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Local adaptation drives population isolation in a tropical seabird

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Abstract

Aim: Understanding the mechanisms of population isolation in marine top predators is challenging owing to their high mobility and the inherent difficulty in quantifying oceanographic variables. In this study, the worldwide distributed brown booby *Sula leucogaster* was used to test the potential role of isolation by distance (IBD) and isolation by environment (IBE) in promoting intraspecific diversity.

Location: A heterogeneous seascape in the south-western Atlantic Ocean, along a latitudinal gradient from 0° to 27°S.

Methods: Population structure was assessed using nine microsatellite loci. Between-colony geographical distances were used to test IBD, while air temperature, sea surface temperature, chlorophyll α concentration, colony density and isotopic niche width were used to test IBE.

Results: Genetic isolation of a remote small colony was associated with local selective pressures on land and in foraging areas. Clustering of the remaining colonies was explained by seascape differences between neritic and oceanic environments.

Main conclusions: Seabirds can easily overcome large geographical distances, but their dispersal ability seems to be lower than their mobility. In this context, gene flow can be disrupted even between relatively close colonies if there are strong selective pressures. Local adaptation and IBE seems to be most plausible explanation for patterns found in brown boobies; this is particularly noticeable for birds at a small offshore archipelago, for which the identification of the key selective forces shaping genetic and phenotypic differences is the main issue.

KEYWORDS
Atlantic Ocean, brown boobies, evolutionary ecology, gene flow, isolation by distance, isolation by environment, marine biogeography, microsatellites, oceanographic dynamics, *Sula leucogaster*

1 | INTRODUCTION

Understanding how biodiversity correlates with environmental features represents a baseline for evolutionary ecologists studying microgeographic adaptation in any ecosystem (Richardson, Urban, Bolnick, & Skelly, 2014). Identifying associations of biological diversity with selection pressures reveals the microevolutionary processes accounting for existing forms and enables one to predict how wild populations will respond to climate changes (Hoffmann & Sgrò, 2011). In general, ecogeographical rules (e.g. Bergmann's rule; Bergmann, 1847) can explain phenotypic variation of a wide range of species, but known exceptions shed light on the complexity of mechanisms shaping biodiversity (e.g. Berke, Jablonski, Krug, Roy, & Tomasovych, 2013; Fisher, Frank, & Leggett, 2010; Nunes, Mancini, & Bugoni, 2017). Mayr (1956) highlighted this conflict and suggested that "the emphasis of research should be shifted to a study of the exceptions." In this context, studies addressing the association of intraspecific diversity and landscape heterogeneity can provide a

better understanding of the drivers of population isolation, and consequently, potential explanations for exceptions of ecogeographical rules (Orsini, Vanoverbeke, Swillen, Mergeay, & Meester, 2013).

Early studies proposed that genetic differentiation among populations increases with geographical distance (e.g. Wright, 1943). Under the isolation by distance (IBD) model, genetic drift causes population differentiation in the absence of selection and with short range dispersal (Wright, 1943). The IBD model has been demonstrated for large spatial scales and applied to organisms with low dispersal capacity, resulting in a pattern of spatial autocorrelation in the distribution of genetic variation (Meirmans, 2012). Explaining population isolation by geographical distance alone, however, is likely to be simplistic, as geography tends to be entangled with environmental heterogeneity (Shafer & Wolf, 2013; Wang & Bradburd, 2014).

In this context, it has been shown that local adaptation can influence gene flow and be a major driver of population differentiation (Sexton, Hangartner, & Hoffmann, 2014). The isolation by environment (IBE) model may be defined "as a pattern in which genetic differentiation increases with environmental differences, independent of geographical distance" (Wang & Bradburd, 2014). Hence, landscape heterogeneity is a basic assumption of the IBE model, and some ecological processes are known to contribute to population isolation, such as non-random gene flow (Edelaar & Bolnick, 2012), and natural and sexual selection against migrants due to local adaptation (Hendry, 2004). Under such circumstances, fine-scale variations in the use of local resources may be sufficient to isolate populations, such as differences in size of seeds for passerines (Ryan, Bloomer, Moloney, Grant, & Delport, 2007), forest types for epiphytic orchids (Mallet, Martos, Blambert, Pailler, & Humeau, 2014) and topography for grasshoppers (Noguerales, Cordero, & Ortego, 2016).

For marine organisms, exposure to a heterogeneous seascape may influence population structure (Selkoe et al., 2016). Ecological barriers are known to generate genetic discontinuity in species with limited dispersal abilities, such as river outflows preventing larval dispersal in wrasses (Rocha, Robertson, Roman, & Bowen, 2005), and shelf fronts disrupting gene flow in marine snails (Piñeira, Quesada, Rolán-Alvarez, & Caballero, 2008). Although large marine vertebrates can cross most of these barriers due to their high mobility, local adaptation is suggested to influence population structure of species inhabiting heterogeneous seascapes, as observed for dolphins using distinct water masses (Möller et al., 2011). Forces driving spatial genetics in large marine predators can be further complicated by population-specific parameters, such as differential habitat use and resource specialization influencing killer whales (Moura et al., 2014). Under such contexts, local pressures can induce adaptation, which, in turn, can affect population dynamics and increase selection against immigrants (Saccheri & Hanski, 2006).

Over the last decade, the field of landscape genetics has been combined with spatial ecology to disentangle eco-evolutionary processes and to demonstrate IBE (Manel & Holderegger, 2013). Nevertheless, assessments of spatial genetics in marine top predators are still scarce when compared with terrestrial populations, presumably because of inherent difficulties in characterizing marine habitats and populations (Selkoe et al., 2016). Seabirds present interesting models for studying relationships between genetic diversity and spatial ecology, as breeding generally takes place on islands and despite the high mobility of these animals, they tend to be highly philopatric (Schreiber & Burger, 2001). Furthermore, seabirds are widely distributed, making it possible to compare populations across environmental gradients. The brown booby, *Sula leucogaster* (Boddaert, 1783), is a strictly marine bird living in tropical and subtropical latitudes in all ocean basins (Nelson, 2005).

Intraspecific differentiation is high in brown boobies, and distinctive populations can even be found within the Atlantic Ocean (Morris-Pocock, Anderson, & Friesen, 2011). In the south-western Atlantic Ocean, there is also evidence of phenotypic population differentiation of brown boobies driven by multi-scale environmental characteristics (Nunes et al., 2017), along with differences in trophic niche width (Mancini, Hobson, & Bugoni, 2014) and population size (Mancini, Serafini, & Bugoni, 2016). Although geographically proximate to each other, the brown booby colonies in the south-western Atlantic are exposed to a heterogeneous environment in terms of latitude, sea surface and air temperatures, primary productivity, and available area for nesting (Nunes et al., 2017; Seeliger & Kjerfve, 2001). Colony-specific conditions (e.g. trophic relationships, aggressive nest defence) could be driving population differentiation by shaping ecological processes. In other words, environmental heterogeneity can lead to ecologically dependent reproductive isolation in brown boobies through natural selection to local conditions, which is known to be one of the primary causes of differentiation in animals (Coyne & Orr, 2004; Hendry, 2004). The evolutionary history of brown boobies has been explained in terms of allopatric divergence (Morris-Pocock et al., 2011); hence it is reasonable to expect that the population structure of brown boobies in the south-western Atlantic Ocean should be more directly correlated with environmental heterogeneity than simply with geographical distance; that is, we would predict lower gene flow between colonies located in distinct environments, such as coastal versus pelagic.

According to this reasoning, we assessed the influence of environmental heterogeneity on the population structure of six colonies of brown boobies residing in the south-western Atlantic Ocean using microsatellites. Additionally, a data set of physical and colony-specific parameters was used to investigate how the environment may promote or disrupt gene flow. The following issues were assessed: (1) population differentiation and structure based on genotypes; (2) asymmetrical dispersal among colonies; and (3) the potential role of IBD and IBE in population isolation of brown boobies in the south-western Atlantic Ocean.

2 | MATERIALS AND METHODS

2.1 | Sampling and study area

Fieldwork was carried out between 2011 and 2014 in six archipelagos along a latitudinal gradient from 0° to 27°S in the south-western

Atlantic Ocean: Moleques do Sul, Cagarras, Abrolhos, Rocas Atoll, Fernando de Noronha, and Saint Peter and Saint Paul, hereinafter referred to as Moleques, Cagarras, Abrolhos, Rocas, FN, and SPSP respectively (Figure 1a). Sampling concentrated on breeding adults, distinguished from juveniles by their plumage coloration (Nelson, 2005), which were assumed to had born in the sampling colony. Boobies were captured on nests by hand or using hand nets, and blood samples (~200 μl) were obtained by puncturing the tarsal vein with a sterile needle, and stored in microtubes containing 70% ethanol. Individuals were banded to avoid resampling, and released on the nests after handling.

2.2 | Genetic diversity and structure

DNA extraction followed the 5 M sodium chloride protocol (Medrano, Aasen, & Sharrow, 1990). All samples were amplified at nine microsatellite loci with primers described by Taylor, Morris-Pocock, Sun, and Friesen (2010). M13(-21) tail was incorporated into each forward primer at the 5′ end (Schuelke, 2000) and consequently to the PCR products. PCR was performed in a 20-μl solution containing 20–30 ng of DNA, 10 pmol of forward primer, 10 pmol of reverse primer, 10 pmol of fluorescent dye label (HEX or FAM), 10 mM of each dNTP, 1.5 mM of $MgCl_2$, 1x PCR buffer and 1 U of *Taq* DNA polymerase. The following PCR profile was used: 94°C for 5 min, followed by 35 cycles of 94°C for 30 s, annealing temperature for 30 s and 72°C for 30 s, with a final extension in 72°C for 10 min. Primer-specific annealing temperature was adjusted as follows: 50°C for Sv2A-95, Sv2A-47 and Sv2B-27; 52°C for Sv2A-2 and Sn2A-123; 54°C for Sn2B-100; and 56°C for Sv2A-26 and Sn2B-83. For Sv2B-138, we used the touchdown programme proposed by Taylor et al. (2010). To avoid biased readings between genotyping rounds, ~5%–10% of genotyped samples were reassayed. PCR products were run on ABI 3730XLs with an internal standard size marker of 400 HD.

Evidence for null alleles, large allele dropouts and scoring errors due to stuttering were checked using MICRO-CHECKER 2.2.3 (van Oosterhout, Hutchinson, Wills, & Shipley, 2004). Genotypic linkage disequilibrium for each pair of loci in each population and across all populations was assessed through Fisher's exact tests using GENEPOP 4.4 (Rousset, 2008). Observed and expected heterozygosities (H_O and H_E), deviations from Hardy–Weinberg equilibrium (HWE; Nei, 1978) and numbers of alleles for each locus (A) were calculated using ARLEQUIN 3.5 (Excoffier & Lischer, 2010). Sequential Bonferroni correction was used as a control for multiple tests (Legendre & Legendre, 2012). Allele frequencies were calculated to assess the proportion of rare alleles for each population (Luikart, Sherwin, Steele, & Allendorf, 1998). Finally, the percentage of polymorphic loci and the inbreeding coefficient F_{IS} (Weir & Cockerham, 1984) were calculated for each population in GENALEX 6.5 (Peakall & Smouse, 2012).

Between-population genetic distance was calculated using D_{SW}, which takes into account the mutational pattern of microsatellites (Shriver et al., 1995). Fisher's exact test with sequential Bonferroni correction (Legendre & Legendre, 2012) was applied to detect intraspecific genotypic differences in GENEPOP 4.4. A phylogenetic tree was built using the neighbour-joining method with 1,000 bootstrap replications (Saitou & Nei, 1987) and D_{SW} as the distance measure in the software POPTREE2 (Takezaki, Nei, & Tamura, 2010). Principal coordinate analysis (PCoA) with standardized data was also carried out in GENALEX 6.5 to explore similarities and groupings among colonies. Additionally, the Bayesian clustering method implemented in the software STRUCTURE 2.3.4 was performed to determine the most plausible number of clusters (*K*) (Pritchard, Stephens, & Donnelly, 2000). Analyses were performed on an admixture model with independent allele frequencies, and location information was not used as prior. Numbers of *K* from 1 to 10 were tested by conducting 20 independent runs for each *K* with a burn-in period of 100,000 steps and 1,000,000 MCMC repetitions. The ad hoc ΔK (Evanno, Regnaut, & Goudet, 2005) was used to detect the best K in

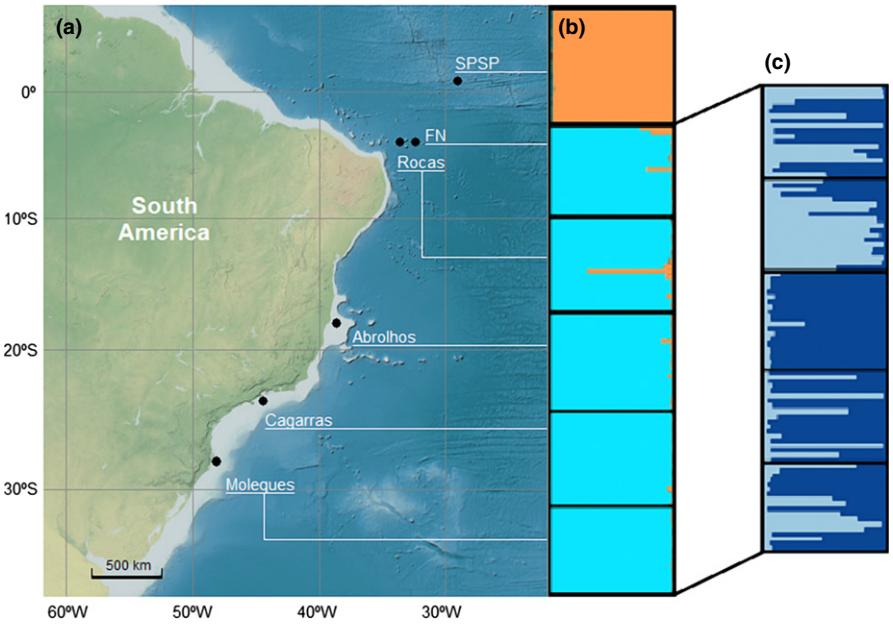

FIGURE 1 Study area with cluster arrangements based on genetic data. (a) Brown booby, *Sula leucogaster*, colonies in the south-western Atlantic Ocean. (b) Bar plot from Bayesian estimates of population structure based on microsatellite data considering two clusters ($K = 2$); and (c) bar plot without brown boobies from SPSP considering two clusters ($K = 2$). SPSP = Saint Peter and Saint Paul Archipelago; FN = Fernando de Noronha Archipelago; Rocas = Rocas Atoll; Moleques = Moleques do Sul. Sample size: SPSP = 24; FN = 19; Rocas = 19; Abrolhos = 20; Cagarras = 19; Moleques = 18. For references to colour, see the online version [Colour figure can be viewed at wileyonlinelibrary.com]

STRUCTURE HARVESTER Web 0.6.94 (Earl & vonHoldt, 2012). The 20 independent runs for the best *K* were merged using CLUMPP 1.1.2 (Jakobsson & Rosenberg, 2007) and a bar plot was generated using DISTRUCT 1.1 (Rosenberg, 2004). Finally, a Bayesian inference of recent bidirectional gene flow was performed using BAYESASS 1.3 (Wilson & Rannala, 2003).

2.3 | Isolation by distance

The geographical coordinates of each colony were used to calculate pairwise geographical distances (km; hereinafter, "GeoDis"). Using this information, we applied a Mantel test to test for correspondence between genetic and geographical distance matrices, which were log-transformed (1+ log[distance]) and linearized (Slatkin, 1995) respectively. The Mantel test was performed with Pearson's correlation and *p*-values were calculated using 5,000 permutations in the "vegan" package (Oksanen et al., 2016) in the R software 3.2.5 (R Core Team, 2016).

2.4 | Isolation by environment

Air temperature (AT; °C), sea surface temperature (SST; °C) and chlorophyll α concentration (Chlα; mg mm^{-3}) for each colony were obtained from Nunes et al. (2017). Briefly, SST and AT were obtained from the nearest oceanographic buoy to each archipelago, considering average values from the launching date until 2015 (2000 for SPSP, FN and Rocas; 2011 for Moleques; 2012 for Cagarras and Abrolhos). Chlα was obtained from the Aqua MODIS, NASA/GSFC, considering average values from 2002 to 2014 within a 40-km radius surrounding each colony. The six colonies were remarkably different both in terms of numbers of individuals, ranging from 140 in Rocas to 2,500 in Cagarras, and the total area of the archipelago, ranging from 0.002 to 17.5 km^2 (this study; Nunes et al., 2017). Population density was calculated as individuals km^{-2}, hereinafter referred to as "Density" (Appendix S1).

Isotopic niche width was estimated for each population using carbon and nitrogen isotopic ratios from whole blood obtained by Mancini et al. (2014), and from samples taken and processed by the authors (Appendix S1). Bayesian ellipse areas were calculated using the package "SIBER" (Jackson, Parnell, Inger, & Bearhop, 2011) and isotopic niche width was defined as the standard ellipse areas adjusted for small sample sizes (SEAc; $‰^2$).

Pairwise Pearson's correlations were calculated among AT, SST, Chlα, Density, and SEAc using sequential Bonferroni corrections (Legendre & Legendre, 2012). Distance matrices for environmental variables were calculated using the Mahalanobis dissimilarity index, and partial Mantel tests were performed between matrices of genetic and environmental distances, controlling for the effect of between-population geographical distances (Legendre & Legendre, 2012). These analyses were performed with the functions provided by the "vegan" package (Oksanen et al., 2016), and *p*-values were calculated based on 10,000 permutations. In addition, a redundancy analysis (RDA) was used to identify the effect of each environmental variable on genetic variation by running the *ordistep* function in the "vegan" package using a backward stepwise procedure, and Akaike's information criterion (AIC) was used to select the best model. *p*-values were calculated based on 10,000 permutations.

3 | RESULTS

In total, 119 individuals were sampled, ranging from 18 individuals in Moleques to 24 in SPSP. MICRO-CHECKER results demonstrated no significant genotyping errors. Only two of 54 loci (six populations × nine loci) deviated from HWE (*p*-value <.05), and three out of 216 locus pairs (6 populations × 36 loci pairs per population) deviated from linkage equilibrium (*p*-value <.05). No linkage disequilibrium was detected when comparing locus pairs across all populations. The nine loci were polymorphic, with 2.6 alleles on average, but boobies from SPSP had low polymorphism (i.e. four out of nine loci were polymorphic with 1.4 alleles per locus on average) when compared to those from Rocas/Abrolhos/Cagarras (eight out of nine polymorphic loci with 2.73 alleles per locus on average) and those from FN/Moleques (all loci polymorphic with 2.75 alleles per locus on average). SPSP boobies also had the lowest H_O and average number of alleles per locus, and a low percentage of rare alleles (~8%; Appendix S2). A mode-shift distortion was observed for Rocas and SPSP (Appendix S2). The inbreeding coefficient (F_{IS}) was close to 0 for all populations.

The PCoA plot was built from coordinates 1 and 2, which explained 73.9% and 18.0% of the genetic variance respectively. Coordinate 1 separated the SPSP colony from the remaining colonies, while Coordinate 2 separated FN and Rocas from Moleques, Cagarras and Abrolhos, hereafter referred to as the "coastal colonies" (Appendix S2). A population structure based on two clusters ($K = 2$) was most strongly supported by the STRUCTURE analysis, with a clear differentiation of SPSP from all other colonies (Figure 1b). SPSP was hence removed from the matrix to detect structure among the other colonies, which was also divided into two clusters ($K = 2$) (Figure 1c; see Appendix S2 for ΔK analyses). The phylogenetic tree reconstructed using the neighbour-joining method and D_{SW} as the distance measure also demonstrated a strong differentiation of SPSP from the other colonies, and split FN/Rocas from the coastal colonies (Appendix S2). The lowest D_{SW} values were observed for the Cagarras–Moleques and Rocas–FN colonies, which also presented no significant genotypic differences (Table 1). The highest rates of gene flow were within clusters (i.e. 14% from Rocas to FN; 23% from Moleques to Cagarras; and 20% from Moleques to Abrolhos), but dispersal from Moleques to FN and to Rocas was as high as 8% and 6% respectively (Figure 2).

Environmental variables showed high heterogeneity (Figure 3). Isotopic niche width ranged from $0.09‰^2$ in FN to $1.29‰^2$ in Abrolhos (Appendix S2). Partial Mantel tests were not significant when comparing matrices of genetic and environmental distances controlling for geographical distances, both with and without SPSP (Appendix S2). Multicollinearity between variables was tested by calculating pairwise correlations and estimating the variance inflation

TABLE 1 Genetic (D_{SW}) and geographical distances among six colonies of brown boobies *Sula leucogaster* in the south-western Atlantic Ocean. Pairwise genetic distances are presented below the diagonal, and pairwise geographical distances (km) are above the diagonal. Bold values represent significant genotypic differentiation based on Fisher's exact test, with adjusted *p*-values based on the sequential Bonferroni correction for multiple comparisons (*p*-values <.001). SPSP = Saint Peter and Saint Paul Archipelago; FN = Fernando de Noronha Archipelago; Rocas = Rocas Atoll; Moleques = Moleques do Sul

SPSP	570	671	2,021	2,626	3,242
0.601	FN	153	1,452	2,058	2,684
0.625	0.072	Rocas	1,375	1,960	2,571
0.526	**0.201**	**0.130**	Abrolhos	655	1,348
0.763	**0.156**	**0.060**	**0.062**	Cagarras	700
0.648	**0.293**	**0.145**	**0.067**	0.053	Moleques

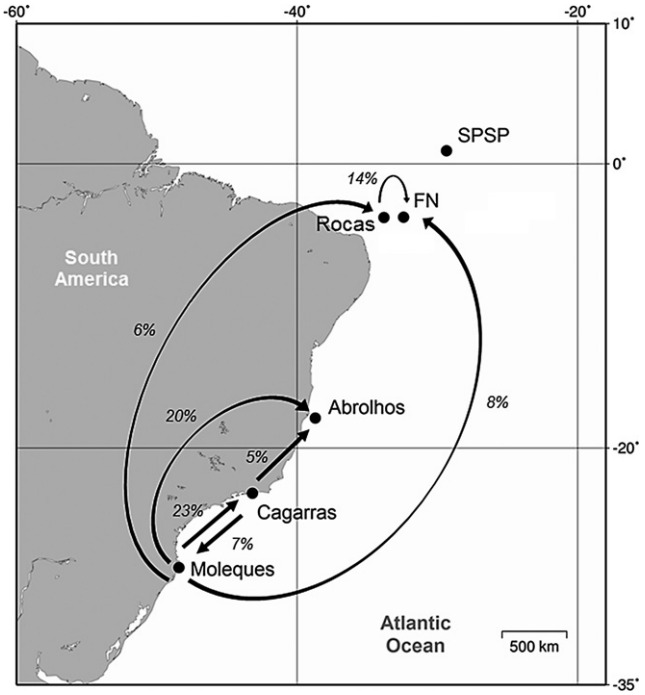

FIGURE 2 Bayesian inferences of dispersal rates among the six brown booby, *Sula leucogaster*, colonies in the south-western Atlantic Ocean. Gene flow is represented by the fraction (%) of individuals in a given population that are immigrants from the remaining populations. SPSP = Saint Peter and Saint Paul; FN = Fernando de Noronha; Rocas = Rocas Atoll; Moleques = Moleques do Sul

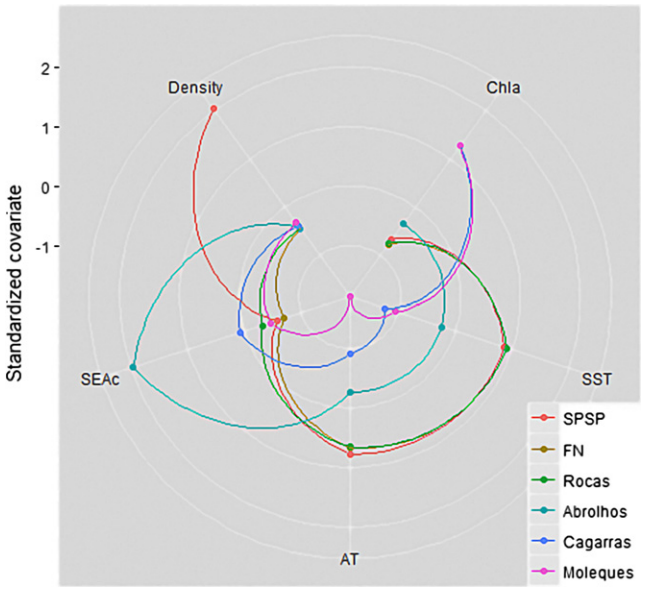

FIGURE 3 Radial plot demonstrating heterogeneity of seascape features and colony-specific parameters across the six brown booby colonies in the south-western Atlantic Ocean. Each radial line corresponds to a standardized environmental covariate with values decreasing towards the centre. Each point on the radial lines corresponds to the population mean (the ellipse "0" corresponds to the mean for each variable). Chlα = chlorophyll α; SST = sea surface temperature; AT = air temperature; density = population density; SEAc = standard Bayesian ellipse areas from isotopic data. For references to colour, see the online version [Colour figure can be viewed at wileyonlinelibrary.com]

factor for each relationship (Zuur, Ieno, & Elphick, 2010). Significant correlation was detected between Chlα-SST, Chlα-AT and SST-AT (*p*-value <.01; Appendix S2) and variance was inflated by a factor of 10.3, 7.4 and 8.6 for these correlations respectively. Therefore, only SST was used in subsequent analyses to avoid multicollinearity. The coefficient of determination for correspondence between genetic and geographical matrices was close to zero (R^2 = .031; *p*-value = .202), but after removing SPSP the correspondence was positive and marginally significant (R^2 = .273; *p*-value = .05; Appendix S2). The reduced model in RDA explained 82.2% of the total variance and was composed by Density+SST (F = 7.18; df = 2; *p*-value = .016), while genetic diversity without SPSP was better explained (20.7%) by the model containing only SST (F = 2.91; df = 1; *p*-value = .083) (Figure 4).

4 | DISCUSSION

In general, brown booby populations exhibited low genetic diversity, with an average of ~3 alleles per locus and heterozygosity (H_O) of ~.4, values consistent with those found for other brown booby colonies (Morris-Pocock et al., 2011), suggesting that brown booby populations can persist with low genetic diversity. Even so, boobies

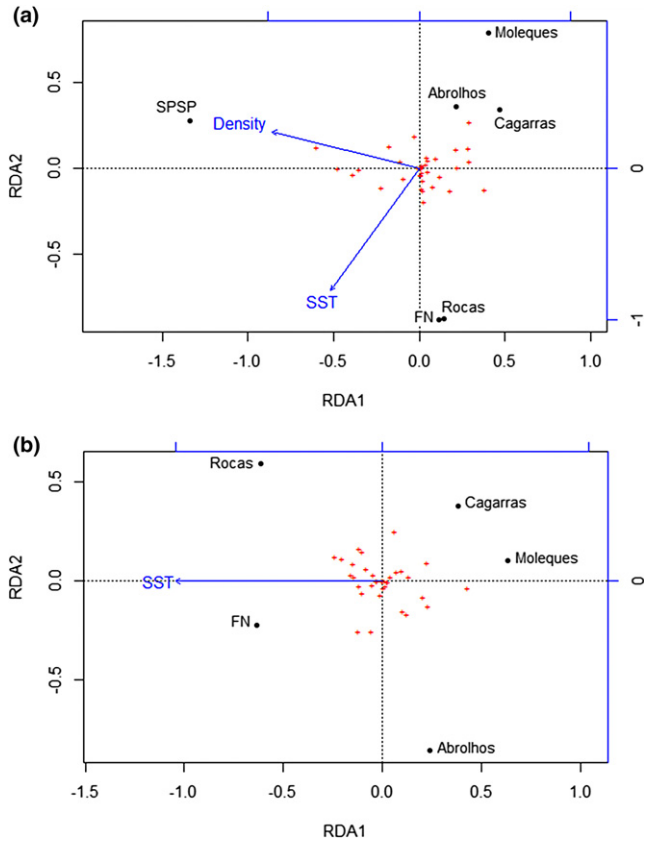

FIGURE 4 Redundancy analyses demonstrating how environmental variables correspond to genetic variation among brown booby colonies in the south-western Atlantic Ocean in scenarios with (a) and without (b) the Saint Peter and Saint Paul Archipelago. Angles between arrows are defined by Pearson's correlation and direction of a projected arrow indicates where the highest values are. Blue arrows represent which environmental variables better explain variations in allele frequencies among colonies. SPSP = Saint Peter and Saint Paul Archipelago; FN = Fernando de Noronha; Rocas = Rocas Atoll; Moleques = Moleques do Sul; SST = sea surface temperature; density = population density. For references to colour, see the online version [Colour figure can be viewed at wileyonlinelibrary.com]

from SPSP presented remarkably low genetic diversity, suggesting the influence of additional evolutionary processes, such as founder effect or a recent bottleneck event.

Mode-shift distortion in the distribution of SPSP allele frequencies could be influenced by the high number of monomorphic loci observed in this population. Selectively neutral alleles at high frequencies can be fixed (i.e. allele frequency = 1) by random events, such as genetic drift, in small and isolated populations (Ridley, 2003). Hence, the high homozygosity and percentage of monomorphic loci observed in SPSP could be a result of: (1) allelic fixation by genetic drift; (2) a recent founding event by a population with already fixed alleles; or (3) inbreeding, although F_{IS} calculations were not consistent with this scenario, probably because this coefficient includes only loci with allele frequency $\neq 1$.

Landscape heterogeneity and the availability of nesting areas directly influence nest density, which could be affecting gene flow between SPSP and all other colonies. Brown boobies prefer flat and slightly sloping ground on the edges of cliffs for nest building, and colonies are composed of scattered groups of nests with irregular spacing, which usually ranges from .6 to 27 m in between (Nelson, 2005). This is the case of brown boobies from Moleques (Branco, Fracasso, & Moraes-Ornellas, 2013) and Cagarras (Alves, Soares, Couto, Efe, & Ribeiro, 2004), which prefer slightly sloping areas; while in Abrolhos, boobies preferably nest on cliff edges (Alves, Soares, Couto, Ribeiro, & Efe, 2000). Conversely, brown boobies from SPSP are mainly based in Belmonte Island, an area of 6,000 m^2 with a maximum altitude of 21 m, and ~250 nests located on the highest portion of the island in an area of only ~700 m^2 (Barbosa-Filho & Vooren, 2010). This aggregation results in a high-density colony with an average between-nest distance of ~1 m (Kohlrausch, 2003), generating fierce competition for space that causes injuries to adults and chicks, including cannibalism (Neves, Mancini, Marques, Nunes, & Bugoni, 2015). Therefore, living in SPSP apparently requires an ability to compete for nesting areas, which could promote population isolation by local adaptation and selection against immigrants.

Although the IBD model was not able to explain genetic diversity in south-western Atlantic brown boobies, geographical distance seems to influence between-colony genetic distance indirectly by influencing within-cluster environmental similarities. For example, the lowest pairwise geographical distances were found between Rocas and FN, as well as within coastal colonies, which are influenced by similar oceanographic dynamics. In tropical ocean waters, such as around FN and Rocas, productivity peaks are mainly associated with topography, creating a patchy pattern of nutrient distribution, as observed in the south-western Atlantic Ocean (Souza, Luz, Macedo, Montes, & Mafalda-Jr, 2013). Conversely, neritic environments, such as Moleques, Cagarras and Abrolhos, are characterized by increased primary productivity, as they are influenced mainly by the input of nutrients from river outflows (Santos, Muniz, Barros-Neto, & Araujo, 2008), continental shelf fronts (Acha, Mianzan, Guerrero, Favero, & Bava, 2004), and vortices generated by winds and slope topography (Odebrecht & Castello, 2001). Around Moleques, waters are fertilized by the Rio de la Plata plume (Möller-Jr, Piola, Freitas, & Campos, 2008) and are influenced by the Subtropical Shelf Front (Piola, Romero, & Zajaczkovski, 2008), which are key processes behind the high local productivity (Odebrecht & Castello, 2001). Input of nutrients around Cagarras is driven mainly by Guanabara Bay runoff, which is highly eutrophic (Kjerfve, Lacerda, & Dias, 2001), and the Cabo Frio upwelling system, which is an ascending process of the South Atlantic Central Water (Valentin, 2001). Finally, boobies from Abrolhos depend on the region influenced by the Caravelas River (Pereira, 2012), a nutrient-rich area supporting the second most complex mangrove system in the north-eastern region of Brazil (Herz, 1991). In summary, there are remarkable differences in oceanographic dynamics between the neritic and pelagic environments where the colonies are located, but high within-cluster similarity. Therefore, shorter geographical distances between archipelagos imply similar

environmental pressures, reducing selection against immigrants and promoting gene flow among nearby colonies.

In addition to differences in seascape features, species-specific behaviour could be contributing to local adaptation and population isolation. Brown boobies usually forage in regions of high productivity near their colonies during the breeding period, but show high variation with respect to foraging areas as they follow prey availability (Castillo-Guerrero, Lerma, Mellink, Suazo-Guillén, & Peñaloza-Padilla, 2016; Nelson, 2005). Breeding in SPSP occurs year-round (Barbosa-Filho & Vooren, 2010) and foraging trips by breeding adults last about 1 h, which take place within a ~9-km radius of the colony (Nunes et al., in prep.). The diet of these south-western Atlantic boobies is composed primarily by five flying-fish species (Both & Freitas, 2001). In comparison, brown boobies from Anguilla, an island in the Caribbean, feed within a ~40-km radius around the colony, with a total trip duration of ~5:30 h (Soanes et al., 2016), while boobies from Isla San Jorge, Gulf of California, prey on up to 36 species (Castillo-Guerrero et al., 2016). These differences in foraging behaviour, along with year-round breeding activities, illustrate that there is plenty of food near SPSP throughout the year, suggesting that it is not necessary for the boobies to fly far from the colony, even during the non-breeding period, to find food. Although there is no information about the non-breeding distribution of brown boobies from SPSP, the high number of non-breeding individuals using SPSP as a resting site suggests that boobies stay in the colony throughout the year (Barbosa-Filho & Vooren, 2010), which is also likely to be a factor for gene flow disruption in seabirds (Friesen, 2015).

Between-colony diet differences seem to be primarily associated with available resources around the colonies, as has been demonstrated by analyses of regurgitated material and stable isotope studies carried out within our study area (Alves et al., 2004; Both & Freitas, 2001; Branco, Fracasso, Machado, Bovendrop, & Verani, 2005; Mancini et al., 2014; Nunes et al., in prep). Nevertheless, isotopic data were insufficient to explain the population structure of brown boobies in the south-western Atlantic Ocean, an observation that could be related to shortcomings of method and sampling design. First, comparing isotopic niches may be deceptive, as it is sensitive to differences in isotopic composition of resources between distinct systems, such as neritic and pelagic (Newsome, del Rio, Bearhop, & Phillips, 2007). A potential way of overcoming this problem would be by transforming δ data in terms of the proportional incorporation of different resources into the boobies' blood (p-space; Newsome et al., 2007), but isotopic data from potential prey for each colony are lacking. Secondly, substantial differences were observed between Abrolhos and the remaining colonies, including the coastal ones, which were expected to have similar niche widths. This could be linked to the fact that comprehensive sampling was carried out during both summer and winter seasons in Abrolhos (Mancini et al., 2014), while Cagarras and Moleques were sampled only during the summer. Seasonal variations in environmental conditions are more pronounced on the continental shelf than in the pelagic tropical archipelagos, where oceanographic dynamics tend to be stable throughout the year (Soares, Oliveira, Codato, & Escobedo, 2012; Souza et al., 2013). As a consequence, isotopic values vary in space and time in coastal colonies in response to oceanographic processes, requiring a sampling design to accommodate these shortcomings (Kurle & McWorther, 2017). Hence, sampling brown boobies at Moleques and Cagarras in both summer and winter could make the isotopic niche width of coastal colonies more comparable and similar, and contribute to explaining genotypic differences between FN/Rocas and coastal colonies.

Interestingly, a trend of northward dispersal was observed in the coastal cluster, with high emigration rates from Moleques. Moleques was also shown to contribute 6% and 8% of each generation to Rocas and FN, respectively. Brown boobies from Moleques are known to be strongly dependent upon shrimp fishery by-catch as a food source (Branco et al., 2005), so that annual fluctuations in shrimp catches influence the number of eggs laid by the population (Branco et al., 2013). Individuals banded in Moleques have already been recaptured at the latitudes of Cagarras, Abrolhos, Rocas and FN (Efe et al., 2006), illustrating the ability to fly over large distances. Foraging plasticity to deal with environmental changes has been demonstrated in brown boobies in the Gulf of California, where diving depths and prey sizes appear to be annually adjusted according to environmental fluctuations (Castillo-Guerrero et al., 2016). Therefore, considering that brown boobies have opportunistic feeding habits and high behavioural plasticity, annual fluctuations in food availability could be influencing the northward dispersal of boobies from Moleques.

Ecotype-based clustering is known to occur not only among seabirds but also in other marine top predators. For example, seascape covariates were demonstrated to influence gene flow among populations of the short-beaked common dolphin (Amaral et al., 2012), the Hawaiian monk seal (Schmelzer, 2000) and the Atlantic bluefin tuna (Riccioni et al., 2013). Spatial autocorrelation among sampling locations is common, so that environmental distance can be confounded with geographical distance. However, gene flow disruption between relatively close breeding sites, as observed between SPSP and FN/Rocas, suggests the importance of additional drivers of population isolation. Finally, identifying evolutionary processes of population differentiation should be of paramount importance for management programmes, as understanding within- and between-colony relationships is crucial for defining management units, as well as local and global conservation priorities.

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BIOSKETCHES

Guilherme T. Nunes is broadly interested in evolutionary ecology with a special focus on the mechanisms of population differentiation in marine top predators. His main projects involve identification of selective pressures shaping phenotypes and genotypes of tropical seabirds.

Leandro Bugoni's research interests include trophic ecology and conservation of marine vertebrates, mainly using stable isotopes and biologging to understand how seabirds and sea turtles use food resources and interact with human-related threats.

Author contributions: G.T.N. and L.B. conceived the ideas; G.T.N. collected samples and data; G.T.N. analysed the data; and G.T.N. and L.B. wrote the paper. This study is part of the Ph.D. Thesis of G.T.N. supervised by L.B.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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