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# Role of environmental factors in the genetic structure of a highly mobile seabird

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## Abstract

**Aim:** Environmental features can act as selection pressures and barriers to gene flow between populations. The genetic structuring of highly mobile but philopatric seabirds creates a paradox, and the role of oceanographic and geographic variables is still poorly understood. In this study, we investigate the influence of environmental and geographic variables in the genetic and phenotypic diversity of a pantropical seabird breeding in islands and archipelagos separated by different geographic distances, up to thousand kilometres, and which differ in environmental characteristics.

**Location:** Islands and archipelagos in the southwestern (SW) Atlantic Ocean.

**Taxon:** *Sula dactylatra*, Lesson, 1831 (masked booby).

**Methods:** The population structure of the species was accessed through mitochondrial and nuclear DNA. To test Isolation by Environment (IBE) versus by Distance (IBD), sea surface temperature, primary productivity and salinity, as well as isotopic niche based on carbon and nitrogen, and distances between colonies and from the continent, were used. We also tested the correlation between the genetic structure and the morphometry of individuals in each colony.

**Results:** We uncover the presence of low genetic structure between populations. Nevertheless, differences were identified between inshore and offshore colonies, with the influence of landscape characteristics of these two types of environment. The morphometric and isotopic niche variations are consistent with this segregation.

**Main Conclusions:** Environmental variables of coastal and oceanic environments seem to influence the genetic structure of masked boobies, even though it is low in the SW Atlantic Ocean, highlighting the role of environmental heterogeneity in shaping biodiversity.

KEYWORDS
isolation by environment, marine biogeography, masked boobies, mitochondrial DNA, morphometry, single-nucleotide polymorphism, *Sula dactylatra*, ultraconserved elements

## 1 | INTRODUCTION

Different environmental features influence biodiversity patterns, which can be shaped by microevolutionary processes related to selection pressures on populations (Richardson et al., 2014). These pressures can interfere on the gene flow and the connectivity of populations, which can be related to the geographic distance between them (Isolation by Distance–IBD; Wright, 1943), especially when it is greater than the mobility and organisms' dispersal ability, as reported for seagrass (Jahnke et al., 2019) and sea clams (Mao et al., 2011).

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However, the influence of IBD has already been observed for species with high displacement capacity, such as fish (Hirase et al., 2020). Genetic differentiation can also be related to the adaptation of individuals to environmental characteristics (Isolation by Environment–IBE; Wang & Bradburd, 2014), such as abiotic conditions, which was already evidenced for passerine birds (Manthey & Moyle, 2015) and cetaceans (Mendez et al., 2010); as well as differences in foraging and dispersal patterns, as identified for cetaceans (Monteiro et al., 2015) and seabirds (Burg & Croxall, 2001; Jacoby et al., 2023). Moreover, populations are under the action of stochastic (e.g. genetic drift) and deterministic (e.g. natural selection) events (Griffiths, 2013) and the influence of historical factors is relevant to understanding population structure (Lombal et al., 2020). Thereby, a complex gradient of features can influence the population structure of animals, as has already been demonstrated for seabirds (Friesen, 2015), marine mammals (Ansmann et al., 2012), and sea turtles (Bowen & Karl, 2007).

Molecular markers, such as mitochondrial DNA (mtDNA) and Ultraconserved Elements (UCEs) of nuclear DNA, can be used to assess interpopulation variation and detect genetic structure (e.g. Zarza et al., 2018). MtDNA does not undergo recombination and has a high mutation rate (Lynch, 2007). In addition to maternal inheritance, mtDNA represents a single genetic locus (Moore, 1995). On the other hand, UCEs are present in high quantities in the genome and have biparental inheritance (Stephen et al., 2008). UCEs represent a highly conserved multi-locus marker but have low levels of purifying selection in their flanking regions, which allows the detection of single-nucleotide polymorphisms (SNPs) (Byerly et al., 2023). Using both mitochondrial and nuclear markers, it is possible to infer population divergence, as well as the role of landscape features in promoting structuring among populations (e.g. Faria et al., 2007) of a wide range of organisms.

Seabirds have high mobility but are mostly philopatric (Schreiber & Burger, 2001). They usually breed on islands, which are environments with unique characteristics. As seabirds spend long periods associated with these ecosystems during their breeding periods (Schreiber & Burger, 2001), a relation between the genetic structure of the group and the variables to which they are exposed is expected (Friesen et al., 2007). Studies have already shown that environmental features (e.g. sea temperature, salinity, primary productivity; Hailer et al., 2011) may play a significant role in shaping populations of seabirds, as well as geographic (e.g. colony distances; Burg et al., 2003), and ecological features (Burg & Croxall, 2001). This last one can be evaluated by the isotopic niche of individuals, which is a proxy of the ecologic niche, and it is also related to primary productivity, seasonality, and complexity of the food web (Fry, 2006). Therefore, the genetic structure of seabird populations may be the result of different selective pressures that are exerted by different environments (Friesen, 2015).

The masked booby, *Sula dactylatra* (Suliformes), is a pelagic seabird with a pantropical distribution over all ocean basins (Steeves et al., 2005a). On the Atlantic Ocean, the species breeds in the Caribbean and the southern Atlantic Ocean (Harrison, 1985). In the southwest Atlantic Ocean (SW Atlantic Ocean), at Brazilian territorial waters, the species breeds in Fernando de Noronha and Abrolhos Archipelagos, Rocas Atoll, Trindade, and Martin Vaz Islands (Fonseca-Neto, 2004; Mancini et al., 2016). Variations in the isotopic niche of the species have already been reported between Brazilian colonies (Mancini et al., 2014). Complementarily, morphological differences, such as distinct morphometry among populations of the same oceanic basin, have already been described (Anderson, 1993; Pitman & Jehl Jr, 1998), but these studies do not test the correlation of the body traits with the diversity and genetic structure among populations. In addition, morphometric analyses were not performed for the different colonies of masked boobies in the Atlantic Ocean and the possible relationship between the morphometry and the genetics of the group has never been evaluated. However, it has already been detected in other seabirds in the Atlantic Ocean (Gómez-Díaz et al., 2009; Nunes & Bugoni, 2017).

These variations may be a result of the influence of non-physical barriers to gene flow, which is still poorly understood (Steeves et al., 2005b), although studies suggest that structuring is related to the local adaptation of individuals (Steeves et al., 2005a), as seen for other Suliformes in the Atlantic Ocean (Hailer et al., 2011; Nunes & Bugoni, 2017). Complementarily, Steeves et al. (2005a) observed low gene flow between masked booby colonies from Isla Monito (Caribe) and Boatswain Bird Island (Ascension), but the causes of differentiation remain unsolved. Despite this, long displacements can be performed by masked boobies, with records of juveniles found in the South American continent, more than ~2000 km from Abrolhos, where they were banded (Efe et al., 2006). Thus, the species is considered wanderer, mainly with juveniles travelling long geographic distances (Anderson, 1993), while adults remain near breeding sites throughout the year (Roy et al., 2021). Determining the genetic structure of masked boobies in the SW Atlantic Ocean and identifying factors related to such structure is relevant to understanding the configuration of populations within this ocean basin and how this species will respond to environmental variations, such as climate change (Orsini et al., 2013).

Here, we investigated the role of environmental, geographic, and ecological variables on the genetic and phenotypic diversity of masked boobies in the SW Atlantic Ocean. We analysed the genetic structure using mitochondrial and nuclear markers; evaluated the contribution of environmental, geographic and ecological factors to the genetic structure; and correlated the morphometric variations with the genetic variability of the species. We hypothesized that: (i) genetic structure among populations of masked boobies in the SW Atlantic Ocean is best explained by IBE, and (ii) phenotypic variation between populations is compatible with the genetic structure of the species.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area and taxon sampling

The five masked booby colonies on SW Atlantic Ocean are located from 3° S to 20° S (Figure 1). They are between 65 km (Abrolhos) and 1188 km (Martin Vaz) from the South American mainland, and the distance between colonies varies from 49 km (between Trindade and Martin Vaz) to 1930 km (between Rocas and Martin Vaz). The

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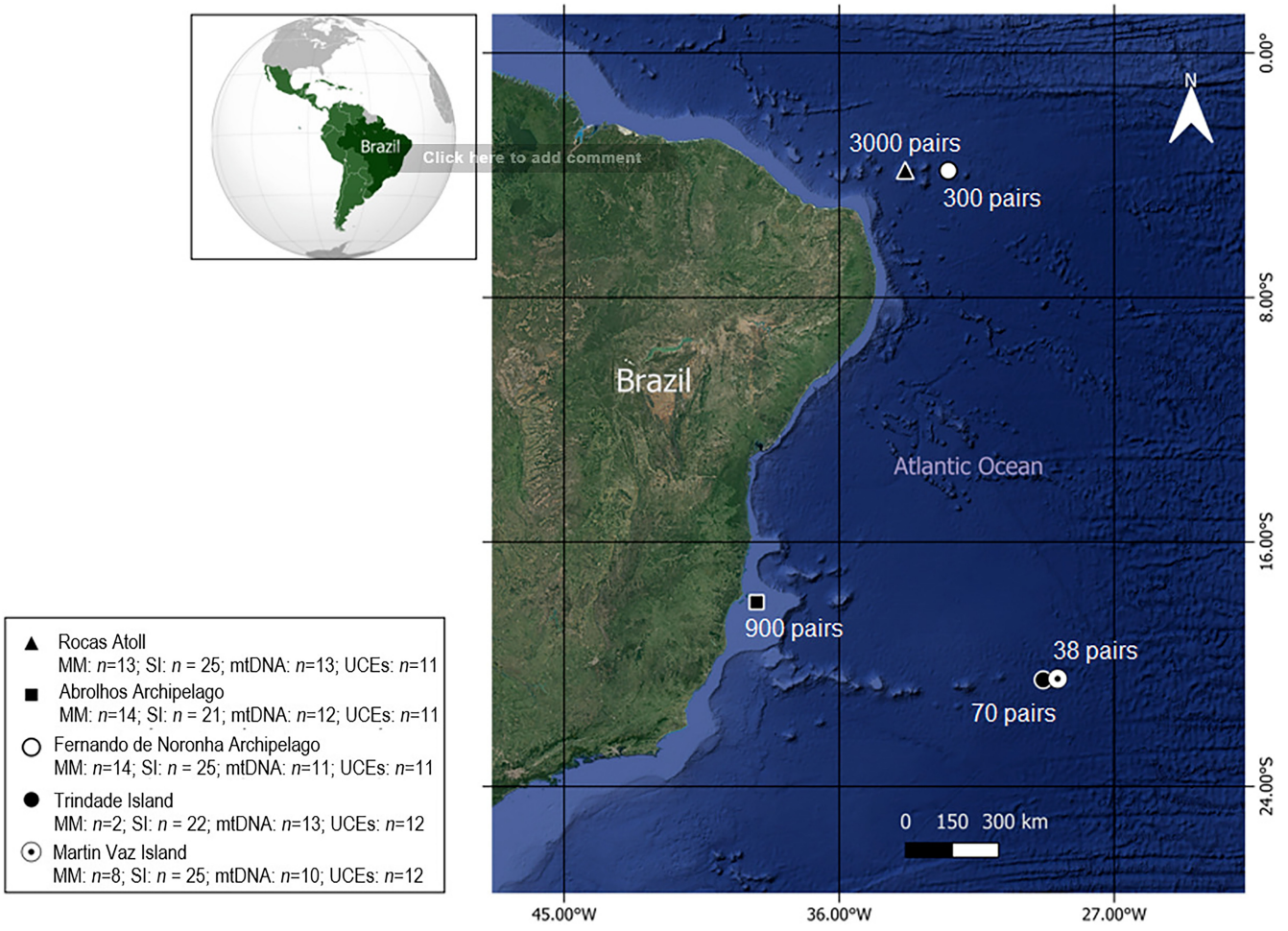


**FIGURE 1** Breeding sites of masked booby, *Sula dactylatra*, in the southwest Atlantic Ocean: Rocas Atoll, Fernando de Noronha and Abrolhos Archipelagos, Trindade Island, and Martin Vaz Island. The number of individuals that compose each of the analyses is mentioned. MM, morphometric measures; SI, stable isotopes; mtDNA, mitochondrial DNA; UCEs, ultraconserved elements of the genome.

oceanographic dynamic around each location is variable, influencing environmental characteristics (Peterson & Stramma, 1991). The largest colony is located at Rocas (3000 pairs), followed by Abrolhos (900 pairs), Fernando de Noronha (300 pairs), Trindade (70 pairs), and Martin Vaz (38 pairs) (Fonseca-Neto, 2004; Mancini et al., 2016).

Adult breeding masked boobies were captured in their nests from 2006 to 2012 and 2022. Blood samples were collected ($n = 122$) and, between 2006 and 2012, a drop of blood was also placed on FTA® cards for sexing (Mancini et al., 2013). Four body measurements were taken: culmen and tarsus lengths with a calliper, wing chord with a metal ruler, and body mass with a spring scale. Birds were individually banded to avoid resampling and released on the nest. Details of the ring number and data obtained of each individual are available in Supporting Information 1.1.

## 2.2 | DNA extraction and sexing

DNA was extracted from blood samples ($n = 122$) with the DNeasy Blood & Tissue QIAGEN® kit, following the manufacturer's protocol, and all samples were quantified with a Qubit Invitrogen fluorometer. For sex determination ($n = 23$), we used the CHD genes through PCR amplification following Griffiths et al. (1996). Mancini et al. (2013) previously carried out the sexing of the other 72 samples using the same protocol. The sex of 27 individuals could not be determined, but they were kept as 'undetermined sex' in the analyses in which the sex identification was irrelevant.

## 2.3 | Amplification and analysis of mitochondrial markers

Fragments of the control region (CR) and cytochrome *b* (CYTB) were amplified. Primers, the whole PCR protocol, and sequencing information are available in Supporting Information 1.2. The resulting chromatograms of Sanger sequencing were filtered with Chromas 2.6.6 (available at technelysium.com.au/wp/chromas), and viable sequences (CR, $n = 95$; CYTB, $n = 75$) were aligned in MEGA v. 11 (Tamura et al., 2021) with MUSCLE algorithm. Individuals whose sequencing of both mitochondrial regions was satisfactory

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($n=59$) had their sequences concatenated with the 'ape' package (Paradis & Schliep, 2019) in R (R Core Team, 2023). The use of both sequences concatenated allowed uncovering more genetic variation. All sequences obtained were deposited in GenBank (numbers PP767486-PP767580 for CR sequences and PP767581-PP767655 for CYTB sequences).

Arlequin 3.5.2.2 (Excoffier & Lischer, 2010) was used to calculate nucleotide ($\pi$) and haplotype ($h$) diversity (Nei, 1987); neutrality indexes of Tajima's $D$ (Tajima, 1989) and Fu's $Fs$ (Fu, 1997); and AMOVA to identify the $F_{ST}$ fixation index with a distance matrix (default) with Holm-Bonferroni corrections for multiple comparisons. Haplotypes were generated using DnaSP v. 6 (Rozas et al., 2017) and the haplotype network analysis was performed using the *median-joining* method (Bandelt et al., 1999) with Network 10.2.0.0 – Phylogenetic Network Software (available at fluxus-engineering.com/sharenet.htm). BEAST v. 1.10.4 (Suchard et al., 2018) was used to estimate a time-calibrated tree genealogy for mtDNA lineages. All analyses were performed assuming a strict molecular clock (Garcia-Moreno, 2004), and two independent runs were carried out and combined in TRACER v. 1.7.1 (Rambaut et al., 2018). Details of the analysis are available in Supporting Information 1.3.

## 2.4 | Bioinformatics pipeline for variant calling of UCEs

The capture sequencing of UCEs ($n=57$) was carried out using the *tetrapod2.5k* probe with 2 million readings per sample. Data preparation followed a protocol adapted from Faircloth et al. (2012), using the 'trimmomatic' package (Bolger et al., 2014), through illumiprocessor (Faircloth, 2013) to process the readings performed by the Illumina platform. 'Phyluce' was used (Faircloth, 2015) to assemble contigs, identify UCEs and align sequences. Non-autosomal UCE loci were removed with BLAST+ (Camacho et al., 2009). Packages 'BWA' (Li & Durbin, 2009) and 'SAMtools' (Danecek et al., 2011) were used to index the reference sequence output and sort bam files for each individual through the GNU parallel tool (Tange, 2018). MarkDuplicatesSpark was used with duplicates, and to perform haplotype calling with HaplotypeCaller (Poplin et al., 2017). The longest sequence obtained was used as a reference in the Genome Analysis Toolkit–GATK (Van der Auwera & O'Connor, 2020) to identify SNPs. Multi-allelic loci were removed, and the first SNP of each locus was selected using 'vcftools' (Danecek et al., 2011) to remove linked loci. SNPs matrix from UCEs loci are available on Zenodo (https://doi.org/10.5281/zenodo.11115786).

## 2.5 | Genetic structure with UCE's loci

The best number of genetic groups (K) was estimated with sNMF command in 'LEA: an R Package for Landscape and Ecological Association Studies' (Frichot & Francois, 2015). 'Hierfstat' (Goudet & Jombart, 2022) in R (R Core Team, 2023) was used to perform the Bartlett's test for homogeneity of variances, calculate the population's pairwise $F_{ST}$ (Weir & Cockerham, 1984) and per-population $F_{IS}$ with Holm-Bonferroni corrections for multiple comparisons. Recent migration rates were calculated in BayesAss-SNPs v. 3.0.4 (Mussmann et al., 2019; Wilson & Rannala, 2003). Additional details of the analysis are available in Supporting Information 1.4.

## 2.6 | Stable Isotope Analysis (SIA)

Blood samples were analysed in two different laboratories (Laboratory of Analytical Chemistry at the University of Georgia and Centro Integrado de Análises at the Universidade Federal do Rio Grande) and values were corrected allowing inter-lab comparisons. The result of isotopic composition is expressed in delta notation ($\delta$) in parts per thousand (‰). Details of stable isotope processing are available in Supporting Information 1.5. The package 'SIBER: Stable Isotope Bayesian Ellipses in R' (Jackson et al., 2011) was used to infer isotopic niches through Standard Ellipse Areas (SEA) and Standard Bayesian Ellipse Areas ($SEA_b$).

## 2.7 | Relationship between genetic, environmental, isotopic and geographical distances

The collinearity between environmental variables with the $F_{ST}$ and genetic diversity data from both markers (mtDNA and UCEs) was evaluated through the 'vegan' package (Oksanen et al., 2020). Because the correlation found does not compromise analyses, all variables were maintained. The geographic distances between colonies and from colonies to the Brazilian coast were obtained by Google Earth. For the environmental data, the sea surface temperature (°C), concentration of chlorophyll α (μg/L) as a proxy of primary productivity (Huot et al., 2007), and salinity (Practical Salinity Scale–PSS) were used as they are often evaluated in studies with seabirds that relate genetic diversity with the heterogeneity of the environment (e.g. Gómez-Díaz et al., 2009; Jakubas et al., 2014; Nunes et al., 2017; Peck et al., 2008). Environmental variables were obtained through the Bio-ORACLE platform and details are available in Supporting Information 1.6. All data were centralized. For all analyses, the 'vegan' package (Oksanen et al., 2020) was used in R environment (R Core Team, 2023). A Mantel's test was performed to assess the relationship between the genetic distance matrices (mtDNA and UCEs) and the matrices of each variable (environmental, isotopic and geographic).

## 2.8 | Sexual size dimorphism and morphometric differences between populations

To evaluate sexual dimorphism, the Markov-Chain Monte Carlo method was used to obtain a posteriori distribution of biometric variables (mass, culmen, wing, tarsus) between males ($n=52$) and

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females ($n=37$). Details of the analysis are available in Supporting Information 1.7. Due to the sexual size dimorphism found, statistical analyses were performed to evaluate the morphometric differences between colonies considering males ($n=50$) and females ($n=37$) separately. Trindade colony was excluded due to logistical difficulties in obtaining morphometric measurements of birds, which resulted in a lack of data. A multivariate analysis of variance (MANOVA) was performed, and the residuals showed multivariate normality. We run a pairwise Hotelling $T^2$ test to compare the set of biometric measurements between islands. Data were centralized, and linear correlation between measurements was assessed using a Pearson's correlation matrix to construct a Principal Component Analysis (PCA) with the 'vegan' package (Oksanen et al., 2020). PCA was performed to reduce the four biometric measurements in just two dimensions using the 'FactoMineR' package (Lê et al., 2008). The Euclidean distance between mean values of the PC1 was used as a proxy of the morphological distance between populations. Finally, a Mantel's test between genetic (mtDNA and UCEs) and morphological distance matrices was performed.

## 3 | RESULTS

### 3.1 | Genetic structure

From mtDNA analysis, 20 haplotypes were found in the metapopulation. We identified one common haplotype among all populations (Hp_1), another one shared by the four oceanic colonies (Hp_4), and a high number of exclusive haplotypes, mainly in Rocas (Figure 2). The highest genetic diversity values were those of Rocas, followed by Noronha, Abrolhos, Trindade and Martin Vaz (Table S1). The $F_{ST}$ values were low for all populations (Table 1). Time-calibrated phylogeny suggests that the most recent common ancestor (TMRCA) for the lineage occurred around 200,000 years ago (Figure S1) with 95% HPD = 105,000–332,000 years.

With UCEs, we obtained 1748 SNPs. Both for the metapopulation and for each of the populations, the expected heterozygosity values were greater than those observed (Table S2). In addition, the percentage of genetic variation was greater within each population than between them. $F_{ST}$ values were low for all populations (Table 1). The highest rate of resident animals was on Martin Vaz (83%) and the lowest was on Trindade (68%). The presence of migration was recorded between all populations, occurring mainly from Trindade to Martin Vaz (19%), and the populations that received the most migrants from other colonies were Martin Vaz and Rocas (Table S3).

The phylogenetic analysis and configuration of the mtDNA haplotype network evidenced genetic segregation between Abrolhos, the only coastal colony, and others, mainly the more oceanic ones (Trindade and Martin Vaz) (Figure 2). This is corroborated by the pairwise comparison of populations from mtDNA, which are higher between Trindade/Martin Vaz with others, and the presence of one shared haplotype only between oceanic colonies (Hp_4).

For UCEs, the best number of clusters was $K=3$. It was observed the presence of three distinct genetic profiles: two of them shared among all colonies (purple and blue), and another shared only among the colonies closest to the coast (green) (Figure 3). $F_{ST}$ values of pairwise comparisons with UCEs showed that a relatively higher structure was found between Martin Vaz and Abrolhos and between Trindade and Abrolhos.

### 3.2 | SIA and morphometry

The colony with the biggest isotopic niche width was Abrolhos, and the smallest was Trindade (Figure S2a). In addition, the greatest overlap of ellipses occurred between Abrolhos and Rocas (Figure S2b), with a general overlap between the three colonies closest to the coast (Abrolhos, Rocas, Noronha). However, there was no significant statistical correlation between the isotopic values and the genetic distances.

Reverse sexual dimorphism was found, that is, females were larger than males for all traits (Figure S3), and all of them were different for both sexes among colonies. Males and females with larger body sizes were found at Abrolhos. The pairwise analysis among populations showed that, for females, the greatest differences were between Abrolhos and Martin Vaz and, for males, between Abrolhos and Rocas (Table S4). For mtDNA and UCEs, we did not observe a correlation between genetic and biometric distances, with the first principal component (PC1) explaning 47.6% of the variance in biometrics for males and 36.9% for females.

### 3.3 | Isolation by environment and by distance

The genetic structure found in UCE data was related to chlorophyll α (Pearson's correlation $r=0.77$) and with geographic distance from the coast ($r=0.88$) (Figure 4). The genetic structure observed in mtDNA was also correlated with the distance from the coast ($r=0.39$) (Figure 4). There was no significant correlation between geographical distances between colonies and genetic structure for both markers (UCEs and mtDNA).

## 4 | DISCUSSION

### 4.1 | Genetic structure

Masked boobies in the SW Atlantic Ocean present low levels of genetic structure among the five colonies, supported by both mitochondrial and nuclear markers, the latter showing even lower detectable structure. This pattern is similar to other reports among various Indo-Pacific populations of the species (Kingsley et al., 2020). Moreover, low structure had been also observed in other seabirds in SW Atlantic Ocean, such as the magnificent frigatebird, *Fregata magnificens*, Suliformes (Nuss et al., 2016),

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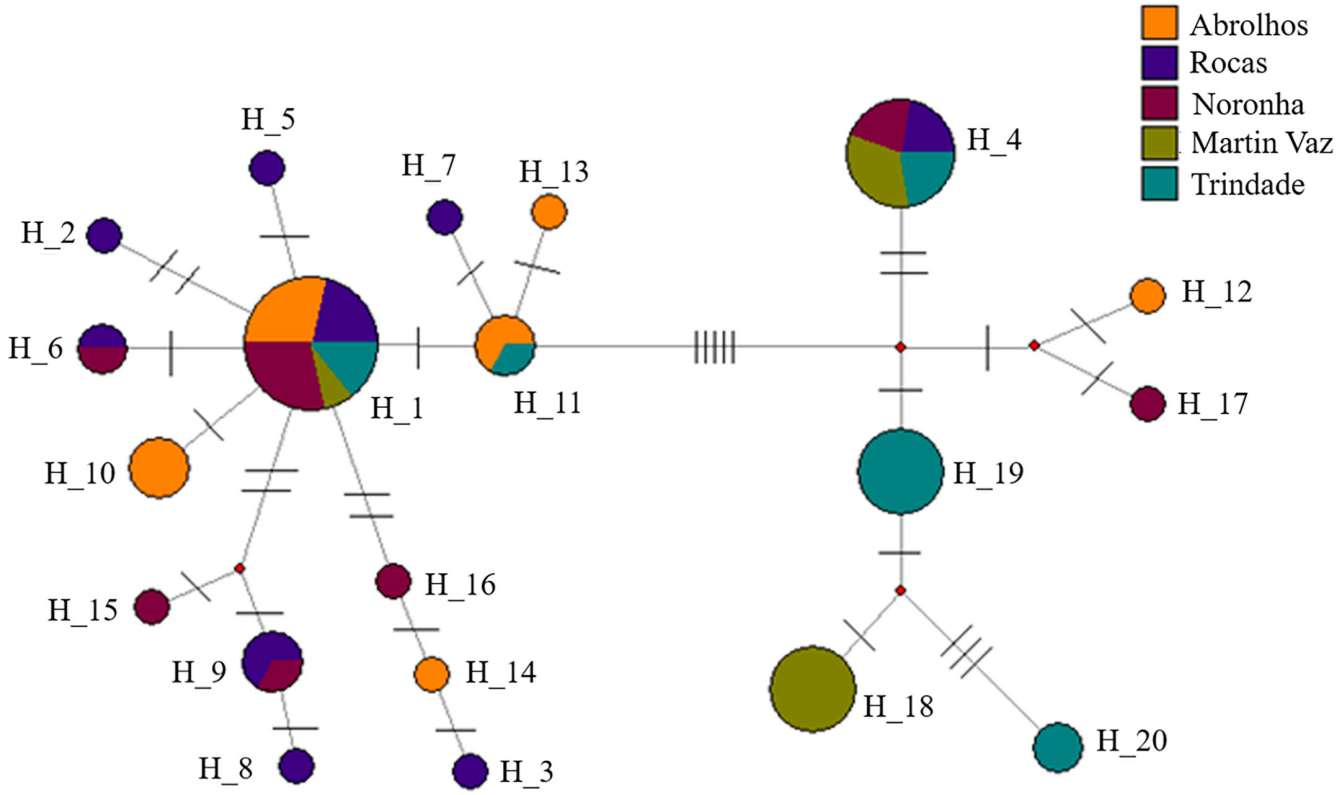


**FIGURE 2** Haplotype network of the five populations of masked booby, *Sula dactylatra*, from the southwestern Atlantic Ocean ($n = 59$) built from control region and cytochrome *b* mtDNA concatenated markers (1214 bp). Roman numerals stand for the 20 haplotypes found. The size of the pie charts demonstrates the number of individuals that present certain haplotypes. Colours indicate the percentage of individuals belonging to each one of the populations. Each mutation is represented by a smaller line perpendicular to the main connecting line. Tiny red dots are mutational steps that are not present in the database but were estimated by the analysis. Rocas–Rocas Atoll ($n = 13$); Abrolhos–Abrolhos Archipelago ($n = 12$); Noronha–Fernando de Noronha Archipelago ($n = 11$); Martin Vaz–Martin Vaz Island ($n = 10$); Trindade–Trindade Island ($n = 13$).

| | Rocas | Abrolhos | Noronha | Martin Vaz | Trindade |
|---|---|---|---|---|---|
| Rocas | – | 0.03 | −0.04 | 0.16* | 0.09* |
| Abrolhos | −0.013* | – | 0.02 | 0.24* | 0.13 |
| Noronha | −0.026* | −0.008* | – | 0.18* | 0.1* |
| Martin Vaz | 0.007* | 0.022* | 0.014* | – | 0.26 |
| Trindade | 0.006* | 0.020* | 0.009* | −0.016* | – |

**TABLE 1** Genetic distances matrix ($F_{ST}$) for the five populations of masked boobies, *Sula dactylatra*, from the southwestern Atlantic Ocean ($n = 59$), calculated through two different markers: mitochondrial DNA (mtDNA) results are above the main diagonal (1214 bp, $n = 59$), and ultraconserved elements (UCEs), below (1748 SNPs, $n = 57$).

*Note*: Fixation indexes were calculated by pairwise differences. Values statistically significant are marked with *, considering $p < 0.05$. Rocas–Rocas Atoll (mtDNA, $n = 13$; UCEs, $n = 11$); Abrolhos–Abrolhos Archipelago (mtDNA, $n = 12$; UCEs, $n = 11$); Noronha–Fernando de Noronha Archipelago (mtDNA, $n = 11$; UCEs, $n = 11$); Martin Vaz–Martin Vaz Island (mtDNA, $n = 10$; UCEs, $n = 12$); Trindade–Trindade Island (mtDNA, $n = 13$; UCEs, $n = 12$).

South American tern, *Sterna hirundinacea*, Charadriiformes (Faria et al., 2010) and Magellanic penguins, *Spheniscus magellanicus*, Sphenisciformes (Bouzat et al., 2009).

The colonies are not completely separated. It could be due to actual genetic flow between populations, which is supported by migration rates between all of them. This possibility was also suggested to masked boobies between the Caribbean and eastern Atlantic Ocean colonies that share haplotypes despite the high levels of genetic structure (Steeves et al., 2003). Furthermore, the low structure and haplotype sharing between populations (Hp_1) may also be due to incomplete lineage sorting (e.g. Silva et al., 2015). The highest genetic diversity of Rocas colony suggests it may be the older colony of the species on the SW Atlantic Ocean, with more time to diverge. It also may be related to the largerd colony size, with more chances of mutation and the emergence of genetic diversification.

The phylogeny suggests a TMRCA for the SW Atlantic Ocean masked booby lineage ~200,000 years ago. A more recent TMRCA was found between the Indo-Pacific and the Atlantic lineages (Isla

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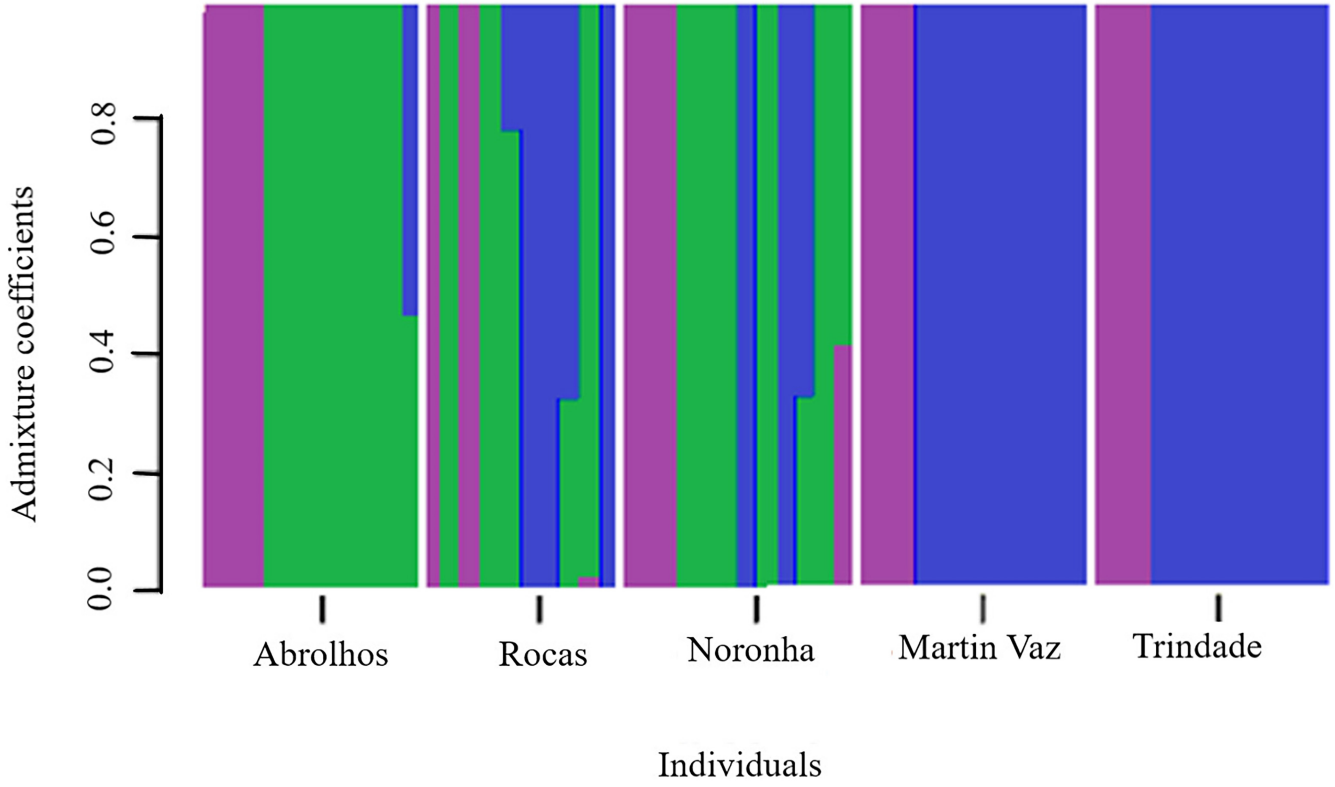


FIGURE 3 sNMF plot indicating $K=3$ for the best number of clusters from the analysis of 1748 SNPs belonging to UCEs loci of the five populations of masked boobies, *Sula dactylatra*, from the southwestern Atlantic Ocean ($n=57$). Rocas–Rocas Atoll ($n=11$); Abrolhos–Abrolhos Archipelago ($n=11$); Noronha–Fernando de Noronha Archipelago ($n=11$); Martin Vaz–Martin Vaz Island ($n=12$); Trindade–Trindade Island ($n=12$).

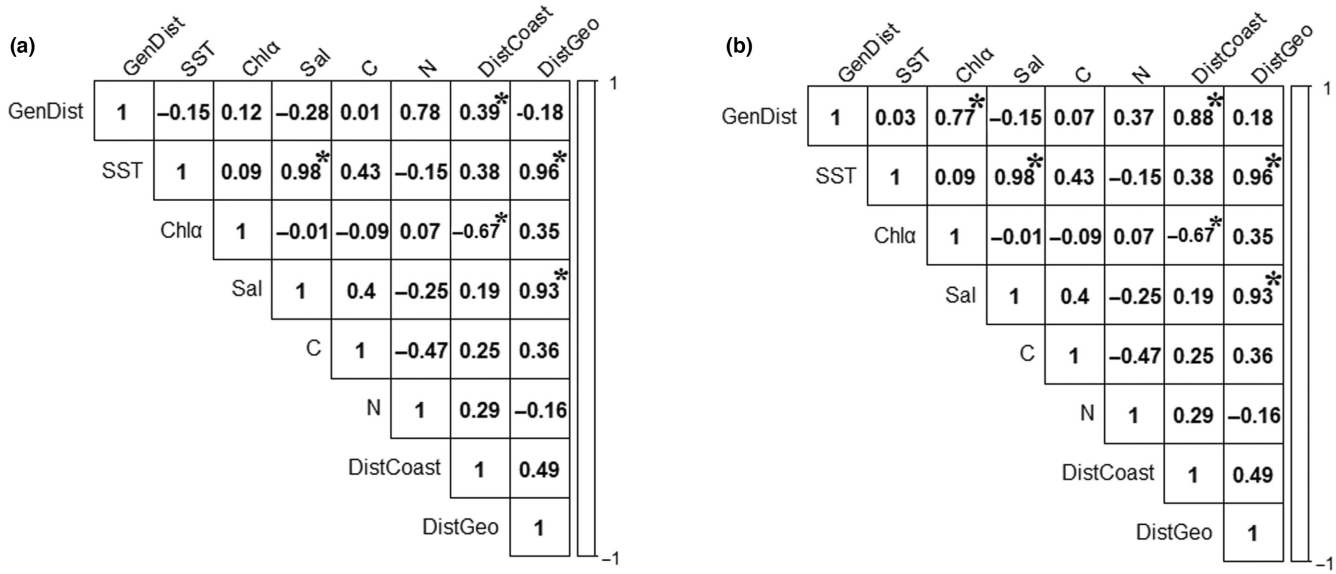


FIGURE 4 Mantel's tests between geographic, environmental, and genetic (mitochondrial and nuclear data) distances of the five populations of masked boobies, *Sula dactylatra*, in the southwestern Atlantic Ocean. (a and b) represent Pearson's correlations between distance matrices calculated through Mantel's tests, using mitochondrial and nuclear data, respectively. The values represent the distance (i.e. divergence) in a pairwise comparison between variables on a scale of 0 (no divergence) to 1 (complete divergence). Values with statistically significant correlations are marked with *. GenDist–pairwise genetic distance ($F_{ST}$) calculated through two concatenated mitochondrial genes (control region and cytochrome *b*, $n=59$, in (a) and nuclear data ($n=57$, in (b); SST, sea surface temperature; Sal, sea surface salinity; C, $\delta^{13}$C blood values ($n=118$); N, $\delta^{15}$N blood values ($n=118$); DistCoast, minimal distance from the central point of each island or archipelago to Brazilian coast; DistGeo, geographical distance between the central point of each pair of islands or archipelagos; Chla, chlorophyll $\alpha$.

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Monito and Botswana Bird Island), about 115,000 years (Steeves et al., 2005a). Compared to other seabirds' lineage, it represents a much recent evolutionary time (e.g. million-year time scale in shearwaters; Torres et al., 2021). Consequently, this may be related to the low genetic differentiation observed in the SW Atlantic Ocean colonies and the haplotype sharing.

Despite the low genetic structure, there is evidence of a genetic segregation between Abrolhos and the oceanic colonies. It was also found for brown boobies, *Sula leucogaster*, in the same study area, with genetic differences between coastal and oceanic populations (Nunes & Bugoni, 2017), which was related to the oceanographic differences between inshore versus offshore environments.

### 4.2 | Phenotypic and ecological variation

The masked booby populations analysed had distinct isotopic values, which may indicate differences in foraging habits, expressing ecological differences, and/or in the isotopic compositions on the baseline waters surrounding each colony, which occurs due to oceanographic features and is reflected at all levels of the food web. The overlap in isotopic niches between the three colonies located closer to the coast (Abrolhos, Noronha, Rocas) is noticeable, and may express similar feeding habits (Jacoby et al., 2023), or the use of feeding areas with similar baseline isotopic composition, which is different from those used by birds from more oceanic islands. It can be related to the influence of the input of nutrients from river outflows (Torrano-Silva & Oliveira, 2013) and continental shelf fronts (Acha et al., 2004) in coastal environments.

In general, all biometric measures differed between islands, and the masked boobies from Abrolhos were bigger than elsewhere. It could be related to the fact that this is the only coastal colony in the SW Atlantic Ocean and is an area with high productivity which may suggest the influence of the environment in this population. Generally, productive areas allow larger organisms due to the decreasing energy path along the trophic web, so the energy transference is optimized (Pinet, 2019). Although Abrolhos was not genetically isolated, it had some of the highest genetic structure values compared to others, suggesting some distinctiveness of this population. The relationship between genetic isolation and morphology was already described in seabirds, such as the population of brown boobies in the São Pedro e São Paulo Archipelago, over the Equator line off the Brazilian coast (Nunes & Bugoni, 2017). This population has larger body sizes than other colonies and is genetically isolated.

Both ecological (segregation between the coastal and oceanic colonies) and phenotypic (Abrolhos is the coastal population with bigger animals) variations highlight the presence of differences between inshore and offshore environments. Despite that, isotopic niche and morphometry did not present a statistically significant correlation with the genetic structure of the species, which may be linked to some artefacts of the technique (e.g. lack of sensitivity, small number of samples).

### 4.3 | Isolation by Environment (IBE)

Genetic correlations with environmental variables suggest that landscape characteristics may influence the genetic structure of the masked booby populations, even though it is low in the SW Atlantic Ocean. Thus, the pool of environmental differences in the coastal and oceanic landscapes, evidenced by distance from the coast and chlorophyll $\alpha$, may act as selective pressures on the organisms.

Steeves et al. (2005a) indicate that, within each ocean basin, populations of masked boobies appear to have diverged due to local adaption and/or genetic drift. In this study, the signs of segregation between the coastal and oceanic colonies, mainly between Abrolhos and others, were corroborated by the genetic data, the isotopic niche, and the morphometry, which suggest the influence of isolation by the environment in the genetic structure. It is known that the dispersal barriers to gene flow in South Atlantic Ocean seabirds are complex, and genetic structure may result from historical, behavioural, and environmental factors (Munro & Burg, 2017). In this way, it highlights the complexity of factors that influence biodiversity.

## 5 | CONCLUSION

Populations of masked boobies in the SW Atlantic Ocean have low genetic structure, which may be related to persisting gene flow between colonies or incomplete lineage sorting. Notwithstanding, there is a divergence between colonies near the coast versus offshore. It demonstrates that environmental variables could be an important selection pressure that acts as a barrier to gene flow, corroborating hypothesis 1. We identified morphometric and isotopic niche variations between populations that reflect the clustering among coastal colonies versus oceanic ones, corroborating hypothesis 2. We highlight the necessity of considering the role of environmental heterogeneity in shaping biodiversity, which is important for understanding the influence of different selection pressures on organisms, in line with identifying how they will respond to climate and environmental changes.

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## CONFLICT OF INTEREST STATEMENT

Authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

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## BIOSKETCH

**Vitória Muraro's** research interests include evolutionary ecology with a special focus on the mechanisms of population differentiation in seabirds. She is also interested in trophic ecology and conservation of marine vertebrates.

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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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