'' \text{ W}$), one of the 21 islets that comprise the Fernando de Noronha Archipelago, located in the western Atlantic Ocean, 360 km off the Brazilian coast (Fig. 1). The archipelago exhibits intra-annual rainfall variation, characterized by a rainy season from March

to July and a dry season from August to January (Castro 2009). Sea surface temperature (SST) exhibits only a mild seasonal variation, with higher values from March to May ($\text{SST} > 28.0^{\circ}\text{C}$) and lower values from August to November ($\text{SST} \sim 26.5^{\circ}\text{C}$; Tchamabi et al. 2017). Meio Island hosts colonies of MBs and brown boobies in areas with herbaceous vegetation and exposed soil, while the RFB colony habitat is characterized by trees and shrub vegetation (Fig. 1; Gaiotto et al. 2022). Between 2017 and 2018, the island underwent rat control measures to mitigate the high density of black rats *Rattus rattus*, which preyed on eggs and chicks and negatively impacted seabird reproduction. Consequently, enhanced breeding performance is expected in the years following rat removal (Le Corre et al. 2015, Saunier et al. 2022).

2.2. Sampling methods

Fieldwork was conducted in April and September between 2015 and 2022. These months correspond to the peak of the chick-rearing periods for MBs and RFBs, respectively (ICMBio 2022, Santos et al. 2024), as well as the rainy and dry seasons (Castro 2009). For MBs, breeding samples were collected in April 2017, 2018, 2019, and 2022 (see Jacoby et al. 2025), and non-breeding samples were collected in September 2015,

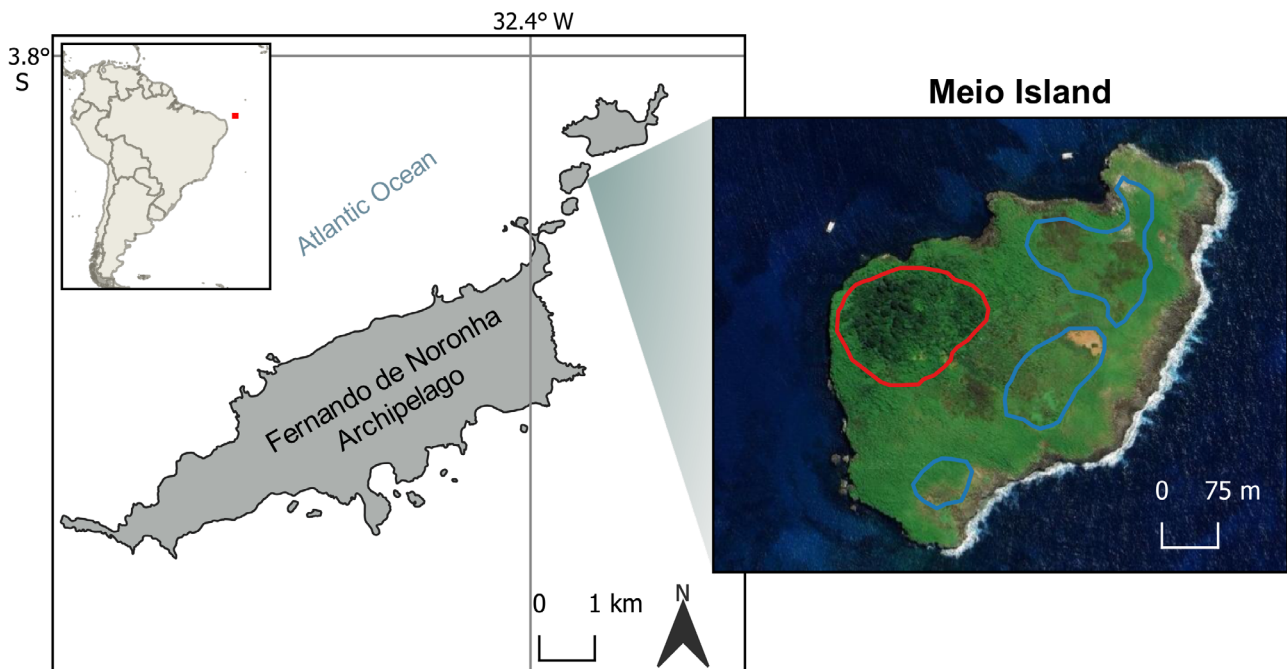


Fig. 1. Fernando de Noronha Archipelago and Meio Island, tropical southwestern Atlantic Ocean. Red polygon: red-footed booby *Sula sula* colony, in areas with tree and shrub vegetation. Blue polygons: masked booby *S. dactylatra* colonies, in areas with herbaceous vegetation and exposed soil

2016, and 2018. For RFBs, breeding samples were collected in September 2015, 2016, and 2018, and non-breeders were sampled in April 2019 and 2022. Whole blood was selected for the study due to its turnover rate of approximately 3–4 wk (Hobson & Clark 1992). Unlike metabolically inert feathers, which may reflect growth periods from different life stages, blood closely represents the dietary intake in the weeks immediately preceding the sampling expeditions (Hobson & Clark 1992, Dalerum & Angerbjörn 2005). Moreover, signs of molting feathers were observed in breeding individuals during handling, further confirming that feathers would not provide a reliable temporal resolution for specific breeding stages.

Breeding individuals were identified within the colony as adults attending chicks at an early stage of development (i.e. featherless or covered with downy feathers, with no development of flight feathers). Non-breeding individuals were sampled opportunistically while roosting near the colonies. The sampling period within each sampling event was carried out over 1–2 d for non-breeders and 3–5 d for breeders. To minimize thermal stress and colony disturbance, captures were conducted between dusk and dawn (18:00–06:00 h). Birds were captured manually or with a fishing pole, with handling time ranging from 5–10 min. For each individual, approximately 0.3 ml of blood was drawn from the metatarsal vein using a sterile syringe and needle, stored in dry microtubes, and frozen at -20°C , as recommended for blood samples for stable isotope analysis (Bugoni et al. 2008). Individuals were banded with metal rings (CEMAVE/ICMBio) and marked with non-toxic wax crayons to avoid recapture in the same sampling event. MBs were sexed based on vocalization, while RFB sex was not determined due to the lack of reliable field diagnostic differences (Nelson 1978).

2.3. Stable isotope analysis

In the laboratory, whole blood samples were lyophilized, ground, and homogenized. Subsamples (~ 0.7 mg) were placed in tin capsules for stable isotope analysis of carbon and nitrogen. The isotopic signatures were determined using an isotope ratio mass spectrometer (IRMS) coupled to an elemental analyzer. Samples from 2015–2019 were analyzed at the Pôle Spectrométrie Océan of the Institut Universitaire Européen de la Mer (PSO-IUEM, France) using an IRMS Delta V Plus with a ConFlo IV interface (Thermo Scientific) and a Flash EA 2000 (Thermo Scientific). Samples from 2022 were analyzed at the Centro Inte-

grado de Análises of the Universidade Federal do Rio Grande (CIA-FURG, Brazil) using an IRMS Delta V Advantage coupled to a Flash EA 2000 (Thermo Fisher Scientific). The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were determined using the equation from Bond & Hobson (2012) and are expressed in δ notation (‰) relative to international standards: Vienna Pee Dee Belemnite for carbon and atmospheric air for nitrogen. Analytical accuracy was verified by repeated measurements of internal standards interspersed between samples: acetanilide at PSO-IUEM ($\pm 0.08\text{‰}$ for $\delta^{13}\text{C}$ and $\pm 0.15\text{‰}$ for $\delta^{15}\text{N}$), and glutamic acid and caffeine at CIA-FURG ($\pm 0.07\text{‰}$ for $\delta^{13}\text{C}$ and $\pm 0.11\text{‰}$ for $\delta^{15}\text{N}$).

The blood of seabirds has an expected low lipid content; therefore, lipid extraction procedures were not performed (Bearhop et al. 2002). Subsequently, the percentage of carbon and nitrogen mass in each sample was calculated to obtain the C:N ratio. Blood samples ($n = 4$) with C:N ratios above 4.0 were removed from the analyses to avoid potential lipid bias in results (Post et al. 2007, Cherel et al. 2014a). While $\delta^{13}\text{C}$ informs spatial aspects of the diet, such as the relationship between the use of inshore or offshore areas (Hobson et al. 1994), $\delta^{15}\text{N}$ reflects trophic level position, offering insights into prey–predator relationships (Fry 2006). Thus, the bi-plot of $\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$ results in a δ -space that represents the isotopic niche, which is a proxy for the trophic niche (Newsome et al. 2007, Jackson et al. 2011).

2.4. Statistical analysis

Isotopic niche position, niche width, and niche overlap were compared across 3 approaches: (1) MB seasonal comparisons (breeding [April] vs. non-breeding [September]) over years; (2) RFB seasonal comparisons (breeding [September] vs. non-breeding [April]) over years; and (3) interspecific comparisons between MBs and RFBs in April and September over years. For the latter, data from April 2017 and 2018 were excluded, as RFBs were not sampled. Sexual differences in isotopic values for MBs in Fernando de Noronha were previously shown to be non-significant in the breeding season (April) using the same data set (Jacoby et al. 2025). To ensure consistency, we additionally tested for sex differences during non-breeding periods using the Mann-Whitney test (see Text S1 at www.int-res.com/articles/suppl/meps15232_supp.pdf). As sex was not determined for RFBs, no sex-based analyses were performed for this species. All statistical analyses were performed in R (v.4.5.1; R Core Team 2025).

Differences in niche position were examined using multivariate and univariate analysis (Hammerschlag-Peyer et al. 2011). Variations in bivariate niche position ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) were assessed by calculating mean Euclidean distance (straight-line distance between 2 points) between the centroids (mean values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of each sampling event (month/year; Layman et al. 2007). Niche positions were considered to be different when the observed Euclidean distance between 2 centroids exceeded the 95th percentile of a null distribution generated via residual permutation procedures (Turner et al. 2010). Univariate differences of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for MBs and RFBs separately between sampling events were assessed using the Kruskal-Wallis test, followed by Dunn's post hoc comparisons with the Holm correction to control for multiple testing (Holm 1979). Additionally, because some MB individuals were sampled more than once across years, we performed a sensitivity analysis to assess the potential influence of repeated individuals on comparisons between sampling events (see Text S1). Results were qualitatively consistent with those obtained using the full data set (see Table S1).

For the interspecific approach, linear mixed models (LMMs) were fitted for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, including species, month (April or September), and their interaction (species $\times$ month) as fixed effects, and year as a random intercept to account for potential interannual variability. Individual identity (ring code) was initially included as a random intercept to account for potential repeated sampling of individuals; however, because this term explained negligible variance (1 resampled individual) and did not improve model fit, it was removed from the final models. Term significance was assessed with type III likelihood ratio tests using the 'anova()' function from the 'car' package (v.3.1.1-5; Fox & Weisberg 2019). Post hoc pairwise comparisons between species in each month were performed using the 'emmeans' package (v.1.11.2-8; Lenth 2025). Furthermore, to explicitly test for pairwise differences among specific sampling events, separate linear models were fitted, including sampling event (month/year) as a fixed effect. Term significance was assessed using type III likelihood ratio tests. Pairwise contrasts among sampling events were similarly estimated using the emmeans package (Lenth 2025).

Isotopic niche width is considered a proxy for the resources consumed and was calculated and compared between sampling events using 2 complementary approaches. First, we calculated the mean distance to centroid (MDC), which represents the average Euclidean distance from each individual sample to the cen-

troid of its respective sampling event. Niche widths were considered significantly different when the observed MDC was greater than expected under a null distribution generated by permutation (Turner et al. 2010). Second, we estimated Bayesian standard ellipse areas (SEA_B) using the 'SIBER' package (v.2.1.9; Jackson et al. 2011). Differences in niche width were assessed by estimating the posterior probability (PP) that the SEA_B of the first group was smaller than the second in pairwise comparisons, with values varying from 0 (no probability that the SEA_B from the first group is smaller than the second) to 1 (the SEA_B from the first group is smaller than the second). Significant differences were inferred when PP values were smaller than 0.05 or higher than 0.95.

Finally, we calculated isotopic niche overlap as a proxy for the similarity in resource use between sampling events, based on standard ellipse areas corrected for small sample sizes (SEA_C) using the 'maxLikOverlap()' function from the SIBER package. Pairwise proportions of overlapping areas, representing the overall proportion of shared niche space, were calculated using Eq. (1):

$$\text{Total overlapped area} = \frac{\text{Overlapped area}}{(\text{Ellipse1 area} + \text{Ellipse2 area} - \text{Overlapped area})} \quad (1)$$

where values range from 0% (no overlap) to 100% (complete overlap).

In addition, the relative proportion of overlap was calculated for each ellipse using Eq. (2):

$$\text{Relative overlap}_i = \frac{\text{Overlapped area}}{\text{Ellipse}_i \text{ area}} \quad (2)$$

where i refers to each group in the pairwise comparison, with values ranging from 0% (no overlap) to 100% (complete overlap). Overlap values were interpreted following Schwartz-Narbonne et al. (2019) and Garcia-Quintas et al. (2024), with <30, 30–60%, and >60% considered as low, moderate, and high, respectively.

3. RESULTS

3.1. Seasonal differences for the MB

A total of 142 whole blood samples were obtained from MBs, including 97 from breeding seasons (April) and 45 from non-breeding seasons (September; Table 1). Niche position differed significantly across all sampling events ($p \leq 0.008$; Table S2). The $\delta^{15}\text{N}$ values varied significantly among sampling events

Table 1. Sample sizes (n), mean $\pm$ SD of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotopic values from blood samples of masked booby *Sula dactylatra* (MB) and red-footed booby *S. sula* (RFB) from the Fernando de Noronha Archipelago, Brazil, separated by sampling event (month and year). Mean distance to centroid (MDC) based on Euclidean distances from bivariate distributions of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and standard ellipse areas corrected for small sample sizes (SEA_C). CS: climatic season; D: dry; R: rainy; Se: season; Br: breeding; NBr: non-breeding

Sampling events	CS	MB						RFB					
		Se	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	MDC	SEA_C	Se	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	MDC	SEA_C
Sep 2015	D	NBr	8	-17.41 ± 0.41	11.49 ± 0.23	0.39	1.93	Br	10	-18.11 ± 0.21	10.96 ± 0.18	0.24	0.79
Sep 2016	D	NBr	22	-17.03 ± 0.13	11.44 ± 0.20	0.21	0.48	Br	29	-17.39 ± 0.18	10.97 ± 0.20	0.21	0.53
Apr 2017	R	Br	30	-16.60 ± 0.08	10.38 ± 0.21	0.18	0.34	—	—	—	—	—	—
Apr 2018	R	Br	34	-16.95 ± 0.15	10.60 ± 0.25	0.26	0.76	—	—	—	—	—	—
Sep 2018	D	NBr	15	-17.00 ± 0.15	11.24 ± 0.21	0.21	0.53	Br	17	-17.45 ± 0.16	10.56 ± 0.19	0.21	0.46
Apr 2019	R	Br	12	-16.66 ± 0.09	10.89 ± 0.30	0.22	0.45	NBr	4	-16.98 ± 0.06	10.36 ± 0.07	0.08	0.12
Apr 2022	R	Br	21	-17.65 ± 0.10	10.82 ± 0.20	0.17	0.36	NBr	6	-17.92 ± 0.03	10.28 ± 0.19	0.15	0.12

(Kruskal-Wallis test, $\chi^2 = 104.87$, $df = 6$, $p < 0.001$), with post hoc pairwise differences indicating significantly lower values in April compared to September sampling events (Fig. 2a; Table S2), with a few exceptions for April 2019 vs. September 2015 ($p = 0.111$), April 2019 vs. September 2018 ($p = 0.326$), and April 2022 vs. September 2018 ($p = 0.099$; Table S2). The $\delta^{13}\text{C}$ values also differed significantly between sampling events (Kruskal-Wallis test, $\chi^2 = 112$, $df = 6$, $p < 0.001$), with most post hoc pairwise comparisons showing higher values in April than in September (Fig. 2a; Table S2). Exceptions included April 2018 vs. September 2015 ($p = 0.113$), April 2018 vs. September 2016 ($p = 1.000$), and April 2018 vs. September 2018 ($p = 1.000$; Table S2). Notably, April 2022 exhibited significantly lower $\delta^{13}\text{C}$ values compared to all other sampling events, except September 2015 ($p = 1.000$; Table S2). Sexual differences during the non-breeding period were found only in September 2016 for $\delta^{13}\text{C}$ (Mann-Whitney $U = 93.00$, $p = 0.008$) and September 2018 for $\delta^{15}\text{N}$ ($U = 31.00$, $p = 0.008$; Table S3). Given these results, sex was not included as a factor in subsequent analyses.

The niche width from September 2015 differed significantly from all other sampling events based on MDC measures ($p \leq 0.024$; Table S2), and also showed a broader isotopic niche area than all other sampling events ($PP < 0.05$ or $PP > 0.95$), based on SEA_B estimates (Table S2). Most total isotopic niche overlap between sampling events was low, with only a moderate overlap observed between September 2016 and 2018 (47.38%; Fig. 3a; Table S4). Relative niche overlap was considered high only among non-breeding periods: September 2016 overlapped 100% with September 2015 and 67.59% with September 2018, which, in turn, overlapped 88.27 and 61.31 % with September 2015 and 2016, respectively (Table S4).

3.2. Seasonal differences for the RFB

A total of 66 RFB samples were analyzed, including 56 from breeding seasons (September) and 10 from non-breeding seasons (April; Table 1). The low sample size for RFBs in April reflects the difficulty in capturing individuals during the non-breeding season, as their arboreal roosting behavior limits accessibility compared to the breeding period. Bivariate niche position differed significantly across all sampling events ($p = 0.001$; Table S2). The $\delta^{13}\text{C}$ values varied significantly among sampling events (Kruskal-Wallis test, $\chi^2 = 41.60$, $df = 4$, $p < 0.001$; Fig. 2b), with pairwise comparisons indicating significant differences in April 2019 vs. September 2015 ($p < 0.001$), April 2019 vs. September 2018 ($p = 0.028$), and April 2022 vs. September 2016 ($p = 0.003$; Table S2). Values of $\delta^{15}\text{N}$ also differed significantly across sampling events (Kruskal-Wallis test, $\chi^2 = 42.05$, $df = 4$, $p < 0.001$), with pairwise differences observed between all breeding and non-breeding sampling events, except for the comparisons of April 2019 vs. September 2018 ($p = 1.000$), April 2019 vs. April 2022 ($p = 1.000$), and April 2022 vs. September 2018 ($p = 0.682$; Table S2).

Based on MDC measures, niche width differences were only marginally significant between September 2015 and April 2019 ($p = 0.054$; Table S2). However, SEA_B estimates indicated that September 2015 had a broader isotopic niche compared to April 2019 ($PP = 1$) and April 2022 ($PP = 1$; Table S2). Additionally, SEA_B values from September 2016 and September 2018 were larger than those from both April sampling events ($PP > 0.99$; Table S2). Total and relative isotopic niche overlap were mostly low, with moderate relative overlap observed only between September 2016 and 2018 (36.21%), and between September 2018 and September 2016 (41.96%; Fig. 3b; Table S4).

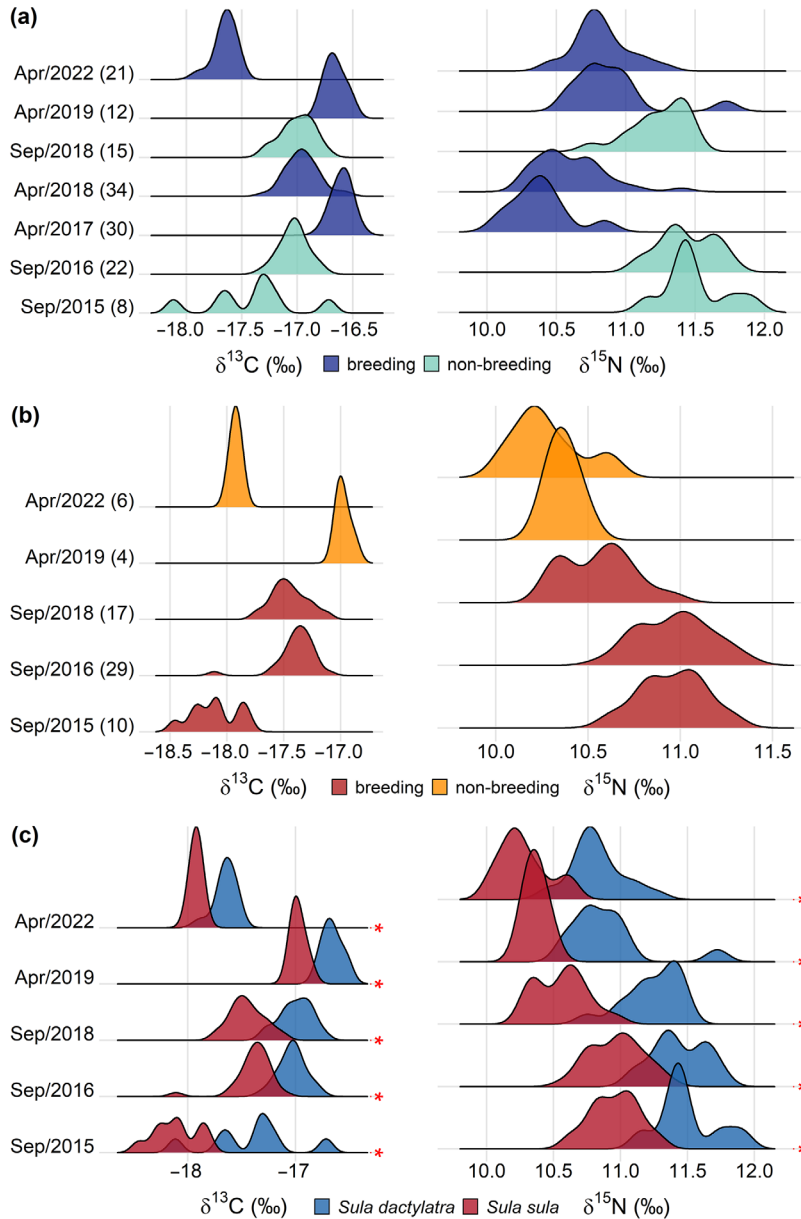


Fig. 2. Variations in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from blood samples of (a) masked boobies *Sula dactylatra* during breeding and non-breeding periods (month/year); (b) red-footed boobies *S. sula* during breeding and non-breeding periods; and (c) both species in each sampling event (month/year) in the Fernando de Noronha Archipelago, Brazil. Sample sizes for each sampling event are shown in parentheses. Red asterisks: significant differences between species in each sampling event based on linear models

3.3. Interspecific niches

A total of 144 samples were analyzed, including 78 from MBs and 66 from RFBs (Table 1). The following results refer to sampling events in which both species were sampled. Niche position differed significantly

between species, based on comparisons of mean centroids ($p = 0.001$; Table 2). The type III ANOVA for the LMM including year as a random intercept for $\delta^{15}\text{N}$ values indicated a significant effect of species ($F_{1,137.08} = 157.69$, $p < 0.001$) and month (April/September, $F_{1,3.22} = 12.99$, $p = 0.033$), while the interaction between these 2 factors was not significant ($F_{1,137.08} = 0.01$, $p = 0.905$; Table 3). Pairwise comparisons showed that MBs had higher $\delta^{15}\text{N}$ values than RFBs in both September and April ($p < 0.001$; Table 3). For $\delta^{13}\text{C}$, significant effects were found for species ($F_{1,136.99} = 103.79$, $p < 0.001$) and the interaction between species and month ($F_{1,136.99} = 4.83$, $p = 0.029$; Table 3). Month alone did not influence mean values ($F_{1,3.01} = 0.05$, $p = 0.083$). Pairwise comparisons showed that $\delta^{13}\text{C}$ values were significantly higher in MBs than in RFBs in both months ($p < 0.001$), with a larger difference observed in September (Table 3). The exploratory linear model treating sampling event as a fixed factor indicated significant differences between species in all sampling events, with higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in MB blood compared to RFB blood ($p \leq 0.002$; Fig. 2c; Table S5).

Niche width, based on MDC, differed significantly between species only in September 2015 ($p < 0.043$; Table 2). However, based on SEA_B ellipses, beyond September 2015 ($PP = 0.03$), MBs also exhibited broader isotopic niches than RFBs in April 2019 ($PP = 0.01$) and April 2022 ($PP = 0.01$; Table 2). Total and relative isotopic niche overlap between species was consistently low across all sampling events ($< 30\%$) (Table 2; Fig. 3c).

4. DISCUSSION

This study revealed a trophic niche partitioning mechanism between 2 sympatric and closely related seabird species breeding on a tropical Atlantic Ocean archipelago. We found consistently low isotopic niche

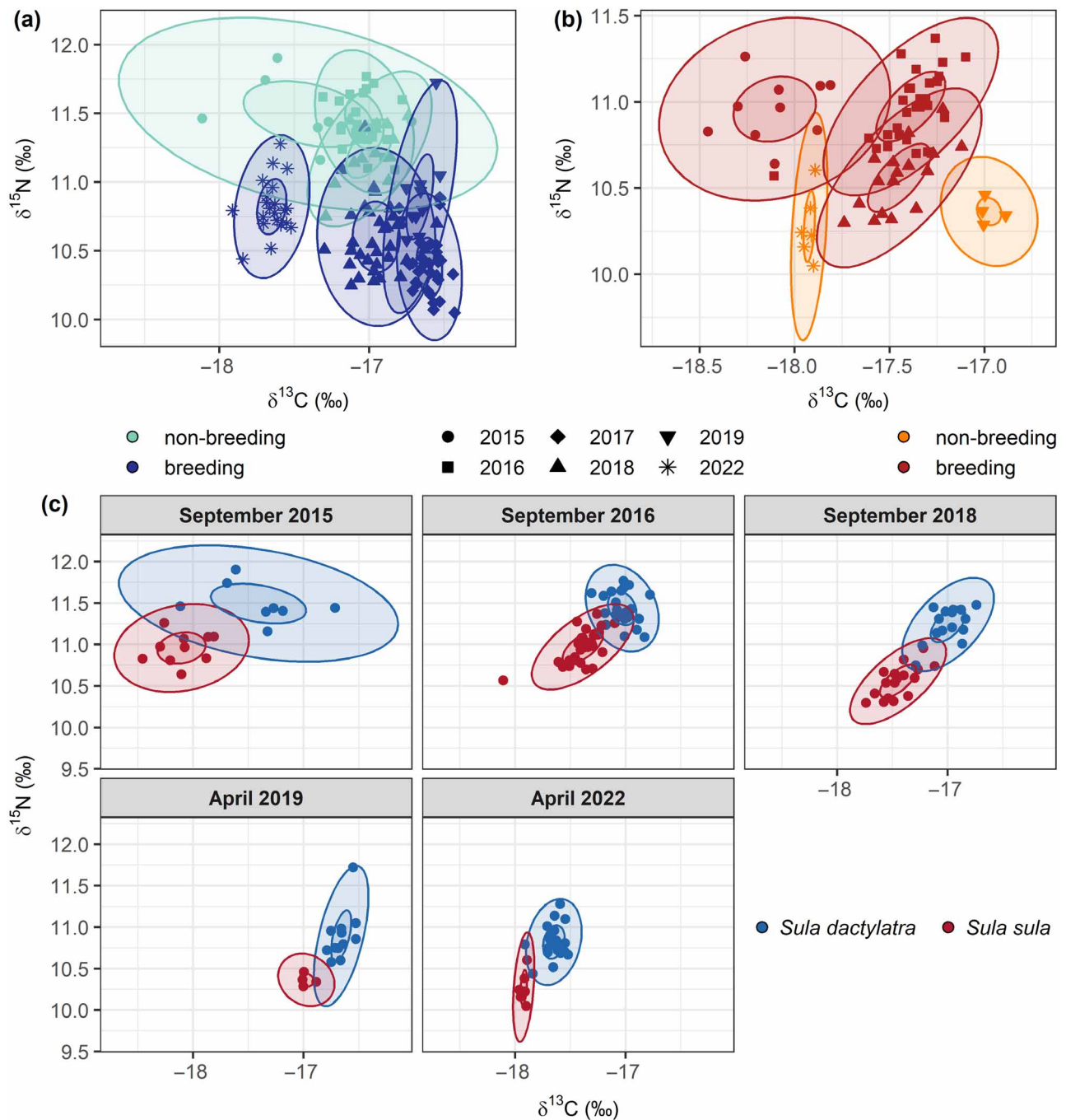


Fig. 3. Isotopic niche ellipses based on carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) values from blood samples of (a) masked boobies *Sula dactylatra* and (b) red-footed boobies *S. sula* during breeding and non-breeding seasons over years; and (c) both species in each sampling event (month/year). Ellipses encompass 40% (inner) and 95% (outer) of the data

overlap between species over seasons (September–April), suggesting that niche segregation plays a key role in facilitating year-round coexistence. This segregation was consistent across sampling events (month/year), despite interannual and intra-annual variations in isotopic values, which are potentially related to the

environmental dynamics of the archipelago. As expected, MBs had higher $\delta^{15}\text{N}$ values than RFBs, but also higher $\delta^{13}\text{C}$ values, likely reflecting the larger body size and mass that drive distinct foraging strategies. Unexpectedly, the MB niche width remained relatively stable between breeding and non-breeding

Table 2. Isotopic niche metrics based on carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) values from samples of masked booby *Sula dactylatra* (MB) and red-footed booby *S. sula* (RFB) from Fernando de Noronha Archipelago, Brazil. Niche position (NP) and Mean Distance to Centroid (MDC) differences (dif) between species were considered significant when exceeding values expected under a null distribution ($p < 0.05$). Posterior Probabilities (PP) indicate the probability (0 to 1) that the Bayesian standard ellipse area of the MB is smaller than that of the RFB. Niche overlap was calculated based on standard ellipse area corrected for small sample sizes, and includes the overlap of total area, representing the overall proportion of shared niche space between species in each sampling event, and the relative overlap, representing the proportion of shared niche space for each species niche. Overlap values <30 , $30\text{--}60$, and $>60\%$ were considered low, moderate, and high, respectively

Species MB vs. RFB	NP		MDC		PP	Overlap of total area (%)	Relative overlap (%)	
	dif	p	dif	p			MB	RFB
Sep 2015	0.88	0.001	0.14	0.043	0.03	7.42	9.74	23.69
Sep 2016	0.59	0.001	0.00	0.901	0.68	14.66	27.03	24.25
Sep 2018	0.82	0.001	0.00	0.995	0.38	10.22	17.36	19.90
Apr 2019	0.61	0.001	0.14	0.100	0.01	3.45	4.21	16.08
Apr 2022	0.61	0.001	0.03	0.717	0.01	1.93	2.52	7.58

periods, despite the release of chick-rearing demands. By contrast, RFBs exhibited an unexpectedly larger isotopic niche during the breeding period than during the non-breeding period, suggesting shifts in foraging strategies or, ultimately, in interspecific pressures.

The low trophic niche overlap observed between species can be driven by multiple additive factors. MBs showed a higher trophic position than RFBs across all compared periods, a pattern primarily at-

tributed to species-specific morphological traits. Trophic position is often strongly correlated with body size, as larger individuals can exploit a broader diversity and size range of prey (Mancini et al. 2014, Petalas et al. 2021). Specifically, the MB has a body mass up to twice that of the RFB, the smallest species in the *Sula* genus (Nelson 1978, Young et al. 2010b). Such disparity is reflected in the higher $\delta^{15}\text{N}$ values observed in MBs compared to RFBs, consistent with previous studies (e.g. Young et al. 2010b, Mancini et al. 2014, Lerma et al. 2024). Furthermore, the larger body size of MBs enables deeper dives, granting access to a comparatively wider array of prey types and sizes (Schreiber & Hensley 1976, Zavala et al. 2007, Kappes et al. 2011).

Altogether, these findings reinforce the role of morphological traits in shaping foraging strategies and contributing to niche segregation among ecologically similar seabird species (Mancini et al. 2014, Petalas et al. 2024).

Differences in foraging strategies and diet composition can also contribute to the low isotopic niche overlap. Spatial segregation is a widespread mechanism used by sympatric seabirds to minimize resource competition (Navarro et al. 2013, Austin et al.

Table 3. Results of linear mixed models evaluating the effects of species, month (April or September), and their interaction on carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) values from blood samples of masked booby *Sula dactylatra* (MB) and red-footed booby *S. sula* (RFB) from Fernando de Noronha Archipelago, Brazil. Models included year as a random intercept to account for inter-annual variability. Pairwise comparisons between species within each month were performed using estimated marginal means

Effect	$\delta^{13}\text{C}$					$\delta^{15}\text{N}$				
	Estimate	SE	df	t	p	Estimate	SE	df	t	p
Fixed effects										
(Intercept)	-17.16	0.34	3.01	-50.68	<0.001	10.86	0.11	3.32	95.85	<0.001
Species (RFB)	-0.29	0.06	137.00	-4.57	<0.001	-0.54	0.08	137.08	-7.11	<0.001
Month (September)	-0.02	0.44	3.02	-0.04	0.971	0.53	0.15	3.36	3.69	0.031
Species $\times$ month	-0.16	0.07	137.00	-2.20	0.030	-0.01	0.09	137.08	-0.12	0.905
Group	Variance	SD				Variance	SD			
Random effects										
Year (Intercept)	0.23	0.48				0.02	0.15			
Residuals	0.03	0.17				0.04	0.21			
Contrast	Estimate	SE	df	t	p	Estimate	SE	df	t	p
Pairwise comparisons										
April (MB $\times$ RFB)	0.29	0.06	137.00	4.57	<0.001	0.54	0.08	137.00	7.11	<0.001
September (MB $\times$ RFB)	0.45	0.04	131.00	12.46	<0.001	0.55	0.04	137.00	13.07	<0.001

2021, Fayet et al. 2023). The consistently lower $\delta^{13}\text{C}$ values in RFBs compared to MBs across all periods suggest that RFBs forage in more oceanic waters, where $\delta^{13}\text{C}$ values are typically low (Cherel & Hobson 2007, Mancini & Bugoni 2014), a pattern well documented in multiple RFB colonies (e.g. Young et al. 2010b, Kappes et al. 2011, Mendez et al. 2017, Almeida et al. 2021). However, while a similar pattern may occur in Fernando de Noronha, caution is warranted, as body size differences between species may significantly influence carbon signatures (Mancini et al. 2014), rather than strictly representing spatial variations. Tracking data for RFBs in the archipelago are still needed to confirm these spatial patterns. Beyond spatial distribution, dietary differences likely play a role in niche segregation. RFB diets often include a higher proportion of squid compared to their congeners (Kappes et al. 2011, Almeida et al. 2021, Lerma et al. 2024), although this is not consistent across all sites (Harrison et al. 1983, Weimerskirch et al. 2006, Young et al. 2010b). While the current methodology cannot determine whether RFBs preferentially consume squid or epipelagic fish, especially given the overlapping $\delta^{15}\text{N}$ values of prey, such as flying fish ($-9.3 \pm 1.2\text{‰}$; Jacoby et al. 2025) and squid ($-9.1 \pm 0.8\text{‰}$; Eduardo et al. 2023), the clear segregation of isotopic niches strongly indicates differences in trophic level or size of prey consumed (Mancini et al. 2014). Therefore, the adoption of distinct foraging strategies likely contributes to trophic niche segregation and facilitates species coexistence.

Contrary to the expectation that central-place foraging constraints would lead to narrower niches during breeding (e.g. Lisnizer & Yorio 2019, Tocker et al. 2023), our findings revealed distinct and unexpected patterns for both species. The relatively stable isotopic niche area of the MB between breeding (April) and non-breeding (September) periods differed from patterns observed in other colonies and booby species (Lerma et al. 2024, Appoo et al. 2026). This stability is noteworthy, as MB individuals tracked in the archipelago increased their trip distances from the colony from ~ 60 km during breeding (Jacoby et al. 2025) to 100–300 km during non-breeding periods (Roy et al. 2021). This expansion in foraging range, however, did not markedly affect niche width or $\delta^{13}\text{C}$ values, suggesting either a lack of predictable, localized prey patches or an absence of significant horizontal carbon baseline variations around the archipelago (Mancini et al. 2014, Magozzi et al. 2017). By contrast, RFBs exhibited a broader niche during breeding (September) compared to the non-breeding period (April). This pattern may reflect a broader

range of foraging areas and an opportunistic diet to meet chick-rearing demands (Cerveira et al. 2020), particularly as the dry season (September) presents lower biological productivity than the rainy season (April) in the archipelago (Silva et al. 2021, Farias et al. 2022). Ultimately, we hypothesize that interspecific competition may also contribute to the opposite pattern observed in RFBs. MBs intensify resource exploitation in April during the breeding peak, potentially restricting the niche of the RFB even during the latter's non-breeding period. This interaction is likely enhanced by the larger body size of MB individuals, which confers competitive advantages over RFBs in resource use (Kappes et al. 2011). Conversely, in September, the reduced pressure from MBs during the non-breeding period may allow for an expansion of the ecological niche of RFBs (Herrmann et al. 2021).

Seasonal and interannual variations may also influence isotopic signatures and foraging dynamics. Both species exhibited higher $\delta^{15}\text{N}$ values in September compared to April. April coincides with the rainy season (March–July), when a shallower thermocline and the intensification of the Central South Equatorial Current (cSEC), a driver of the island mass effect in the archipelago, contribute to increased local productivity and plankton biomass (Campelo et al. 2018, Silva et al. 2021, Farias et al. 2022). Differences in productivity between rainy and dry seasons can influence $\delta^{15}\text{N}$ baseline values, given multiple factors such as freshwater inputs, guano runoff, and nitrogen sources in the system (Dorado et al. 2012, McMahon et al. 2013, Campelo et al. 2018). As the distribution and diversity of fish around the archipelago remain relatively stable throughout the year (Salvetat et al. 2022), the seasonal differences in $\delta^{15}\text{N}$ values of both species likely reflect baseline shifts rather than actual changes in foraging strategies.

Beyond seasonal patterns, marked interannual variations were observed in both species, reflecting spatiotemporal complexities that can also influence isotopic baseline values (MacKenzie et al. 2019). While local SST and other environmental conditions remain relatively stable interannually (Assunção et al. 2016, 2020), large-scale climatic events, such as El Niño–Southern Oscillation (ENSO), can weaken zonal winds and cSEC velocity, significantly reducing primary productivity around Fernando de Noronha (Campelo et al. 2019). Establishing direct correlations remains challenging due to the limited availability of long-term, high-resolution oceanographic and climatic data at the specific spatiotemporal scales required to detect corresponding isotopic responses. Yet large- or small-scale dynamics can alter isotopic

baselines across the complex trophic web of Fernando de Noronha (Eduardo et al. 2023) or even influence prey availability and distribution. This was evidenced by the transition in the diet of the MB from flying fish *Hirundichthys affinis* to false herring *Harengula clu-peola* in 2022, associated with foraging closer to the colony (Jacoby et al. 2025). Despite such variability, the consistently low isotopic niche overlap between MBs and RFBs across years reinforces the robustness of their trophic segregation, supporting previous findings (Mancini et al. 2014).

Small sample sizes can introduce bias in stable isotope analysis, but it can be partially compensated for by statistical approaches and sampling methods. Univariate and multivariate analyses of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and frequentist measures of isotopic niche width (e.g. MDC) can be sensitive to sample sizes, which may influence niche width estimations, such as the lower niche width in the non-breeding period observed for RFBs in April 2019 ($n = 4$) and April 2022 ($n = 6$). However, this issue is minimized by corrections (i.e. SEA_C) or the Bayesian approach (i.e. SEA_B), which are less sensitive to sample size, allowing reliable results even for RFBs during the non-breeding period (Jackson et al. 2011). Despite limited sample sizes, our methodology offers key advantages. First, unlike most studies that infer non-breeding diet from feathers collected during the breeding season, our study includes whole blood samples from both seasons. Blood reflects recent dietary intake (~ 3 wk), offering a finer temporal resolution and reducing uncertainty in isotopic interpretation (Cherel et al. 2014b, Navarro et al. 2015, Petalas et al. 2024). Second, while most booby studies rely on feathers to characterize food resource use in the non-breeding season (e.g. Young et al. 2010a, Pontón-Cevallos et al. 2017, Lerma et al. 2024), feathers only represent the dietary intake from the specific period when they were synthesized, as they become metabolically inert once fully formed (Hobson & Clark 1992). In sulids, feathers can be molted even during the breeding season (Nelson 1978, Grace et al. 2020, authors' unpubl. data). Therefore, using whole-blood samples to represent the non-breeding period in stable isotope analysis offers a more temporally accurate representation of the specific periods sampled, enhancing the reliability of isotopic interpretations, even when sample sizes are limited.

This study highlights the outcome of a local adaptation process that enables the coexistence of 2 species with similar ecological requirements in tropical environments. The consistent segregation patterns observed over seasons and years, combined with the

atypical seasonal shifts in RFB niche width, raise questions regarding the interplay between life-history traits and niche partitioning. Specifically, the relationship between these ecological patterns and the asynchronous breeding peaks observed in the archipelago remains to be further elucidated: MBs from March to May (ICMBio 2022), RFBs from July to September (Santos et al. 2024), and brown boobies from November to January (Silva 2008). We tentatively hypothesize that these distinct phenologies may be coupled with a competitive hierarchy, where the MB, as a larger and potentially dominant species, occupies a breeding window aligned with periods of higher resource availability (Campelo et al. 2018, Farias et al. 2022). Such dynamics underscore the plasticity of seabirds in modulating both trophic and breeding strategies to facilitate coexistence (Soanes et al. 2021, Fromant et al. 2022). However, a comprehensive understanding of this seabird assemblage, including the brown booby (which was not examined in the present study), requires long-term, community-level studies integrating complementary approaches, such as breeding monitoring, diet analysis, and tracking data across multiple colonies in the archipelago. Such approaches would be especially valuable in the context of climate change, as seasonal and interannual variability in oceanographic processes (e.g. SST, precipitation, current intensities) may trigger cascading effects on the trophic web and interspecific interactions. Seabirds remain outstanding models for studying niche segregation, as their ecological strategies span multiple spatial, temporal, and trophic dimensions (Petalas et al. 2024). In tropical oceanic regions, where oligotrophic conditions challenge population persistence and species coexistence, understanding these ecological relationships within trophic networks is essential to shed light on the processes that promote and sustain biodiversity.

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