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RESEARCH

Absence of genetic structure among ecologically diverse populations indicate high plasticity in a pantropical seabird

Mariana Scain Mazzochi[1,2] · **Vitória Muraro**[1,2] · **Nelson Jurandi Rosa Fagundes**[3,4] · **Leandro Bugoni**[1,2]

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Abstract

Genotype and phenotype in mobile organisms can be defined by various factors such as environmental, biological and geographical. Brown noddies *Anous stolidus* are pan-tropical seabirds breeding at different times, with migratory and resident populations in six islands throughout 20° of latitude in the Southwestern Atlantic Ocean. If environmental heterogeneity plays a key role in their population biology, we would expect significant genetic structure among colonies. However, absence of genetic structure between phenotypically different populations could play a scenario of ecological plasticity. To test these hypotheses, we used a model-based integrative approach combining genetic (mtDNA and ultraconserved elements) and morphological data of the brown noddy ($n = 122$) along with environmental variables and isotopic niches. We uncovered low levels of genetic structure, with 16 haplotypes for mtDNA and a signal of an ancient population expansion. Ultraconserved elements indicated that all colonies belong to the same genetic population ($K = 1$) and revealed substantial endogamy. However, phenotype differed both by biometric measures and isotopic niches between most pairs of populations. Although individuals from the northernmost colony are larger than the others, they are genetically similar, indicating a wide reaction norm for this species. Our results indicate the Southwestern Atlantic populations of the brown noddy are panmictic, but ecologically and morphologically diverse.

Keywords Gene flow · Panmictic · Phenotypic plasticity · Reaction norm · Seabird paradox

Introduction

Genetic structure may arise in ecologically homogeneous populations if gene flow is limited by intrinsic biological features of the species, like low dispersion capacity, which would set up a case of isolation by distance (Wright 1943). Interruption of gene flow may be facilitated by ecological heterogeneity and local adaptation in isolation by environment (Wang and Bradburd 2014). On the other hand, the absence of genetic structure in the presence of ecological heterogeneity would be indicative of phenotypic plasticity: the ability of a single genotype of creating different morphological, physiological or behavioural states in response to environmental conditions (West-Eberhard 1989).

Different combinations of factors lead to contrasting and unexpected patterns of genetic structure between species of seabirds: some with great dispersal potential, such as the wedge-tailed shearwater *Ardenna pacifica*, may maintain genetically isolated populations throughout their distribution (Herman et al. 2022); whereas less mobile species may either present contemporary gene flow (Faria et al. 2010) or fine-scale genetic structure due to ecological constraints (Garrett et al. 2020). For this reason, this group includes unique model organisms to investigate the interaction between genetic and ecological structures. Although seabirds are mostly philopatric, they are still highly mobile species (Coulson 2001), and thus other notorious factors may

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✉ Mariana Scain Mazzochi
marianasmazzochi@gmail.com

[1] Programa de Pós-Graduação em Oceanografia Biológica, Instituto de Oceanografia, Universidade Federal do Rio Grande – FURG, Rio Grande, Rio Grande do Sul, Brasil

[2] Laboratório de Aves Aquáticas e Tartarugas Marinhas, Instituto de Ciências Biológicas, Universidade Federal do Rio Grande – FURG, Campus Carreiros, Rio Grande, Rio Grande do Sul, Brasil

[3] Programa de Pós-Graduação em Genética e Biologia Molecular, Universidade Federal do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brasil

[4] Programa de Pós-Graduação em Biologia Animal, Universidade Federal do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brasil

affect their gene flow: physical barriers, oceanographic factors, demographic history and biotic features, e.g. allochronic reproduction and morphology (Lombal et al. 2020).

Pan-tropical seabirds, such as the brown noddy *Anous stolidus*, are under varying oceanographic and environmental conditions throughout their distribution. This species is one of the most common seabirds globally, distributed all over the tropical region. Estimated population size ranges from 800,000 to 14,000,000 individuals (BirdLife International 2023) adapted to different environments, from zero-latitude to cold-temperate islands (40°S). In the Southwestern Atlantic Ocean, brown noddies aggregate at six archipelagos and islands throughout 20° of latitude. One archipelago is on the continental shelf while the others are further offshore, so oceanographic factors (e.g. chlorophyll α production, sea surface temperature) are different between their surroundings (data via Bio-ORACLE), as well as their degree of geographic isolation. In this oceanic region, brown noddy populations also present ecological variation between populations: they exhibit at least three different breeding schedules (in Trindade Island, birds breed at a unique period) and both migratory and resident groups, sometimes even varying between these two behaviours (Fig. 1). Dispersal capacity and dispersion patterns are not well known for brown noddies, except for some records of supposedly vagrant individuals. Understanding the interplay between environment, genotype and phenotype is essential to delimitate evolutionary significant units, especially in ecologically diverse species.

Different genetic markers can be used to understand genetic structure and historic processes in populations of seabirds (e.g. Byerly et al. 2023; Goméz-Díaz and González-Solís 2007; Obiol et al. 2021). Mitochondrial DNA (mtDNA) facilitates the detection of demographic events (e.g. Peck and Congdon 2004), but its exclusive maternal inheritance and non-recombining nature may affect some statistics, which generally are expected to exceed nuclear ones (Zink and Barrowclough 2008). Ultraconserved elements (UCEs), on their turn, represent multiple loci and are near-universal conserved in distinct taxa due to high levels of purifying selection in their core. Flanking regions, however, tend to be less subjected to selection and thus maintain information about evolutionary history of species (Winker et al. 2018). UCEs are useful for recovering from phylogenetics to shallower-level population relationships (Winker et al. 2018). Furthermore, this tool allows assessment of the genetic variation in non-model organisms and has recently gained popularity in studies with birds (e.g. Mason et al. 2018; Oswald et al. 2016).

Genome-wide markers have already successfully detected genetic structure in invertebrates such as waterfleas (Orsini et al. 2012), in marine (Lah et al. 2016) and terrestrial mammals (von Takach et al. 2022), and also in birds (Zarza et al. 2016; Harvey et al. 2017). In seabird populations, genetic structure has been assessed using genomic (Rexer-Huber al. 2019) and conventional methods (Herman et al. 2022). Absence of gene flow had been detected both between (Morris-Pocock et al. 2010) and within (Nuss et al. 2016) ocean basins. Some populations of terns (Charadriiformes: Sternini) present genetic structure between distant colonies (Byerly et al. 2023) but also between temporally isolated individuals breeding at the same location (Garrett et al. 2020). Genetic isolation had also been reported between

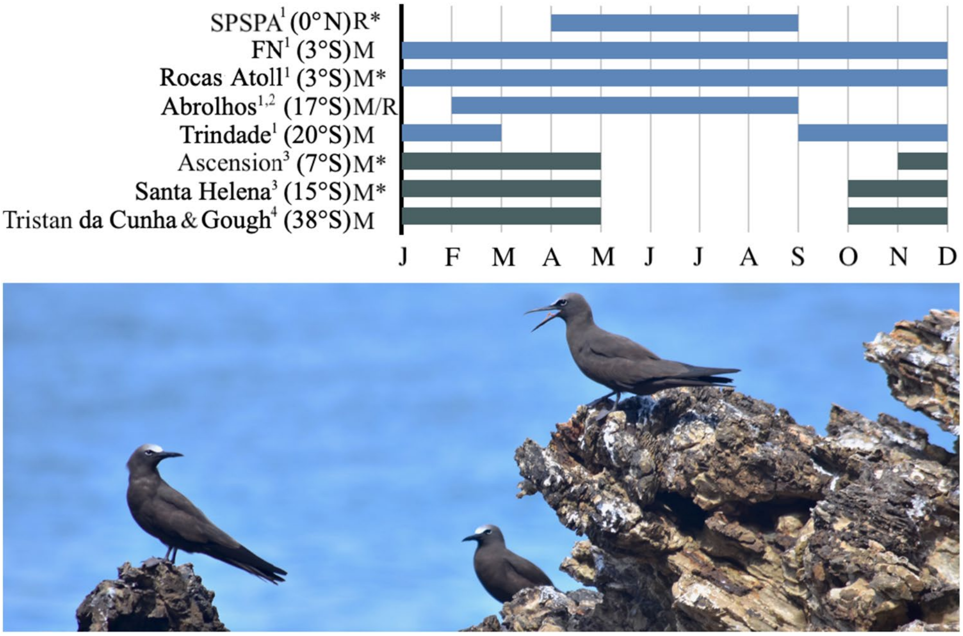

Fig. 1 Breeding phenology of brown noddies *Anous stolidus* on South Atlantic islands. In blue, the populations included in this work. Horizontal axis presents the months. M – migratory; R – resident; * – uncertain (Murphy 1936; Branco 2004). SPSPA - São Pedro e São Paulo Archipelago; FN - Fernando de Noronha Archipelago. [1]Mancini et al. (2016); [2]Campolina et al. 2002; [3]Dorward and Ashmole (1963); [4]Wilson et al. (2010). Below, individuals at Santa Bárbara Island, Abrolhos Archipelago. Photo by MSM

populations of other seabird species breeding at the same colonies of brown noddies at Southwestern Atlantic Ocean (Nunes and Bugoni 2017). Here, we use data from mtDNA and UCEs to estimate the degree of genetic structure among those six brown noddy populations and its relationship with oceanographic factors and isotopic niche, breeding phenology and morphology. We expected that populations exhibiting phenotypic differences would likely constitute distinct genetic units, particularly when they are ecologically different, such as Trindade and Martin Vaz colonies.

Materials and methods

Study area

The six populations of brown noddies (Fig. 2) are distributed in the Southwestern Atlantic Ocean on a latitudinal gradient from 0° (SPSPA) to 20° (Trindade), and the distances from the islands to the coast are between 65 km (Abrolhos) and 1200 km (Trindade). Distances between colonies vary from ~49 km (between Trindade and Martin Vaz) to ~2400 km (between SPSPA and Trindade). Between 2010 and 2012, colony sizes were ~300 (SPSPA), ~500 (Trindade), ~600 (FN), ~4000 (Rocas) and ~4700 (Abrolhos) individuals

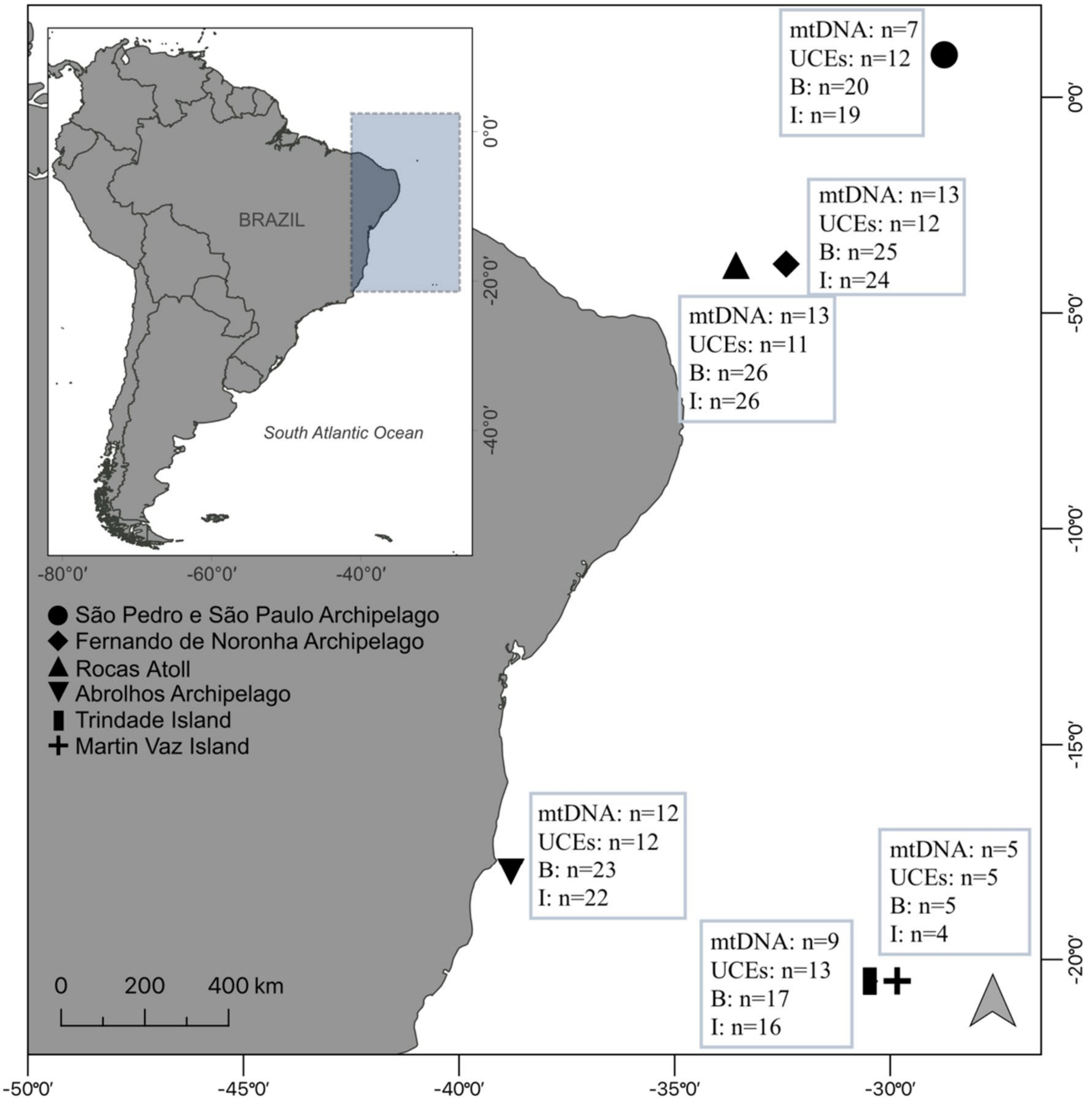

Fig. 2 Colonies of brown noddies *Anous stolidus* in the Southwestern Atlantic Ocean, where sampling had occurred. Sample sizes for each data set are indicated inside squares. B – biometric measures; I – stable isotope analysis

(Mancini et al. 2016). “Colony” was considered as a synonym of “population” throughout the methodology description.

Sampling, DNA extraction and sexing

We sampled 122 individuals from the six colonies between 2007 and 2012 ($n = 113$) and in 2021 and 2022 ($n = 9$). Individuals were captured with dip nets and contained for sampling. Blood was collected from the tarsal vein and stored in absolute ethanol, and a drop of blood from the 2007–2012 samples was also added to FTA® cards for sex determination (Mancini et al. 2016). We obtained measures from individuals in all colonies, except Trindade: culmen and tarsus, measured with a caliper; and tail and wing length, using metal rules. Tail length was not measured for birds in Martin Vaz colony. Individuals were also weighed with Pesola® spring scales.

We extracted DNA from blood samples using the DNeasy Blood & Tissue Kit (QIAGEN) following the manufacturer’s protocol. DNA samples were quantified with a Qubit Invitrogen fluorometer. The sex of individuals was determined through the PCR amplification of CHD genes following Griffiths et al. (1996). Some individuals ($n = 78$) were sexed using the same method, and reported in Mancini et al. (2016).

Mitochondrial markers

Mitochondrial DNA fragments of the ATP synthase 6 and 8 (ATPase 6/8) and NADH dehydrogenase 2 (ND2) genes were amplified by PCR. These markers are among the most variable mitochondrial markers for birds (Faria et al. 2007). Primers and whole PCR protocols are available in Supplementary Online Material 1. PCR products were checked by eye using agarose gel electrophoresis with GelRed® and purified with ExoSAP-IT™ prior to sequencing.

PCR products were Sanger sequenced at Macrogen, Inc. (South Korea). Chromatograms were filtered with SnapGene v. 6.0 (Insightful Science; available at snapgene.com) and those with low quality were discharged. We obtained $n = 65$ sequences for ATPase6/8 and $n = 109$ for ND2, and aligned with Molecular Evolutionary Genetics Analysis v. 10.2.6 (MEGAX; Stecher et al. 2020). Sequences were concatenated in RStudio v. 1.4.1717 (RStudio Team 2023) with the package *ape* (Paradis and Schliep 2019) for the individuals of which both markers were successfully sequenced ($n = 59$).

We used DNA Sequence Polymorphism v. 6 (Rozas et al. 2017) to prepare data for Arlequin 3.5.2.2 (Excoffier and Lischer 2010), in which we calculated Tajima’s D (Tajima 1989), Fu’s Fs (Fu 1997), a molecular analysis of variance (AMOVA) using pairwise differences and standard genetic diversity indexes. We calculated these metrics for both individual genes and for the concatenated dataset. Pairwise differences were used to calculate F_{ST} between populations with Holm-Bonferroni corrections for multiple comparisons. We also used the packages *pegas*: Population and Evolutionary Genetics Analysis System (Paradis 2010) and *adegenet* (Jombart 2008) to build the median-joining haplotype network.

To estimate the effective population size change over time we performed a Bayesian Skyline Plot (BSP; Drummond et al. 2005) with the concatenated genes in BEAST 2 (Bouckaert et al. 2014) and Tracer v. 1.7.1. (Rambaut et al. 2018). We obtained the best nucleotide substitution model for each marker using all codon positions in MEGAX under the Akaike’s information criterion (HKY for both markers). We chose a strict molecular clock because it is often used in analyses of data at the intraspecific level (Ho and Duchêne 2014). We used different rates for each gene (and their confidence intervals) estimated from mean body mass of sampled individuals, following Nabholz et al. (2016). We estimated the species’ generation time based on estimates of sexual maturity (3–7 years; Brown and Robertson 1975; Chardine et al. 2020), mean survival rate (88%; Morris and Chardine 1995; Chardine et al. 2020) and lifespan (maximum of 25 years; Brown and Robertson 1975; Clapp et al. 1982), resulting in an estimate of 9.6 years/generation. We run the MCMC for 50,000,000 iterations, sampling every 1000 iterations and discarding the initial 5,000,000 of the chain as burn in. Effective sample sizes (ESSs) for all relevant parameters were > 200, as was estimated within Tracer, considering ESS > 200 as representative of *a posteriori* distributions.

Bioinformatics pipeline for variant calling of ultraconserved elements

Samples of 67 individuals were sequenced by Rapid Genomics LLC using the *tetrapod2,5k* probe and 2 million reads per sample. We used *illumiprocessor* (Faircloth 2013) with the package *trimmomatic* (Bolger et al. 2014) to process reads from Illumina and performed the assembly of contigs, identification of UCEs and alignment of sequences with *phyluce* (Faircloth 2015). We then ran BLAST+ (Camacho et al. 2009) with the probe set against the zebra finch *Taeniopygia guttata* total mitochondrial genome (NCBI; ref: NC_007897.1) and Z chromosome (NCBI; ref: NC_044241.2) in order to remove non-autosomal UCE loci. Then, the longest sequence was used as a reference in the Genome Analysis Toolkit 4.3.0 (Van der Auwera and O’Connor 2020) to call single nucleotide polymorphisms (SNPs) for each individual. We used the packages BWA (Li and Durbin 2009) and SAMtools 1.9 (Danecek et al. 2021) to index the reference sequence, output and sort bam files for each individual through GNU parallel (Tange 2018). Duplicates were removed with MarkDuplicatesSpark and performed haplotype calling with HaplotypeCaller 4.3.0 (Poplin et al. 2017).

We filtered genotypes with vcftools (Danecek et al. 2011) setting the minimum Q, DP and GQ values to 30. Base quality score recalibration was performed with BaseRecalibrator and ApplyBQSR. We were not able to filter variants by quality score recalibration because high-quality sets of known variants to use as training and truth resources are not available for brown noddies. Instead, we performed hard filtering with VariantFiltration. Finally, we removed multiallelic loci and, to avoid retaining linked variants in the final dataset, we selected the first polymorphism detected in each locus with vcftools.

Genetic structure with UCE's loci

We estimated genetic structure among brown noddy populations using three different methods. Firstly, we used STRUCTURE (Pritchard et al. 2000) software to estimate the most adequate number of genetic groups (K) through log-normal probability of data (LnK). We performed analysis with $K = 1$ to 7 with 250,000 Markov chains via Monte Carlo (burn-in: 100,000), and 5 iterations per K. We evaluated performance through Structure Harvester (Earl and vonHoldt 2012) and CLUMPAK (Kopelman et al. 2015), and chains which presented outlier variance of likelihood values were substituted by new ones. We also compared STRUCTURE results with sNMF (Frichot et al. 2014) from the LEA package (Frichot and Francois 2015) with $\alpha = 100$ and 100 repetitions. Then, we performed a discriminant analysis of principal components with the packages *adegenet* (Jombart 2008) by retaining 67 principal components in the principal component analysis and 40 in the discriminant analysis. We selected the best K based on Bayesian information criterion.

A Bartlett test of homogeneity of variances between the values of expected and observed heterozygosity (for the metapopulation and for the six populations) was calculated for all UCEs loci with the package *hierfstat* (Goudet and Jombart 2022) in RStudio. We also performed an AMOVA to estimate F_{IS} and F_{ST} over all loci with Arlequin 3.5.2.2 (Excoffier and Lischer 2010). Pairwise F_{ST} (Weir and Cockerham 1984) and per population F_{IS} were calculated with the same package. We estimated effective population size (N_e) using the linkage disequilibrium method of Waples and Do (2010) as implemented in NeEstimator V2.1 (Do et al. 2014). Migration rates between each pair of populations were calculated in BayesAss-SNPs v. 3.0.4 (Wilson and Rannala 2003; Mussmann et al. 2019) with 20,000,000 iterations (burn-in: 10,000,000) and spacing 2,000 iterations between samples. To check for convergence, we performed two runs with different seeds and combined them in Tracer v. 1.7 (Rambaut et al. 2018). We also estimated theta ($\theta = 4N_e\mu$) with Migrate (Beerli et al. 2019). Due to computational constrains, we thinned the full 2062 SNPs database in four files of ~500 SNPs. We ran each file using 2,000,000 iterations (burn-in: 10,000) and 200 iterations between samples, assuming a finite sites mutation model and a constant mutation rate. Genome mutation rate was estimated using the equation in Lynch (2010) assuming a haploid genome size of 1.2 Gbp based on data for the South American tern *Sterna hirundinacea* (Sternini), which is the closest taxon with available information for the genome size (NCBI; ref: PRJNA558062).

Relationship between genetic, environmental and geographical distances

We obtained values for sea surface temperature (SST; °C), salinity (PSS) and chlorophyll α concentration (μg/L) (the last two measured at the top of the water column) from Bio-ORACLE with RStudio, using the package *sdmpredictors* (Bosch and Fernandez 2022). We extracted monthly means between 2000 and 2014 with 0.25 arc degrees of resolution and cropped raster files using the package *raster* (Hijmans 2022), following a maximum foraging range (a circular area around the colonies) of 100 km (Surman and Wooller 2003; Perez-Correa et al. 2020). Chlorophyll α concentration was used as a *proxy* for primary productivity (Huot et al. 2007).

Carbon and nitrogen stable isotope values were used to infer foraging area and trophic level of populations (Fry 2006), which are related to primary productivity, seasonality and complexity of trophic web, and thus could result from different selective pressures exerted by the distinct environments (Friesen 2015). We lyophilized total blood samples, weighted them on a precision scale and then transferred to tin capsules. Part of samples ($n = 72$) had stable isotopes analyzed at the Laboratory of Analytical Chemistry from University of Georgia (see Mancini et al. 2014), while others ($n = 40$) were analyzed at Centro Integrado de Análises from Universidade Federal do Rio Grande (CIA-FURG). We expressed values as ‰ in delta (δ) notation:

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

in which R = $^{13}C/^{12}C$ or $^{15}N/^{14}N$. International standards for carbon and nitrogen were VPBD (Vienna Pee Dee Belemnite limestone) and atmospheric air, respectively. Laboratory standards were analyzed every 12 samples: at CIA, cane and beet sugar for carbon, and glutamic acid, caffeine and ammonium sulfate for nitrogen; at LAC, bovine liver for carbon and poplar leaf for nitrogen. Because there were differences in $\delta^{13}C$ and $\delta^{15}N$ values measured between labs (Student's paired t-test = − 2.59 for $\delta^{13}C$ and 4.46 for $\delta^{15}N$,

$n = 10$, $p < 0.05$) we adjusted values from CIA to LAC labs using a linear regression, making values from different labs comparable. We estimated isotopic niches through standard ellipse areas (SEA) with 40% confidence intervals and standard Bayesian ellipse areas ($\mathrm{SEA_b}$) using the package SIBER: Stable Isotope Bayesian Ellipses in R (Jackson et al. 2011). Overlap between ellipses was estimated as a proportion of the non-overlapping area of each two ellipses by using 95% prediction intervals.

Finally, we estimated geographic distances between pairs of islands and between each island and the South American coast in Google Earth by marking a central point in each island or archipelago. Because the relationship between genetic and geographical distances is not linear, we divided the geographic distance matrix in five different intervals, so we could obtain a more accurate description of the spatial patterns (Diniz-Filho et al. 2013). We centralized these values and performed a Mantel's correlogram with 1000 permutations with Pearson's correlation. We also performed conventional Mantel tests using Pearson's correlation between centralized genetic (mtDNA and UCEs), environmental and geographical distances. Environmental variables and distances between each island and the continent were transformed into Mahalanobis distances. All analyses were performed in *vegan* (Oksanen et al. 2020).

Relationship between genetic structure and breeding phenology

We performed an AMOVA considering four different population groupings (Fig. 1). To our knowledge, there are no records of brown noddies breeding at Martin Vaz. However, we have registered adult individuals apparently returning to the same rocks in consecutive days on February 2022 (BA Linhares, FURG, pers. comm.). Thus, we performed two alternative groupings for Martin Vaz: one pooled with Trindade Island assuming both populations reproduce at the same period due to their proximity; and another assuming that they breed on a different period. Also, individuals from SPSPA and Abrolhos have overlapping breeding seasons (but not exactly the same period). Therefore, we performed one AMOVA pooling and another considering different reproductive periods. We used Holm-Bonferroni corrections for multiple comparisons.

Sexual size dimorphism and morphometric differences between populations

We generated *a posteriori* values from morphometric measures of males and females via MCMC ($n = 95$; except for tail length which was $n = 91$, as this trait was not measured for Martin Vaz birds). As we have not measured Trindade island individuals, this population was excluded. We used jagsUI (Kellner 2019) in RStudio (RStudio Team 2023) to generate three chains with 12,000 iterations (burn-in: 2000). *A priori* distributions were vague: $\tau \sim$ Gama (0.01, 0.01) and $\mu \sim N^*(mA, 10^{-6})$, with mA being the mean of each sampled morphometric measure by sex. Intervals of 95% maximum density from *posteriori* distributions were calculated using *HDInterval* (Meredith and Kruschke 2020), and we compared distributions through Bayes Factor (Kinas and Andrade 2010) considering identical *a priori* chances for or against the hypotheses that females and males present the same biometrical measures.

Because males and females differed in size, a multivariate analysis of variance (MANOVA) was performed for each sex between islands. As the residuals deviated from multivariate normality and normalization was not effective, we executed non-parametric multivariate tests using the package *npmv* (Burchett et al. 2017): to compare all populations, a MANOVA with Muller's approximation to Pillai's trace; to perform post-hoc comparisons, an ANOVA-type non-parametric test (with F-approximations). P-values were estimated through permutations and, when too low, we were not able to estimate them ($p < 0.001$).

Finally, to test the association between genetic distances and differences in biometrical measures, we separated biometric data by sex. Individuals from Martin Vaz and Trindade were not included, for which some measurements were not available. We performed a Principal Component Analysis using vegan (Oksanen et al. 2020), and used the Euclidean distance between mean values of the first principal component (for males and females) as an estimate of the morphological distance between populations. We then performed a Mantel's test between genetic (both mtDNA and UCEs) and morphological distance matrices.

Results

Mitochondrial markers

We obtained a ~ 520 bp fragment for ND2 and a ~ 820 bp fragment for ATPase6/8. There were 11 haplotypes for the first marker ($n = 109$) and 9 for the second one ($n = 68$), respectively, which combined ($n = 59$) into 16 haplotypes (diversity values for individual markers are in Supporting Online Information Tables S1 and S2). Lowest diversity values were the ones found in Abrolhos population, followed by Rocas, SPSPA, Trindade and Martin Vaz (Supporting Online Information 2 table S3). We found a deviation from neutrality in the metapopulation (Tajima's $D = 1.44$, $p = 0.04$; Fu's $Fs = -6.9$, $p = 0.005$), suggesting a demographic expansion, which is in agreement with the estimates from the Skyline plot (Supporting Online Information 2 Figure S1) and the star-shaped haplotype network. AMOVA showed

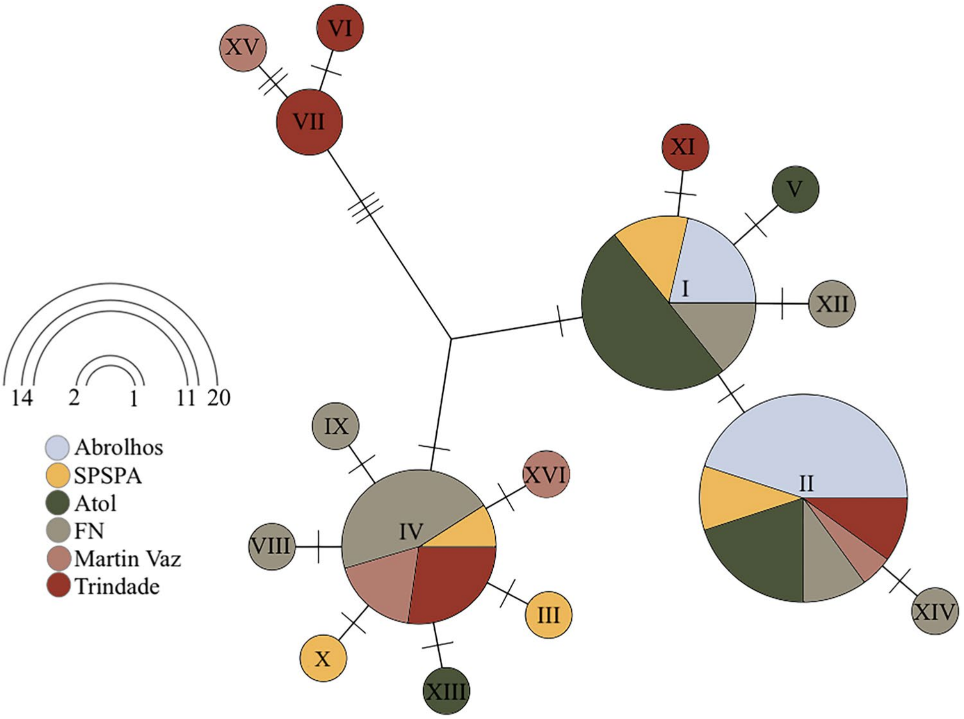

Fig. 3 Haplotype network of six populations of brown noddies from Southwestern Atlantic Ocean built from ND2 and ATPase6/8 markers. Roman numerals stand for the sixteen haplotypes. Pie charts size represent the number of individuals that present a certain haplotype, and colors indicate the percentage of individuals belonging to each population. Each smaller line perpendicular to the main connecting lines represents a mutation. SPSPA - São Pedro e São Paulo Archipelago; FN - Fernando de Noronha Archipelago; Rocas - Rocas Atoll

Table 1 Genetic distances matrix (F_{ST}) of ND2 and ATPase 6/8 genes for six populations ($n = 59$) of brown noddies from the Southwestern Atlantic Ocean, calculated by pairwise differences

	FN	Abrolhos	Rocas	SPSPA	Trindade
Abrolhos	**0.37**				
Rocas	0.18	0.17			
SPSPA	− 0.07	**0.32**	0.08		
Trindade	0.07	**0.37**	**0.22**	0.03	
Martin Vaz	− 0.01	**0.52**	**0.32**	− 0.01	− 0.08

FN Fernando de Noronha Archipelago; *Rocas* Rocas Atoll; *SPSPA* São Pedro e São Paulo Archipelago

Bold values are statistically significant ($p < 0.05$)

Table 2 Pairwise fixation indexes (F_{ST}) estimated from 2062 SNPs belonging to UCEs loci of six populations ($n = 67$) of brown noddies *Anous stolidus* in Southwestern Atlantic Ocean. All values are statistically significant ($p < 0.05$)

	FN	Abrolhos	Rocas	SPSPA	Trindade
Abrolhos	0.044				
Rocas	0.009	0.041			
SPSPA	0.009	0.047	0.017		
Trindade	0.022	0.056	0.028	0.029	
Martin Vaz	0.077	0.043	0.090	0.081	0.050

FN Fernando de Noronha Archipelago; *Rocas* Rocas Atoll; *SPSPA* São Pedro e São Paulo Archipelago

that 18% of the genetic variation occurs among populations while 82% occurs within populations ($F_{ST} = 0.18$, $p < 0.05$). In relation to pairwise genetic distances between populations, Trindade and Martin Vaz against Abrolhos and Rocas were the highest values of F_{ST} and Abrolhos was the only population showing statistically significant values against all remaining populations (Table 1). Most haplotypes were common to all populations (Fig. 3).

UCEs

After quality filtering and retaining one SNP per UCE locus, our final dataset included 2062 SNPs. The best number of genetic populations were $K = 1$ in both STRUCTURE and DAPC (Supporting Online Information 2 Figure S2), while for sNMF the best value was $K = 2$ (Supporting Online Information 2 Figure S3). However, individuals showing high loads for either genetic ancestry component were found in different islands, and no obvious geographic pattern exists for $K = 2$ (Supporting Online Information 2 Figure S4). There was a deficit of heterozygosity in all populations except Martin Vaz (F_{IS} range: 0.39–0.44) and a low effective population size (NeEstimator range: 42.1–72.7; Migrate range: 390–1604, Supporting Online Information Table S4). AMOVA showed that most genetic structure occurs due to inbreeding rather than population structure ($F_{IS} = 0.42$ vs. $F_{ST} = 0.03$, $p < 0.005$ for both estimates), in agreement with pairwise estimates of population genetic structure (Table 2). Genetic assignment of individuals as residents vs. migrants suggested that the population with the highest rate of residents is Rocas, which is also the source of most migrants towards other populations (Supporting Online Information 2 Table S5), even though the overall genetic similarity among populations may complicate these estimates.

Relationship among genetic, environmental and geographical distances

Isotopic niche areas (Standard Bayesian Ellipses Areas) ranged from 8.82×10^{-2} at Martin Vaz to 6.18 at Fernando de Noronha, and the proportional highest overlap of standard/Bayesian ellipse areas was between Rocas Atoll and Fernando de Noronha Archipelago (0.24; Fig. 4a, b).

Using mtDNA data, population pairs separated by intermediate distances (~ 1000–1500 km) had the highest modular value of Mantel's correlation, although not statistically significant (Supporting Information 2 Figure S5, Table S6). For the conventional Mantel's tests, mtDNA genetic distances only presented statistically significant correlation ($p < 0.05$) with the matrix of distances from the coast ($r = 0.53$, $p = 0.006$, Supporting Information 2 Figure S6a), whereas none of the matrices correlated with nuclear genetic distances ($p < 0.05$). Some environmental variables dissimilarity indexes were also correlated (Supporting Information 2 Figure S6a), as well as the Z-scores of salinity and SST (Supporting Information 2 Figure S6b).

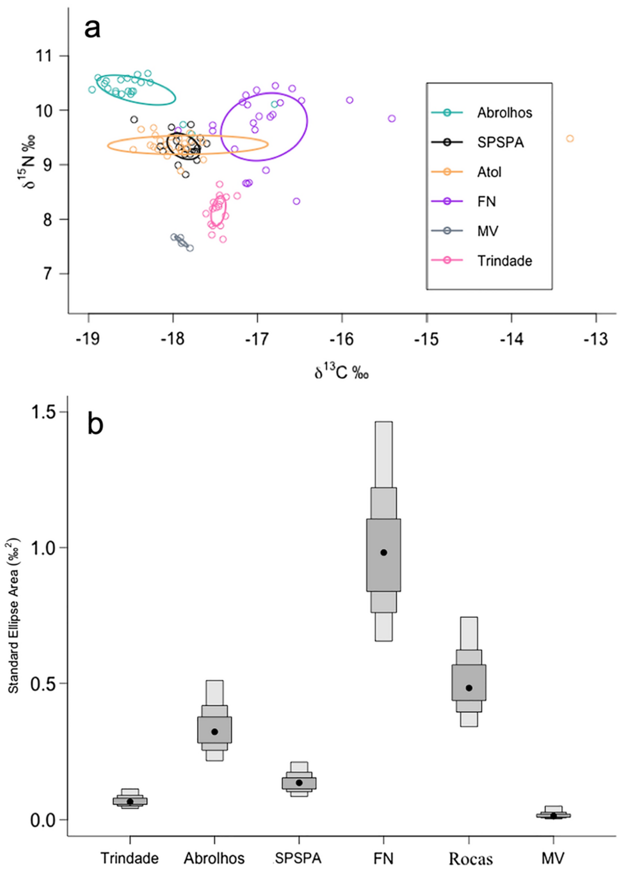

Fig. 4 **a** Estimates of isotopic niche breadth (δ^{13}C e δ^{15}N) of the brown noddy *Anous stolidus* at Southwestern Atlantic Ocean, represented by Standard Ellipses Area – SEA with 40% confidence intervals. **b** Posterior Bayesian estimates of isotopic niche represented by Standard Bayesian Ellipses Area - SEA_b. Black circles are the modes for the posterior distribution of each population, and boxes represent confidence intervals of 50%, 75% and 95%. SPSPA - São Pedro e São Paulo Archipelago; FN - Fernando de Noronha Archipelago; Rocas - Rocas Atoll; MV - Martin Vaz

Relationship between genetic structure and breeding phenology

Analysis of molecular variation showed that the grouping with highest percentage of variation between populations was that including Fernando de Noronha with Rocas Atoll and Trindade with Martin Vaz (16.3%; Supporting Information 2 Table S7). However, this value was lower than the one observed when groupings were formed with the original individual populations (18%).

Sexual size dimorphism and morphometric differences between populations

We identified 50 females and 65 males. For all measurements and their respective posterior distributions, males were larger than females (Supporting Information 2 Figure S7, Table S8). For both sexes, grouping of the five measures was statistically different among populations (non-parametric MANOVA, males: $V = 4.97$ and $p < 0.001$; females: $V = 2.91$ and $p = 0.002$; Supporting Information 2 Figure S8). In the pairwise comparisons, the largest difference was between SPSPA and Rocas for males; and between SPSPA and Abrolhos for females (Table 3). In the PCAs, PC1 retained 46.6% and 50.1% of the variance for males and females, respectively. Variable that most contributed to PC1 was wing for both males and females, with 28% and 28.1%. Correlations between matrices of nuclear/mitochondrial genetic distances and biometric measures of males and females were absent.

Discussion

We uncovered low levels of genetic structure between brown noddy colonies within most of their breeding range in the Southwestern Atlantic Ocean. F_{ST} values are low for all comparisons using SNPs (Table 2), and for most comparisons using mtDNA (Table 1). However, mtDNA revealed a larger structure between Trindade/Martin Vaz and other populations. Neither geographic distance nor environmental factors seem to have a role in interrupting gene flow, even though colonies experience different recent or ongoing

Table 3 ANOVA-type non-parametric test (with *F*-approximations) for biometrical measures of brown noddy *Anous stolidus* populations ($n = 91$) in the Southwestern Atlantic Ocean. Results for males are below the main diagonal, and females are above. Statistically significant values are bold. *P*-values are presented between brackets and, when they were too low ($p < 0.001$), we were not able to estimate them (-)

	Abrolhos	Rocas	FN	SPSPA
Abrolhos	*	**3.71 (0.036)**	3.71 (0.153)	**13.84 (<0.001)**
Rocas	**3.42 (0.02)**	*	0.54 (0.683)	**7.59 (0.005)**
FN	**3.97 (0.01)**	**7.89 (<0.001)**	*	1.55 (0.346)
SPSPA	**12.98 (<0.001)**	**19.14 (<0.001)**	**7.27 (<0.001)**	*

SPSPA São Pedro e São Paulo Archipelago; *FN* Fernando de Noronha Archipelago; *Rocas* Rocas Atoll

Bold values are statistically significant ($p < 0.05$)

local pressures, which is reflected in their different isotopic niches. Allochronic populations were also pooled as a single genetic unit, which suggests ecological plasticity in breeding phenology; furthermore, the biometric assessment of phenotypes reveals significant differences among most of the pairs of islands, providing the first general description of the pattern of phenotypic expression of a single genotype across a range of environments (the reaction norm) for this species.

UCEs loci point to a single metapopulation of brown noddies, with a lack of genetic structure in the Southwestern Atlantic Ocean ($K = 1$). This pattern may represent recently isolated populations with limited gene flow, or contemporary gene flow among historically separated populations, similar to the one observed for the more coastal South American tern (Faria et al. 2010). The minimal genetic structure observed can be attributed primarily to endogamy rather than spatial distribution. F_{ST} values were all close to zero, different from the relatively higher values estimated from mtDNA, especially for Abrolhos colony vs. others. This indicates a low, but noticeable, mito-nuclear discordance. Similar patterns have been found for populations of other marine species, and have been suggested to be caused by male-mediated dispersal, high effective population size or demographic expansion or selection on mtDNA (Larmuseau et al. 2010).

According to mitochondrial evidence, the brown noddy metapopulation had undergone an expansion between 40,000 and 20,000 years ago. Radial (star-like) shape of the haplotype network and *Fs* and *D* values agree with this demographic pattern, similarly to what has been demonstrated for another Sternini in coastal Southwestern Atlantic Ocean (Faria et al. 2010). Despite the absence of ice sheets covering tropical environments throughout the Last Glacial Maximum (LGM), sea surface temperatures were 1–3 °C lower than present (CLIMAP Project Members 1976), affecting physicochemical oceanographic features and, therefore, distribution and population dynamics of tropical seabirds (Peck and Congdon 2004). A similar pattern of a demographic expansion prior to the LGM was suggested for the snow petrel *Pagodroma nivea* (Carrea et al. 2019).

The models of isolation by environment and distance do not seem to apply to Southwestern Atlantic brown noddies. The diverse blood isotopic values between populations may represent different diets or distinct isotopic baselines influenced by oceanographic features around each colony. Rocas Atoll, Fernando de Noronha and São Pedro e São Paulo Archipelago had the highest overlap of standard ellipses, which may represent the similar environmental features in their surroundings. The isolated isotopic niches of Trindade and Martin Vaz colonies probably reflect both their different foraging range and breeding period, which occurs during the austral Summer, opposite to the other populations that feed around their breeding areas mostly during the austral winter. The effects of seasonality on isotopic values have been previously reported in seabird colonies (Mancini et al. 2016). The lack of overlap between Trindade and Martin Vaz niches also suggest that, despite of their relatively high proximity and the absence of information of breeding individuals at Martin Vaz, they may be ecologically different populations; or it may reflect insufficient sample size at MV.

Abrolhos is the only archipelago located on the continental shelf, which is also the closest one to the coast (approximately 60 km). In addition, this region under influence of river discharges presented the most productive waters throughout our study range (0.45 mg/m^3 between 2000 and 2014, whereas oceanic islands further offshore had surrounding waters with chlorophyll α levels between 0.045 and 0.15 mg/m^3; Global Ocean Biogeochemistry Array, Copernicus). Matrix of distances from the coast was the only significant correlation with genetic distances, which could reflect contrasting features of this continental shelf island, such as the relatively higher primary productivity surrounding Abrolhos. However, this feature does not seem to disrupt gene flow in the studied populations. Other seabirds, such as brown booby *Sula leucogaster* (Nunes and Bugoni 2017) and Cook's petrel *Pterodroma cookii* (Rayner et al. 2011), had shown genetic differentiation between populations breeding on islands with waters differing in primary productivity levels, likely due to local adaptation.

The most distinct mtDNA haplotypes found were VI, VII and XV, diverging by five, four and six mutations from haplotype I, respectively. Trindade birds breed from September to March, a unique breeding period in comparison to others in this study. Some allochronic seabird populations are genetically distinct, such as sympatric populations of band-rumped storm-petrels *Hydrobates* spp. (Taylor et al. 2019) and sooty terns *Onychoprion fuscatus* on Ascension Island, even with breeding periods differing by only 42 days (Garrett et al. 2020). Brown noddies from Ascension Island breed in the same period as Trindade. Trindade and Martin Vaz populations together also have the highest number of exclusive haplotypes. These different alleles may represent genetic admixture between Trindade and Ascension populations or a case of incomplete lineage sorting due to recent breeding time switch in Trindade population (Taylor et al. 2019), which must be tested by genetic analysis with samples from Ascension. These mutations could also have occurred by chance or appeared through sexual bias in migration. Still, F_{ST} obtained for Trindade and MV populations against Abrolhos and Rocas are relatively high, and their isotopic niches are also isolated. Trindade and Martin Vaz colonies may also be historically separated from the other populations, presenting a contemporary gene flow. The lower sample size of Martin Vaz population decreases reliability of the results, but the high haplotype and nucleotide diversity observed in the two islands may also be a signal of an ancient population (Hamilton 2021). However, these allochronic populations with low genetic differentiation may also exist due to ecological plasticity (Taylor et al. 2019), which may emerge through competition for food (Monteiro and Furness 1998).

Most biometric measures differed between pairs of islands, whereas genetic distances were limited. There was also no correlation between biometric differences and pairwise F_{ST}. Similar to brown boobies at São Pedro e São Paulo Archipelago (Nunes et al. 2017), brown noddies are also larger in this place than elsewhere. Therefore, it seems that similar factors influence both species, i.e. there are important factors shaping seabird body size at SPSPA, other than heat dissipation, which was supposed to be the major one according to Bergmann's rule. This archipelago is a small rocky seamount with unique conditions such as vortices on its east side, which facilitates retention of nutrients around (Araujo and Cintra 2009). However, different from brown boobies (Nunes and Bugoni 2017), brown noddies from SPSPA show no genetic differences in comparison to other populations. This is the first description of the range of phenotypic answers for the same genotype in a gradient of environments for the brown noddy, i.e. its reaction norm. Interrelationships between genetic and environmental traits are complex to define, but it seems that there is a multi-trait reaction norm describing phenotypic expression in brown noddies. These multiple features could depend on various theories concerning the genetic architecture of plasticity, such as pleiotropy, epistasis; and the concept of plasticity functioning as an inverse proportion to heterozygosity (Pigliucci 2005), which seems to apply here, as all populations had low estimated values for this parameter.

Effective population sizes from NeEstimator represent more recent estimates than those from Migrate. When compared to the latest censuses in the studied populations (Mancini et al. 2016; ICMBio 2020), they represent approximately 1.3% of the real population size of Abrolhos, 22% of SPSPA, 1.7% of Rocas and 8.3% of Trindade (missing census data for Martin Vaz and Fernando de Noronha). Recent censuses at Abrolhos indicate that the population decreased at least by approximately 1600 individuals (2011–2019; Mancini et al. 2014, ICMBio 2020). Although this could be due to migrants leaving the colony, we had no evidence of such an event in our analyses. The observed trend, along with our results indicating endogamy, may suggest a real decline and hence a need of attention to this metapopulation in the Southwestern Atlantic. More studies are needed in order to understand if this is a global pattern or if it is restricted to the studied area.

Migration rates between islands suggest that the population with the higher number of residents is Rocas Atoll, while it also provides the most important contribution of migrants for all other islands. There are previous reports of brown noddies banded in Rocas recovered elsewhere along the South American coast, suggesting that some individuals move long distances from there (Schulz-Neto 2004). Previous censuses also demonstrate a steep population decline in this colony, which could be due to a large proportion of individuals leaving the atoll (Mancini et al. 2016). This evidence suggests that this population acts as one of the sources for other Southwestern Atlantic colonies. Sandy flat areas with soft substrate in the atoll differ from the rocky substrates commonly used in other Brazilian nesting areas, or other hard substrate elsewhere (Chardine et al. 2020), which may not be equally suitable for nesting. For those reasons, we hypothesize that Rocas Atoll serves as a stepping-stone for migrating individuals from nearby colonies, such as those in the Caribbean, to the other Southwestern Atlantic populations. This is a common mechanism for the Sternini, since they frequently change breeding sites in response to habitat changes (Faria et al. 2010). This hypothesis could be tested through a population genetic analysis including other colonies in the Atlantic.

Our method for estimating migration rates assumes that they are low, so the proportions of non-migrants have an inferior limit of 2/3 due to biological constraints of migration (Meirmans 2014). This probably makes our proportion of residents overestimated for several populations; however, it is likely that the proportions would be maintained if more accurate values had been estimated. Along with other parameters previously discussed, the estimates of migrants between all populations seems to be high and similar enough to consider that the Southwestern Atlantic colonies of brown noddies form a single panmictic metapopulation with a possible source of migrants from Rocas Atoll.

The studied populations represent a unique genetic group, but ecologically, morphologically and phenologically variable, suggesting high phenotypic plasticity. However, phenotypic features might also be related to genetic variability in different regions of the genome that were not covered by this study. Tracking individuals from all populations could clarify if there is any recently isolated population, and confirm the estimated migration patterns. Noddies, although being mostly tropical species, are also found at high latitudes, and the ecological differences highlighted in this study could be even more evident in those areas. It is noticeable that the largest birds were found at SPSPA, similarly to brown boobies, but this occurred in spite of lacking the genetic differences found on boobies. Species such as these are models to understand the relationship of ecological plasticity with micro- and macro-evolutionary processes.

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Data availability DNA sequences are available at GenBank under the accession numbers: PP176671-PP176781 and PP179903-PP179967 for mtDNA (ND2 and ATPase6/8, respectively). SNPs matrix from UCEs loci are available on Zenodo (https://doi.org/10.5281/zenodo.10524760). Stable isotope analysis results and biometric measures are provided as supplementary material.

Declarations

Competing interests The authors declare no competing interests.

Ethical approval For this work was provided by Animal Use Ethics Committee from Universidade Federal do Rio Grande (FURG) under the process number 23116.002603/2021-87 and report PRF037/2022. Sampling was conducted under the approval from Sistema de Autorização e Informação em Biodiversidade (license numbers 76,380 and 22,697).

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