

## Population connectivity of vulnerable Brazilian parrotfishes

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### ABSTRACT

Parrotfishes are iconic tropical and subtropical reef fishes, where they consume primary producers and contribute to reef bioerosion. Despite their ecological importance, parrotfishes have been threatened by overfishing worldwide. Understanding patterns of genetic diversity and connectivity is therefore essential for identifying conservation priorities and guiding management strategies for parrotfishes. Here, we evaluated the genetic diversity, connectivity, and gene flow of *Sparisoma frondosum* and *S. axillare*, two vulnerable and endemic Brazilian parrotfishes. A total of 104 samples of *S. frondosum* and 173 of *S. axillare* were collected along the Brazilian coast (from 00°50'S 44°15'W to 27°30'S 48°31'W). By assessing 11 microsatellite loci in *S. frondosum* and 16 in *S. axillare*, we found  $H_o < H_e$  with strong structuring near the southern end of its distribution at the subtropical reefs of Rio de Janeiro state (RJ) for *S. frondosum*, and in the isolated Trindade and Martim Vaz Archipelago (IT) for *S. axillare*. No significant correlation was found between genetic differentiation and geographical distance, suggesting that factors other than spatial distance play key roles in shaping their genetic structures. Both species respond differently to marine barriers, and the observed patterns were discussed in light of how overfishing may be influencing genetic connectivity. Coastal populations require coordinated management along the Brazilian coast, while the genetic structuring in distant islands and at the southern range limits highlights connectivity constraints and potential vulnerability to environmental change.

### 1. Introduction

Parrotfishes (Labridae: Scarinae) are iconic and ecologically significant components of reef environments worldwide. While fulfilling a unique ecological role in reef systems (Bonaldo et al., 2014), they also serve as an important resource for fisheries. Among the nominally herbivorous fishes, parrotfishes are by far the most studied (Bonaldo et al., 2014; Hoey and Bonaldo, 2018). Ten species of scarine labrids occur in the southwestern Atlantic, with seven being endemic to the Brazilian Province (Pinheiro et al., 2018). The larger-body species belonging to the genera *Scarus* (2 species) and *Sparisoma* (4 species), are all classified

as being under some level of threat (Queiroz-Véras et al., 2023). Besides being distributed from tropical to subtropical reefs along the Brazilian coast and oceanic islands (Ferreira et al., 2004; Araújo et al., 2020), overfishing was widely reported (Bender et al., 2014; Roos et al., 2016, 2020; Morais et al., 2018).

Fishing 'down' marine food webs (Pauly et al., 1998) has intensified pressure on herbivore and detritivore fish families, with the strongest implications for parrotfishes (Taylor et al., 2014). In the Indo-Pacific and South Pacific, overexploitation of parrotfishes has been shown to shift dominance in response to overfishing (Dulvy and Polunin, 2004; Clua and Legendre, 2008; Taylor et al., 2015). In Brazil, fishing pressure on

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parrotfishes has led to the inclusion of the greenbeak parrotfish, *Scarus trispinosus*, on the IUCN Red List of Threatened Species in the endangered category (Padovani-Ferreira et al., 2012). In addition to *Sc. trispinosus*, the species *Sc. zelindae*; *Sparisoma axillare*; *Sp. frondosum*; and *Sp. rocha* are listed as vulnerable according to the Brazilian red list of threatened species (MMA 148/2022) (Brasil, 2022). Investigating the genetic diversity of these vulnerable endemic parrotfish is therefore particularly important in Brazil, where their distribution range is nearly restricted to approximately 4000 km of coastline, all under the jurisdiction of a single country.

The distribution of marine species is shaped by biological limitations, ecological traits, geographic barriers—whether permeable or not—and historical events (Spalding et al., 2007; Bowen et al., 2016). The Brazilian marine province is biogeographically defined by different ecological barriers: (1) the Amazon-Orinoco plume, which separates the Brazilian and Caribbean provinces (Rocha, 2003; Rocha et al., 2007; Floeter et al., 2008; Araujo et al., 2022); (2) the mid-Atlantic barrier, whereby distance divides the Brazilian province from the tropical eastern Africa (Rocha et al., 2005a, 2007; Robertson et al., 2006); (3) the South Equatorial Current at around 5°S latitude, splitting into the southward Brazilian Current and northward North Brazil Current (Cortinhas et al., 2016); and (4) the coastal upwelling. Within the Brazilian province, freshwater and sediment plumes from rivers like the Amazon, São Francisco, Paraguaçu, Jequitinhonha, Doce, and Paraíba do Sul (Floeter et al., 2008; De Biasi et al., 2023) contribute as barriers of dispersion. Likewise, the Vitória-Trindade seamount chain at 20.5°S latitude is the main step-in-stone connecting coastal population through time with the Trindade Island (Pinheiro et al., 2017; Mazzei et al., 2021; Simon et al., 2021). The current distribution of fauna in the Brazilian Province was also influenced by sea-level fluctuations during the Pleistocene glacial maxima, when the coastline was approximately 100 m lower than it is today (Miller et al., 2005, 2011).

Research on snapper species (*Lutjanus*) has shown high genetic variability and significant gene flow, possibly driven by population expansions during these sea-level changes (Souza et al., 2015, 2019; da Silva et al., 2015, 2016; Evangelista-Gomes et al., 2020; Veneza et al., 2023). However, *Lutjanus synagris* exhibited low genetic polymorphism throughout the western South Atlantic, indicating a different pattern (Silva et al., 2018; Evangelista-Gomes et al., 2020). Parrotfish genetic substructure has been identified in *Scarus trispinosus* populations between the northeast and east coasts of Brazil (Bezerra et al., 2018). This pattern was consistent with findings from other marine taxa as crustaceans, mangrove species, hermatypic corals, and turtles (see Martins et al., 2022). In a previous study with the *S. axillare* using Single-Nucleotide Polymorphism (SNP) markers, genetic substructure was attributed to the isolation of oceanic islands from the mainland (Verba et al., 2023). This finding aligns with studies on coral and reef fish species that have consistently shown a genetic break between oceanic islands and the mainland locations due to geographic distance and ocean currents, as seen for the corals *Mussismilia hispida* (Peluso et al., 2018), *Favia grandidieri* and *Siderastrea radians* (Nunes et al., 2011), and reef fish in general, such as the brown chromis *Azurina multilineata* (Cunha et al., 2014) and the bridled goby *Coryphopterus glaucofraenum* (Volk et al., 2021).

Global studies indicate that understanding connectivity can help assess fishing threats to populations due to overfishing (Reiss et al., 2009; Gandra et al., 2021), identify source populations (Merella et al., 2010) and understand colonization patterns (Bariche and Bernardi, 2009; Velasco-Montoya et al., 2022). In this context, the objectives of this study were to describe the genetic diversity, connectivity, and gene flow of *S. frondosum* and *S. axillare* among coastal and oceanic reefs within the Brazilian Province. This study is the first to assess *S. frondosum*, while *S. axillare* has already been studied using SNPs markers (Verba et al., 2023). Here, we expand on those findings by using microsatellites, which offer greater genetic detail due to their multi-allelic nature, in contrast to the diallelic SNPs, which are abundant

but less informative (Schaid et al., 2004). We expect to find high genetic connectivity on a large scale through coastal waters (based on Bezerra et al., 2018; Endo et al., 2019; Verba et al., 2023), alongside regional patterns of genetic diversity. Additionally, we will test whether any genetic variation observed can be explained by geographic distance. This approach also enables comparisons with co-distributed species using consistent molecular markers, adding depth to our understanding of shared environmental influences on genetic structure.

## 2. Materials and methods

### 2.1. Target species and study site

The Agassiz's parrotfish, *S. frondosum* and the gray parrotfish, *S. axillare* are both widely distributed and abundant along the Brazilian coast, with higher abundances found in the northeastern coast (Ferreira et al., 2004; Feitosa and Ferreira, 2015; Cordeiro et al., 2016; Roos et al., 2019). Specifically, their distribution ranges from the tropical reefs of Parcel de Manoel Luis on the northeastern coast (00°50'S 44°15'W) to the subtropical reefs on the southern coast of Santa Catarina (27°30'S 48°31'W) (Fig. 1). They are also found on all Brazilian oceanic islands, with established populations in Rocas Atoll (3°52'S 33°49'W), Fernando de Noronha Archipelago (3°51'S 32°25'W), Trindade and Martim Vaz Archipelago (20°31'S 29°19'W) and São Pedro and São Paulo Archipelago (0°55'N 29°20'W) only as vagrants (Pinheiro et al., 2018). *Sparisoma frondosum* had extended its distribution beyond the Amazon plumes' and the mid-Atlantic ridge barriers, with vagrants being detected in the southern Caribbean (Humann and DeLoach, 2002; Freitas et al., 2014), and a recent population established at subtropical reefs of Cape Verde in the Central East Atlantic (00°56'N 29°22'W; Freitas et al., 2014). *Sparisoma axillare* had also been confirmed to inhabit reefs of the southern Caribbean as vagrants (Robertson et al., 2006; Rocha et al., 2008).

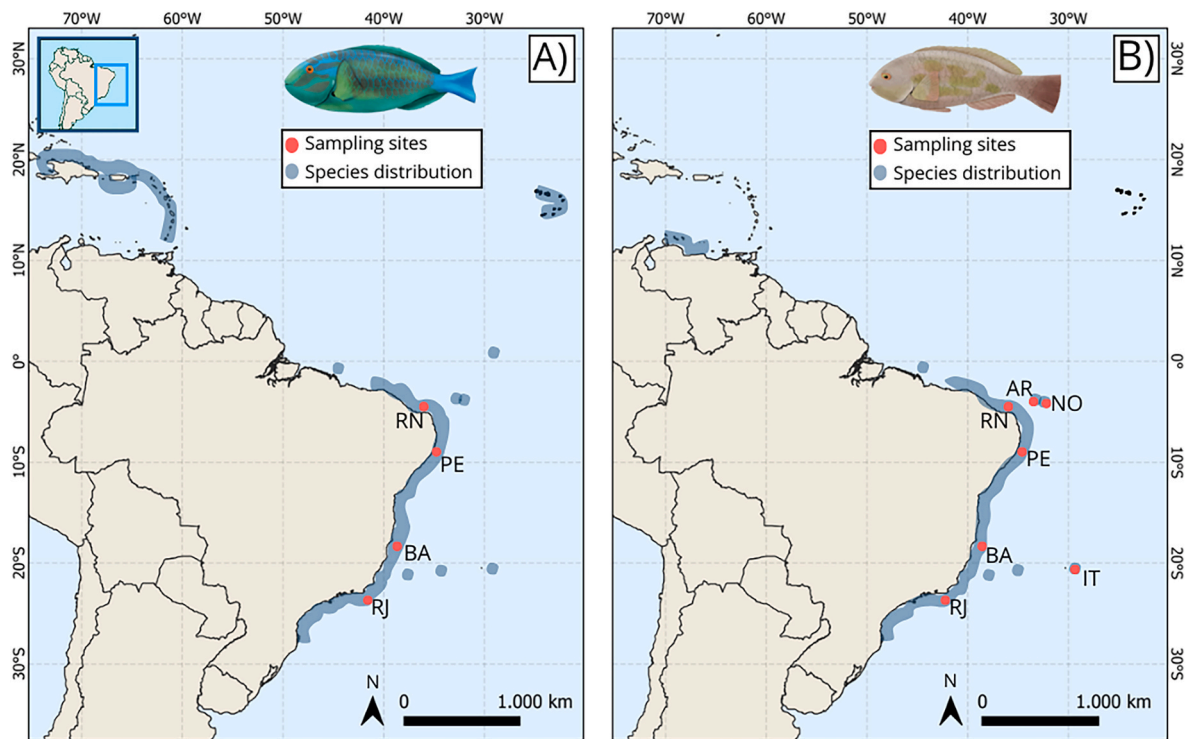
### 2.2. Sampling, extraction, and quantification

A total of 104 samples of *S. frondosum* from the states of Rio de Janeiro (RJ), Bahia (BA), Pernambuco (PE), and Rio Grande do Norte (RN) were used. The samples of *S. axillare* (N = 173) are from RJ, BA, PE, RN, and the oceanic islands of Fernando de Noronha Archipelago (NO), Rocas Atoll Biological Reserve (AR) and Trindade and Martim Vaz Archipelago (IT). Samples used in this study were obtained between the years 2019 and 2021 from fish markets and scientific sampling.

The samples consist of a piece of fin: dorsal, anal, or caudal, which were stored in 95 % ethanol until the DNA extraction. All samples used in this study are stored in the Laboratory of Conservation and Marine Ecology (LECoMar) tissue collection at the Federal University of Southern Bahia (UFSB) in Porto Seguro-BA. Extractions were performed following the protocol of the PureLink™ Genomic DNA Mini Kit from Invitrogen™, and to verify the quantity and quality of the DNA, we used the Qubit 1.4.

### 2.3. Amplification and genotyping

All microsatellites used in this study are listed in Supplementary material (Table S1 in SM) and were developed for this research using samples of *Sparisoma amplum*, *S. axillare* and *S. frondosum*. The multiplex were prepared by diluting 1 µl of each Forward primer and 0.1 of each Reverse primer, 1 µl of each primer's respective fluorescence, and ultrapure H<sub>2</sub>O to complete a 50 µl solution. Reactions were performed using the Type-it Microsatellite PCR Kit™ with adjustments to the manufacturer's protocol, containing 1 µl of DNA, 3.125 µl of Type-it, 0.625 µl of primer Mix, and 2 µl of ultrapure water. Amplifications were conducted following the protocol: 1 cycle of 95 °C for 5 min, followed by 30 cycles of 95 °C for 30 s, 57 °C for 90 s, and 72 °C for 30 s, followed by eight cycles of 95 °C for 30 s, 53 °C for 90 s, and 72 °C for 30 s, with a final extension at 68 °C for 30 min.



**Fig. 1.** Distribution ranges of studied species. **1.A.** *Sparisoma frondosum*. **1.B.** *Sparisoma axillare*. The red dots indicate the sampling sites: Rio de Janeiro (RJ), Bahia (BA), Pernambuco (PE), Rio Grande do Norte (RN), Fernando de Noronha Archipelago (NO), Rocas Atoll Biological Reserve (AR) and Trindade and Martim Vaz Archipelago (IT).

To prepare the genotyping, 1.5  $\mu$ l of PCR product was diluted in 0.2  $\mu$ l of LIZ 600 + 8.3  $\mu$ l of formamide. After the dilutions, the formamide was dried by placing the samples at 95 °C for 3 min, followed by a thermal shock in ice for 2 min.

#### 2.4. Data analysis

The genotyping products were evaluated using the SeqStudio/Applied Biosystems genetic analyzer. Allele identification was performed using Geneious 7.1.9.9 software (Kearse et al., 2012) and the genescan-600 LIZ marker (Thermo Fisher Scientific).

Subsequently, loci and individuals with over 20 % missing values were excluded using the package “poppr” (Kamvar et al., 2014). Genotypic uniqueness and multilocus genotype was assessed using the “poppr” package (Kamvar et al., 2014). Through the “adegenet” (Jombart, 2008) package the polymorphism of the loci was assessed. The package “graph4lg” (Savary et al., 2021) was used to generate an archive to be used in the MICRO-CHECKER. The MICRO-CHECKER v2.2.3 software was used to assess the presence of null alleles, false alleles, and allelic dropout (Van Oosterhout et al., 2004).

Locus polymorphism was assessed by computing the polymorphic information content (PIC) using packages “poppr” (Kamvar et al., 2014), “pegas” (Paradis, 2010), “polysat” (Clark and Jasieniuk, 2011) and, “tidyverse” (Wickham and Wickham, 2017). Various indices, such as the number of alleles ( $A$ ), number of private alleles ( $A_p$ ), mean allelic richness ( $A_r$ ), allelic private richness ( $A_p$ ), observed heterozygosity ( $H_o$ ), expected heterozygosity ( $H_e$ ), Hardy-Weinberg equilibrium (HWE), linkage disequilibrium, were calculated to gauge the genetic diversity of the species. To obtain all the diversity indices R packages function *div-Basic* from the “diversity” (Keenan et al., 2013), “tidyverse” (Wickham and Wickham, 2017) and “poppr” (Kamvar et al., 2014) were used. A Monte Carlo permutation test (999 replicates) was checked to assess whether  $H_e$  in each population was significantly greater than in every other population, using the *Hs.test* function of the “poppr” package

(Kamvar et al., 2014). Hardy-Weinberg equilibrium was tested for each population using an exact test with 1000 permutations, followed by Bonferroni correction for multiple comparisons using the “pegas” package (Paradis, 2010), and loci with adjusted  $p > 0.05$  were considered in equilibrium.

To test evidence of bottleneck, we use the Stepwise Mutation Model (SMM: Cornuet and Luikart, 1997), the Infinite Allele Model (IAM: Maruyama and Fuerst, 1985) and the combination of both with 70 % SMM and 30 % IAM (Di Rienzo et al., 1994; Spencer et al., 2000), using the software Bottleneck v.1.2.02. (Piry et al., 1999).

Furthermore, fixation indices, including  $F_{st}$  and pairwise  $F_{st}$  estimators (Weir and Cockerham, 1984) for overall genetic structure and locus-specific measures, were computed. R packages “hierfstat” (Goudet et al., 1996; Weir and Goudet, 2017) and “pegas” (Paradis, 2010), with significance assessed through bootstrap resampling using “adegenet” (Jombart et al., 2018) were used to compute  $F_{st}$ . Additionally, a Spearman correlation coefficient test between inbreeding coefficient ( $F_{is}$ ) and locus-specific  $F_{st}$  was performed, and a Wilcoxon Rank Sum Test investigated significant differences between  $F_{st}$  values with and without effective number of alleles (ENA) correction. Pairwise  $F_{st}$  significance was determined through 10,000 bootstrap replications. Also, FreeNA results of  $F_{st}$  were presented in Supplementary Material (Tables S2–S5). To evaluate the statistical power of our microsatellite dataset to detect population structure, we conducted simulations using POWSIM 4.1 (Ryman and Palm, 2006) (see Supplementary Material for simulation details).

The Mantel test using 9999 permutations in the R package “ade4” (Chessel et al., 2004) was used to test the Isolation-By-Distance (IBD) hypothesis to determine if genetic variation ( $F_{st}$  pairwise) could be explained by geographic distance (km). Jost’s ( $D_{st}$ ) index was used to compute population differentiation values (Jost et al., 2018) due to its reduced bias for highly polymorphic markers such as microsatellites.

For assessing genetic structure, a Bayesian model-based clustering analysis was executed in STRUCTURE v2.3.4 (Pritchard et al., 2000)

with ten replications for each inferred subpopulation, each with 1,000,000 MCMC steps with 100,000 burns-in iterations. Of the resulting runs, to select the optimal  $K$  (Evanno et al., 2005), we used an ad hoc statistic  $K$  based on the second-order rate of change in  $\text{LnP}(D)$  between successive  $K$  values using the web app “pophelper 2.3.1” (Francis, 2017). To identify genetic patterns within the regions, a discriminant analysis of principal components (DAPC) was done. To estimate the ideal number of clusters ( $K$ ) for the DAPC, the Bayesian information criterion (BIC) technique was used (Jombart et al., 2010; Jombart and Ahmed, 2011). For running and visually assessing DAPC results, the R packages “ade-genet” (Jombart, 2008; Jombart et al., 2010; Jombart and Ahmed, 2011), “factoextra” and “ade4” were used (Chessel et al., 2004). The extent and direction of gene flow were estimated by calculating the relative migration rate and direction, assuming asymmetrical bidirectional gene flow, based on Nei’s  $G_{ST}$  and 1000 bootstraps. We conducted a hierarchical analysis of molecular variance (AMOVA) utilizing the R package “poppr” (Kamvar et al., 2014) with 999 permutations. The analysis for *S. frondosum* assessed the distribution of genetic variation considering all samples from the four locations as putative subpopulations ( $K = 4$ ) and considering just RJ different ( $K = 2$ ). In the case of *S. axillare*, the analysis assumed that IT constituted distinct subpopulations from the the rest ( $K = 2$ ) and that IT, AR + NO, PE + RN and, BA + RJ each constituting a putative subpopulation ( $K = 4$ ).

### 3. Results

To assess *Sparisoma frondosum* populations ( $N = 104$ ; RN: 19, PE: 49, BA: 22, RJ: 13), eleven microsatellite loci were used after we eliminated the locus Spa487, which had a substantial amount of missing data (44 %) of the total dataset. Sixteen microsatellite loci were used to assess *S. axillare* populations ( $N = 173$ ; AR: 9, IT: 14, NO: 8, RN: 37, PE: 35, BA: 37, RJ: 33).

MICRO-CHECKER revealed no evidence of allelic dropout, though it did identify the presence of false alleles and null alleles in the samples, suggesting a potential Wahlund effect. All loci were assessed through FreeNA for *S. frondosum* (S. Tables S2 and S3) and for *S. axillare* (Tables S4 and S5). POWSIM tests indicated that the microsatellites dataset, for both of the species, had enough statistical power to detect even a weak genetic differentiation (Fig. S1).

For *S. frondosum*, the polymorphic information content (PIC) values spanned from 0.11 to 0.88, with a mean PIC of  $\sim 0.55$  (Table 1, Table S6). Loci Spa007, Spa470, and Spa433 demonstrated particularly high PIC values, indicative of substantial genetic polymorphism (Table S6). In *S. axillare*, individual loci exhibited a range of PIC values from 0.035 to 0.94, with a mean PIC of  $\sim 0.40$  (Table 1, Table S6). For *S. frondosum* some loci exhibit higher allelic richness (e.g., Spa007, Spa470 in BA; Spa007, Spa470 in PE), meanwhile, some loci deviate

from HWE (as indicated by asterisks in Table S7). Positive  $F_{IS}$  values (e.g., Spa033, Spa197 in BA) suggest a tendency toward heterozygote deficit, while negative values (e.g., Spa376 in BA) may indicate excess heterozygosity (Table S7). Samples from PE have private alleles ( $A_p$ ) in several loci, contributing to their higher allelic richness ( $A_r$ ) (Table S7). Overall, the subpopulations (BA, PE, RJ, RN) show variability in  $A_r$ ,  $H_o$ , and deviations HWE, suggesting subpopulation-specific genetic dynamics (Table 1). Instead, *S. axillare* showed a mean  $A_r \sim 2.72$ , with most of the loci conform to the HWE, private alleles ( $A_p$ ) are absent in populations of AR and RN, and its  $F_{IS}$  values can be assessed on Supplementary Material (Table 1, Table S8).

In *S. frondosum*, the assessment of Hardy-Weinberg Equilibrium (HWE) for specific loci after Bonferroni corrections reveals a mixed pattern of adherence and departure from the equilibrium expectations. Loci Spa197 and Spa106 exhibit  $p$ -values  $> 0.05$ , suggesting that they are in HWE, aligning with the expected genetic equilibrium within the subpopulations (Table S7). Conversely, multiple other loci, including Spa033, Spa007, Spa042, Spa470, Spa318, Spa433, Spa434, and Spa376, display  $p$ -value = 0, indicating a significant departure from HWE (Table S7). These departures may signify the influence of evolutionary forces such as selection or other complex genetic dynamics acting on these loci.

In *S. frondosum*,  $F_{IS}$  values ranged from  $-0.156$  (Spa105) to  $0.951$  (Spa376), with 9 of 11 loci exceeding  $F_{IS} > 0.2$ .  $F_{ST}$  values showed a median of  $0.098$  (range:  $0.0003$ – $0.3225$ ), with Spa033 ( $0.227$ ) and Spa376 ( $0.276$ ) as maxima (Table S9). Observed heterozygosity (median  $H_o = 0.380$ ) was lower than subpopulation expectations (median  $H_{pop} = 0.561$ ).  $F_{IT}$  values ranged from  $-0.156$  to  $0.965$ , correlating with  $F_{IS}$  trends. In *S. axillare*, the assessment of HWE for specific loci Spa042, Spa487, Spa470, Spa318, Spa433, Spa033, Spa323, Spa007, Spa452, Spa449, and Spa105 exhibit  $p$ -value = 0 even after Bonferroni correction, resulting in significant deviations from HWE. On the other hand, Spa197, Spa106, Spa460, Spa434, Spa099, and Spa105 have  $p$ -values  $> 0.05$ , suggesting adherence to HWE (Table S8). *Sparisoma axillare* revealed distinct patterns across loci (Table S10).  $F_{IS}$  values showed a broad range ( $-0.046$  to  $1.000$ ), with 10 of 16 loci exhibiting positive inbreeding coefficients ( $F_{IS} > 0$ ). Particularly, Spa042, Spa452, and Spa449 reached complete fixation ( $F_{IS} = 1.000$ ), while Spa099 showed the strongest heterozygote excess ( $F_{IS} = -0.046$ ). Population differentiation was generally low (median  $F_{ST} = 0.052$ ), though Spa433 ( $F_{ST} = 0.301$ ) and Spa449 ( $F_{ST} = 0.157$ ) demonstrated higher divergence. The median observed heterozygosity ( $H_o = 0.286$ ) was lower than the expected within subpopulations ( $H_{pop} = 0.419$ ), consistent with the median inbreeding coefficient ( $F_{IS} = 0.308$ ). Extreme values of total inbreeding ( $F_{IT}$ ) mirrored  $F_{IS}$  patterns, ranging from  $-0.039$  to  $1.0$ .

For *S. frondosum*, bottleneck tests revealed population-specific signatures under different mutation models. The IAM detected significant

**Table 1**

Genetic diversity indices for *S. frondosum* and *S. axillare* samples analyzed. It includes the number of individuals ( $N$ ), number of alleles ( $A$ ), allelic richness ( $A_r$ ), private alleles ( $A_p$ ), observed ( $H_o$ ) and expected ( $H_e$ ) heterozygosity. Additionally, the inbreeding coefficient ( $F_{IS}$ ) and overall polymorphic information content (PIC). Locations are: Rio de Janeiro (RJ), Bahia (BA), Pernambuco (PE), Rio Grande do Norte (RN), Fernando de Noronha Archipelago (NO), Rocas Atoll Biological Reserve (AR) and Trindade and Martim Vaz Archipelago (IT).

Species	Location	$N$	$A$	$A_r$	$A_p$	$H_o$	$H_e$	$F_{IS}$	PIC
<i>S. frondosum</i>	RN	19	58	4.26	6	0.41	0.54	0.2479	0.40
	PE	50	72	4.23	6	0.38	0.54	0.2897	
	BA	22	59	4.19	4	0.34	0.56	0.3952	
	RJ	13	50	3.96	2	0.37	0.51	0.273	
<i>S. axillare</i>	AR	9	53	2.73	0	0.33	0.41	0.182	0.55
	IT	14	34	1.93	1	0.21	0.29	0.288	
	NO	8	62	3.08	3	0.33	0.4	0.167	
	RN	37	89	3.2	0	0.29	0.41	0.307	
	PE	35	86	3	6	0.29	0.41	0.275	
	BA	37	86	3.21	6	0.28	0.42	0.33	
	RJ	33	86	3.19	2	0.31	0.42	0.25	

heterozygosity excess in populations RN ( $k = 5.18$ ;  $p = 0.023$ ) and RJ ( $k = 4.45$ ;  $p = 0.021$ ), while the *SMM* identified a bottleneck in PE ( $k = 6.18$ ;  $p = 0.020$ ) (Table S11). In *S. axillare* the *IAM* detected significant heterozygosity excess only in population AR ( $k = 3.31$ ;  $p = 0.021$ ). In contrast, the *SMM* identified bottlenecks in PE ( $k = 5.38$ ;  $p = 0.025$ ), BA ( $k = 5.38$ ;  $p = 0.045$ ), and RJ ( $k = 5.38$ ;  $p = 0.030$ ). The *TPM* confirmed signals in PE ( $k = 5.38$ ;  $p = 0.027$ ) and RJ ( $k = 5.38$ ;  $p = 0.029$ ), while population BA showed borderline significance ( $k = 5.38$ ;  $p = 0.051$ ). Populations of NO and RN showed no bottleneck signatures across all models, despite their low allelic diversity ( $k = 3.88$ – $5.63$ ).

For both species, *S. frondosum* ( $p = 0.7829$ ,  $R^2 = -0.27$ ) and *S. axillare* ( $p = 0.681$ ,  $R^2 = -0.1626$ ) there is no evidence that genetic differentiation increases with geographical distance (Fig. S2). Jost's D values highlight the genetic distinctiveness among *S. frondosum* subpopulations across all regions (Table 2). An exception between RN and PE who exhibit greater genetic similarity overlapping in the same cluster in the DAPC complemented by the Structure analyses suggest at least two clusters ( $K = 2$  or  $K = 4$ ) representing genetically distinct groups (Fig. 2A). In BA, all three clusters are present, though one stands out as the dominant genetic pattern in the area, while in RJ a single cluster predominates, indicating greater genetic homogeneity compared to the other regions analyzed. For *S. axillare*, Jost's D values (Table 2) indicate significant differentiation between IT and all other regions sampled. The structure analyses in conjunction with the Evano method identified the formation of at least four genetic clusters  $K = 4$ . Within them, IT exhibits higher levels of genetic homogeneity and forms a separated cluster from the rest (Fig. 2B).

The relative migration network, based on Nei's  $G_{st}$  (Fig. 3A), reveals strong connectivity within PE and RN for *S. frondosum*, with  $G_{st} > 0.96$ . Additionally, it illustrates that the subpopulation of RJ is minimally connected to the other regions, receiving only marginal genetic input ( $G_{st} = 0.11$ – $0.18$ ) and exhibiting limited outgoing connections. For *S. axillare*, given the more diverse regions sampled, the network is understandably more intricate. However, a noteworthy observation is the distinctiveness of IT from the other locations (Fig. 3B). Genetic flux analysis indicates a connection between NO and AR ( $G_{st} = 0.5$ – $0.68$ ), substantial flux among all the locations of the continental coast (RN, PR, BA, and RJ), and a moderate genetic exchange between the oceanic islands of NO and AR with the continental coast (Fig. 3B). In both species, *S. frondosum* and *S. axillare*, the components "Between Samples Within Subpopulations" and varied from 29 to 34 %, while "Within Samples" from 53 to 62 % (Table 3) identified as significant in the analysis of molecular variance (AMOVA), demonstrating that they were key factors in shaping the genetic variability of these subpopulations (Table 3). Oppositely, the component of variation "Between Subpopulations" was considered a minimal contributor to molecular variance in both species (Table 3).

#### 4. Discussion

We investigated the genetic structure and connectivity of two endemic and vulnerable *Sparisoma* species, namely *S. frondosum* and *S. axillare*, along over ~2300 km of the Brazilian coast, using micro-satellite markers. The choice of these markers was grounded in their high variability and suitability for assessing intra-specific genetic diversity (Schlötterer, 2000; Ellegren, 2004). They revealed the existence of a substructure in *S. frondosum* population in which the limit of coral reef formation (~20° S) seems to be affecting genetic flow, separating southernmost location (RJ) from others. On the other hand, the isolation of IT from other islands and the coast seemed to restrict gene flux in *S. axillare*.

##### 4.1. Insights on the genetic diversity and connectivity patterns on co-distributed congeners species

By examining the genetic characteristics of *S. frondosum* and *S. axillare* along the Brazilian coast, different patterns have emerged. *Sparisoma frondosum* showed notable genetic diversity characterized by high number of private alleles ( $A_p$ ) and high allelic richness ( $A_r$ ), except in PE and BA. In RJ, which had lower genetic diversity, possibly indicating a less stable subpopulation or reduced density. The lower abundance of *S. frondosum* in RJ and southwards along its distribution range (Ferreira et al., 2004) can result in reduced genetic diversity, as smaller populations are more susceptible to endogamic depression (Peery et al., 2012; Trask et al., 2021). It is noteworthy to mention that at RJ (23°S) there is a prominent environmental change, in terms of reef formation with the presence of rocky reef instead of biogenic (Ferreira et al., 2004; Pinheiro et al., 2018), and climatic changes in terms of temperate waters in a region that is influenced by upwelling periods along the year and typically affected by cold waters (Ferreira et al., 2001). These environmental conditions ultimately can act as filters to the genetic diversity of a primarily tropical reef fish.

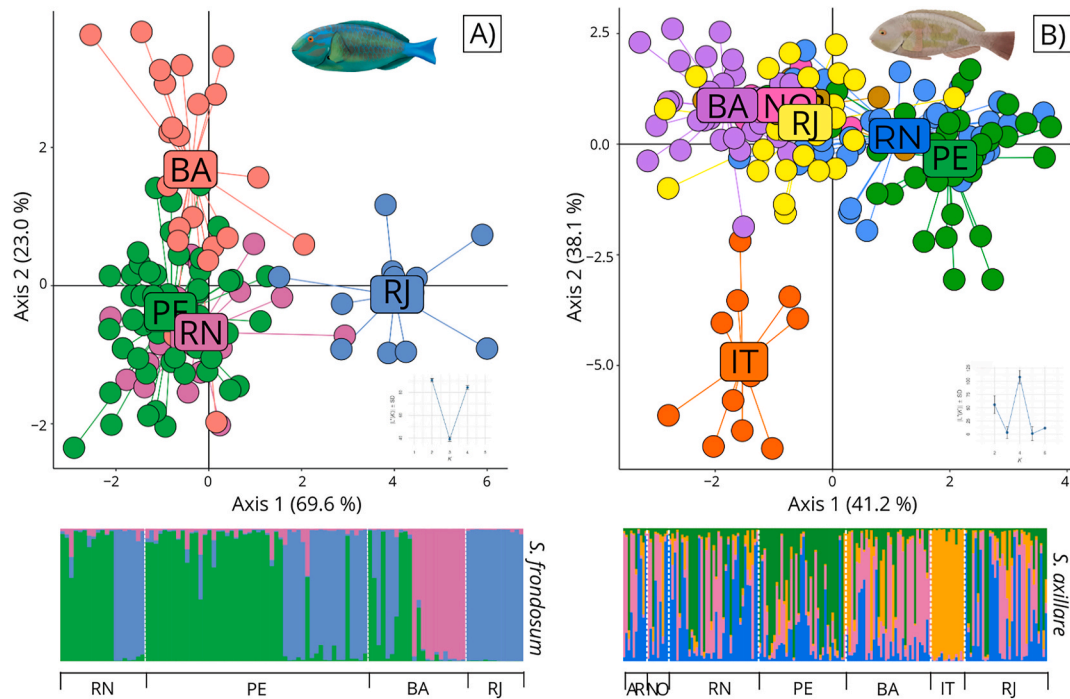
*Sparisoma axillare*, on the other hand, exhibited reduced allelic richness ( $A_r$ ) implying that this species is conditioned to less genetic variation. Moreover, private alleles ( $A_p$ ) are restricted to IT and NO islands, indicating the unique contribution of these islands to maintaining the genetic diversity of *S. axillare*. In addition, the relatively similar heterozygosity ( $H_o$ ) among the oceanic islands also indicates major genetic connectivity and stability within these subpopulations. This result demonstrates stable genetic diversity that is not significantly influenced by latitudinal distribution, and stability can be attributed to its larger population sizes (Ferreira et al., 2004), habitat flexibility (Feitoza et al., 2005; Araújo et al., 2020), and continuous gene flow here shown.

Despite the distinct biomass characteristics across their distribution ranges (Roos et al., 2019), both species exhibit observed heterozygosity lower than expected ( $H_o < H_e$ ), bringing the hypothesis that they could

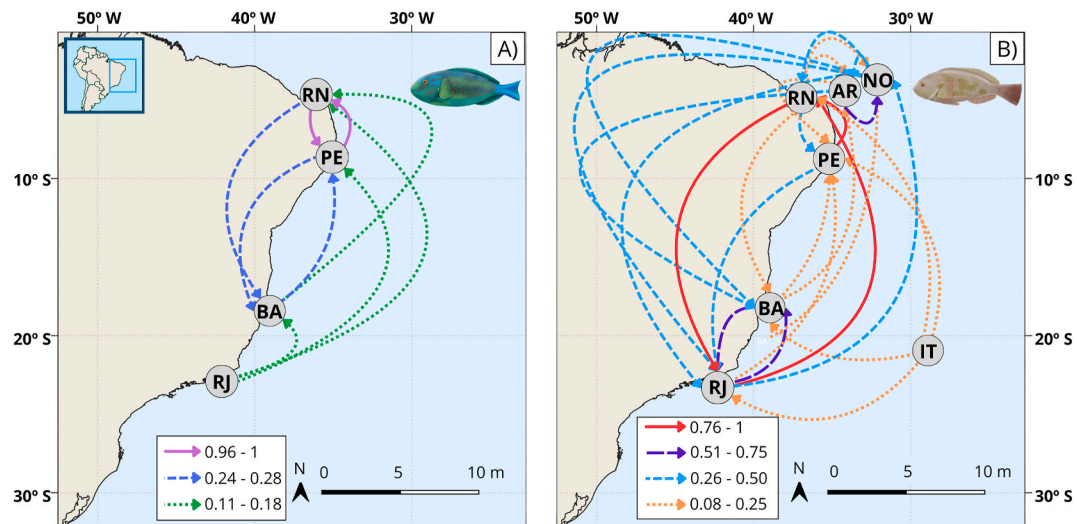
**Table 2**

Genetic Differentiation Metrics for *S. frondosum* and *S. axillare* subpopulations. Jost's D values quantify the divergence in allelic frequencies, providing insights into the relative degree of differentiation. The comparisons are made between subpopulations on the Brazilian coast of the states of Pernambuco (PE), Bahia (BA), Rio de Janeiro (RJ) and Rio Grande do Norte (RN); and oceanic islands of Fernando de Noronha Archipelago (NO), Rocas Atoll Biological Reserve (AR) and Trindade and Martim Vaz Archipelago (IT). Bolds means statistical difference.

<i>S. frondosum</i>		RJ		BA		PE	
	BA		<b>0.3386</b>				
	PE		<b>0.3076</b>		<b>0.1064</b>		
	RN		<b>0.2900</b>		<b>0.1236</b>		0.0078
<i>S. axillare</i>		AR	IT	NO	RN	PE	BA
	IT	<b>0.1678</b>					
	NO	<b>−0.0992</b>	<b>0.1592</b>				
	RN	0.0401	<b>0.1718</b>	<b>0.0443</b>			
	PE	<b>0.0878</b>	<b>0.1837</b>	<b>0.0611</b>	<b>0.0329</b>		
	BA	<b>0.0423</b>	<b>0.1434</b>	0.0363	<b>0.0535</b>	<b>0.0944</b>	
	RJ	0.0247	<b>0.1455</b>	<b>0.0299</b>	<b>0.0193</b>	<b>0.0647</b>	<b>0.0211</b>



**Fig. 2.** Bayesian analysis of the subpopulation structure. **2.A.** *Sparisoma frondosum* genotyped using 11 microsatellite markers. **2.B.** *Sparisoma axillare* genotyped using 16 microsatellite markers. Above is shown a principal component discriminant analysis (DAPC) of possible subpopulations, each different color dot representing individuals from different sampling regions. The genetic structure analyses were made considering the regions of the coastal waters of Rio de Janeiro (RJ), Bahia (BA), Pernambuco (PE), Rio Grande do Norte (RN); and oceanic islands of Fernando de Noronha Archipelago (NO), Rocas Atoll Biological Reserve (AR) and Trindade and Martim Vaz Archipelago (IT).



**Fig. 3.** Directional relative migration network among sampling regions based on Nei's  $G_{ST}$  of **3.A.** *S. frondosum* and **3.B.** *S. axillare*. Arrows indicate the direction, line colors and patterns indicate the intensity of gene flow between studied subpopulations. Absent arrows in some directions are due to migration rates being too low or negligible to be detected. Each gray dot represents the subpopulation Rio de Janeiro (RJ), Bahia (BA), Pernambuco (PE), Rio Grande do Norte (RN), Fernando de Noronha Archipelago (NO), Rocas Atoll Biological Reserve (AR) and Trindade and Martim Vaz Archipelago (IT).

be experiencing not only recent population bottleneck events (Templeton and Read, 1994; Gu et al., 2014), but also a reflect of either true inbreeding or Wahlund effect from population structure (Waples, 2015; De Meeus, 2018). Regarding Wahlund effect, we recognised that undetected population subdivision, potentially due to genetic stratification, may persist even when sampling is carried out randomly (Garnier-Géré and Chikhi, 2013) as may be the case in this study. We are cautious in interpreting this possibility and acknowledge its relevance when evaluating heterozygosity patterns. It is worth noting that a

previous study conducted on *Scarus trispinosus* also found lower observed heterozygosity than expected (Bezerra et al., 2018), even though that study used a different set of microsatellites markers than in this research. This suggests that such patterns may reflect biological processes rather than marker-specific biases, further supporting our cautious interpretations of the observed heterozygosity deficit.

The lack of significant correlation between genetic differentiation and geographical distance in both species (*S. frondosum*:  $p = 0.7829$ ,  $R^2 = -0.27$ ; *S. axillare*:  $p = 0.681$ ,  $R^2 = -0.1626$ ), suggests that factors

**Table 3**  
Analysis of molecular variance of *S. frondosum* and *S. axillare*.

<i>S. frondosum</i>	<i>K</i> = 2		<i>K</i> = 4	
	Sigma	Percent	Sigma	Percent
Between Subpopulations	1.48	18.75	0.67	9.71
Between Samples Within Subpopulations	2.16	27.42	2.03	29.21
Within Samples	4.25	53.82	4.25	61.09
Total	7.89	100.00	6.95	100.00

<i>S. axillare</i>	<i>K</i> = 2		<i>K</i> = 4	
	Sigma	Percent	Sigma	Percent
Between Subpopulations	0.57	8.12	0.18	2.73
Between Samples Within Subpopulations	2.32	33.02	2.27	34.52
Within Samples	4.13	58.86	4.13	62.74
Total	7.01	100.00	6.58	100

beyond spatial distance play major roles in shaping their genetic structures. Ecological influences significantly affect patterns of connectivity in reef fishes. Factors such as habitat occupancy can mediate discordant patterns in congeneric species (Félix-Hackradt et al., 2013). Specifically, the life history aspects of each species and the regional biogeography marked by features like seamounts and the Brazilian current, emerge as critical determinants (Sadler et al., 2023). While both species occupy the same habitats and the pelagic larval duration is assumed similar and close to 57–60 days (Robertson et al., 2006), it is essential to consider that *S. axillare* exhibits a larger size and longer lifespan (Queiroz-Véras et al., 2023) and is a more generalist herbivore (Ferreira and Gonçalves, 2006; Leitão et al., 2023) than its congener *S. frondosum*. These life history and ecological traits may promote wider habitat use and greater gene flow of *S. axillare*, buffering the species against rapid genetic drift or local loss of diversity. In contrast, *S. frondosum* has more specialized habitats leading to vulnerability to local demographic fluctuations. Furthermore, previous studies have shown that life history traits and habitat type influence patterns of genetic diversity (Martinez et al., 2018).

In terms of marine barriers impeding the gene flow of reef fish along the Brazilian coast, the division caused by the South Equatorial Current, particularly its interaction with Cape São Roque (Martins et al., 2022) is among the most influential. This soft barrier, identified as pivotal in restricting gene flow for the parrotfish *Sc. trispinosus* (Bezerra et al., 2018), underscores the profound impact of ocean currents on population connectivity. Research on wrasses, belonging to the same family as parrotfishes (Labridae), has shown that, while certain species exhibit the capacity to maintain genetic connectivity across vast distances of thousands of kilometers, they may face challenges in traversing equal or shorter distances between continents and oceanic islands (Rocha et al., 2005b). The presence of *S. frondosum* in the Cape Verde Archipelago (Freitas et al., 2014), facilitated by the equatorial undercurrent (Joyeux et al., 2001), highlight its exceptional capacity for long-range dispersal and colonization, despite the rarity of species migration from Brazil to the Tropical Eastern Atlantic (Floeter et al., 2008). In *S. frondosum*, there is a robust gene flow between PE and RN, while BA exhibits relatively reduced connectivity with PE in both directions. Following this pattern of diminishing gene flow at higher latitudes, RJ appears isolated, primarily exporting genes with minimal reciprocal flow, suggesting an early stage of genetic structuration. Finally, our findings on *S. frondosum* align with those on greenbeak parrotfish *Sc. trispinosus* (Bezerra et al., 2018) and other species sensitive to environmental features along the northeastern and eastern Brazilian coasts like molluscs (*Anomalocardia brasiliensis*: Arruda et al., 2009) and fishes (*Rhizoprionodon porosus*: Mendonça et al., 2011). The Cabo Frio upwelling likely acts as a disruptive barrier, separating warmer tropical reefs in the north from colder subtropical rocky reefs in the south, creating an ecological transition zone (Santos et al., 2006; Peluso et al., 2018; Volk et al., 2021).

*Sparisoma axillare* is the most abundant and widely distributed parrotfish in the Brazilian coast. His habitat generalist behavior (Ferreira

and Gonçalves, 2006; Leitão et al., 2023) allows its distribution beyond coral reef domain, extending until Santa Catarina rocky coast, at southern Brazil. In this work, genetic diversity of *S. axillare* was more influenced by the Vitória-Trindade Chain barrier. Reef fish assemblages across the seamounts and oceanic islands of the Vitoria-Trindade Chain are highly shaped by stepping-stone processes (Mazzei et al., 2021). Seamounts can facilitate reef organism dispersal, yet the species' dispersal capabilities directly influence genetic connectivity between seamounts and islands (Cho and Shank, 2010). This influence is evident in gene flow patterns and genetic structuration, where IT shows clear separation from other subpopulations. Additionally, NO and AR display interconnected gene flow, with BA acting as a bridge for gene exchange along the coastal waters continuum. A genetic break between continental coastal populations and oceanic islands is evidenced in *S. axillare*, a pattern commonly observed among reef fishes and corals of the Brazilian province (Nunes et al., 2011; Peluso et al., 2018; Volk et al., 2021; Verba et al., 2023).

These findings emphasize the variability in genetic response among co-distributed species within the Brazilian marine fauna, even among closely related species (Nunes et al., 2011). *Sparisoma viride*, which is widely distributed across the Caribbean biogeographic province, shows no evidence of genetic structure and symmetrical migration rates, suggesting a panmictic population throughout its range (Loera-Padilla et al., 2021). Furthermore, a study on a congener *S. aurofrenatum* in the Caribbean found high levels of genetic diversity, with asymmetrical east-to-west unidirectional gene flow (Velasco-Montoya et al., 2022). The large population sizes may help explain the high genetic diversity observed in this species, reducing the risk of local extinctions. This is likely due to the stronger effects of larval dispersal migration compared to genetic drift. However, if unidirectional gene flow diminishes due to anthropogenic interventions such as fisheries, genetic drift could become more pronounced, potentially disrupting population connectivity (Pinsky and Palumbi, 2014). This nuanced analysis highlights the distinct responses of *S. frondosum* and *S. axillare* to critical marine barriers, emphasizing the role of both ocean currents and geographic features in shaping genetic connectivity and gene flow along the southwestern Atlantic.

4.2. Overexploitation of parrotfishes and its consequences on genetic structure

The genetic diversity patterns observed for *S. frondosum* and *S. axillare* might be directly influenced by fishing activities along the Brazilian coast. Fishing negatively impacts population abundance and genetic structure (Allendorf et al., 2014), potentially contributing to the patterns discussed in this study. For *S. frondosum*, the lower genetic diversity observed in the RJ region might be attributed not only to physical and environmental barriers but also to selective fishing practices, such as spearfishing, which targets specific individuals. In RJ, key fisheries have declined, including bluefish (*Pomatomus saltatrix*), groupers (*Mycteroperca bonaci*, *M. acutirostris*, *M. microlepis*, *Epinephelus marginatus*), and the greenbeak parrotfish (*Sc. trispinosus*), primarily due to line and spearfishing (Bender et al., 2014).

Fishing pressure on *Sparisoma* species varies across regions: in southeastern Brazil and BA, spearfishing is the primary method, whereas in PE and RN, fish traps are more commonly used (Bender et al., 2014; Roos et al., 2016; Queiroz-Véras et al., 2023). These pressures likely contribute to the observed genetic structuring in both species, particularly the clustering in PE and RN, where the fishing of these two species is historical, occurring since the 1970s and demonstrating a significant expansion in recent decades, both to the north and south of the initial areas and to deeper locations on the continental shelf (Queiroz-Véras et al., 2025).

*Sparisoma frondosum* and *S. axillare* rank as the most heavily fished parrotfishes after *Sc. trispinosus* (Cunha et al., 2012; Roos et al., 2016; Freire et al., 2021; Queiroz-Véras et al., 2023), which can be the cause to

$H_o < H_e$  patterns observed in all Brazilian parrotfish species studied so far. Our data also revealed recent population reductions in both studied species, specially in PE for *S. frondosum*, and in PE, BA and RJ for *S. axillare*. According to Queiroz-Véras (unpubl. data), when modelling fishing effects on *S. axillare* populations from northeast Brazil, it is possible to see that this species had been facing reductions in number until 2000's, due to high levels of fishing pressure. However, since then, they are recovering to sustainable population levels (above fisheries reference points as MSY or Biomass target yield) despite high fishing effort. This fishing model best explains the bottleneck evidence observed in *S. axillare* in our study, as well as the lower genetic diversity compared to *S. frondosum*.

Overfishing has been shown to alter the demographic structure of fish species (Hidalgo et al., 2011), and rapidly erode genetic diversity (Pérez-Ruzafa et al., 2006). Even small reductions, such as a 2 % decrease in heterozygosity and a 10 % loss in allelic richness can lead to significant population declines over just a few generations (Pinsky and Palumbi, 2014), limiting the species' ability to adapt to environmental changes, including those driven by climate change (Allendorf et al., 2014). In line with these genetic and evolutionary concerns, significant shifts in body size, abundance, and sex ratios of parrotfish under varying fishing pressures, have been documented, providing clear demographic evidence of overfishing on these species (Rivas et al., 2022).

#### 4.3. Conservation considerations

Given our results, including the lower genetic diversity of *S. axillare* compared to *S. frondosum*, and their different response to marine barriers, conservation strategies should be tailored to each species. In *S. frondosum* which comprehends at least two genetic stocks divided by the 20°S marine barrier (congruent with Martins et al., 2022). This species faces overexploitation in northeastern Brazil (traps: Queiroz-Véras et al., 2025) and in RJ (speargun: Bender et al., 2014.), eroding both genetic stocks. Management of this threatened species requires concomitant strategies: habitat restoration, improved water quality and fishing reduction before extremely measures like artificial propagation may need consideration in the future (Tringali and Bert, 1998).

While *S. axillare* show signs of genetic 'stability' (e.g., private alleles) observed in oceanic islands may indicate reduced fishing pressure, RN has been identified as a significant exporter of parrotfishes (Roos et al., 2016; Queiroz-Véras et al., 2023, 2025). Notably, in this region, *S. axillare* lacks private alleles ( $A_p$ ), suggesting that subpopulations may have been homogenized. Although overfishing may not be the sole factor responsible, it is certainly a contributing force to this pattern. This loss of genetic distinctiveness could reduce its resilience and increase its vulnerability to extinction. There are more fishing methods targeting *S. axillare* throughout the coastal continental extension, so even if we consider a single genetic stock, it has been eroded by extensive and intensive fishing pressure (Queiroz-Véras et al., 2023, 2025). Thus, we recommend adopting step-by-step strategies with short and long term goals (Grant et al., 2017) beginning with improving recruitment (Botsford et al., 2003; Gascoigne and Lipcius, 2004); limiting harvests of the stock (Grant et al., 2017), and finally habitat restoration or modification (Buckley, 1989). Ultimately, by increasing and directly supporting Brazilian MPAs, we can enhance parrotfish population resilience. This includes improving abundance, biomass, fish size and recruitment stock (Anderson et al., 2014; Hackradt et al., 2014), and can promote population genetic diversity, as fish within MPAs often maintain significantly higher allelic richness (Pérez-Ruzafa et al., 2006; Bezerra et al., 2018). However, recent studies indicate that, for *Sc. trispinosus*, the largest and most threatened parrotfish, no-take MPAs alone may not be sufficient to ensure its persistence (Roos et al., 2020). It is crucial to acknowledge that the low investment in MPAs and the prevalence of 'paper parks' in Brazil likely contribute to these findings.

## 5. Conclusion

In terms of genetic diversity both studied species exhibit  $H_e < H_o$ , shaped by levels of genetic structuring that were not supported by geographic distance. *Sparisoma frondosum* exhibited higher genetic diversity in northern regions, with signs of genetic structuring driven by environmental barriers such as the upwelling system at Cabo Frio-RJ. Reduced genetic diversity in the southeastern population, particularly in RJ, suggests potential impacts from fishing pressure and environmental changes. Conversely, *S. axillare* showed lower allelic richness overall, with stable genetic diversity in oceanic islands. The observed genetic break between continental and oceanic populations highlights the role of the Vitória-Trindade seamount chain in shaping connectivity patterns.

We demonstrate that even when congeneric species are co-distributed, this is not enough to suggest the same degree of genetic connectivity and gene flow. Ecological traits, geographical barriers, potential larval dispersal, and overexploitation come into perspective. While *S. axillare* demonstrated to be very susceptible to geographical features. The heavily structured IT subpopulation, isolated from the rest, confirmed the seamounts of Trindade and Martim Vaz Archipelago as an important barrier to Brazilian marine currents, contributing to this isolation.

Overfishing is a critical factor influencing genetic diversity and population structure. The decline in genetic diversity observed in *S. frondosum* may be exacerbated by targeted fishing practices, particularly in southeastern Brazil. Given its lower overall genetic diversity, *S. axillare* requires special conservation attention to ensure the long-term stability of its populations.

Our findings reinforce the need for region-specific conservation strategies. Marine Protected Areas alone may not be sufficient to counteract the genetic consequences of overfishing. Understanding the genetic patterns of *S. frondosum* and *S. axillare* provides valuable insights into the broader dynamics of marine biodiversity in the southwestern Atlantic, contributing to more effective conservation and management efforts for reef fish species.

#### CRedit authorship contribution statement

**Karis Itchel Tuñón Valdés:** Writing – original draft, Methodology, Investigation, Formal analysis, Data curation. **Juliana Beltramin De Biasi:** Writing – review & editing, Methodology, Formal analysis, Data curation. **Natalia C. Roos:** Writing – review & editing, Resources. **João Lucas Leão Feitosa:** Writing – review & editing, Resources. **Luísa V.M. V. de Queiroz-Véras:** Writing – review & editing, Resources. **Guilherme O. Longo:** Writing – review & editing, Resources. **Carlos E.L. Ferreira:** Writing – review & editing, Resources. **Alexandre Schiavetti:** Writing – review & editing, Supervision, Resources, Funding acquisition. **Carlos Werner Hackradt:** Writing – review & editing, Validation, Resources, Funding acquisition, Conceptualization. **Fabiana César Félix-Hackradt:** Writing – review & editing, Validation, Resources, Methodology, Funding acquisition, Data curation, Conceptualization.

#### Conflict of interest

The authors declare that there are no conflicts of interest regarding the data submitted.

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#### Declaration of competing interest

The authors declare no known competing financial interests or

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2025.107293>.

## Data availability

Data will be made available on request.

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