



# Environmental and geographical drivers of reef fish beta diversity across the depth gradient

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**ABSTRACT:** The swift decline of coral reefs stands out as a significant biodiversity challenge confronting our generation, and mesophotic coral ecosystems (MCEs; reefs between 30 and 150 m) have been proposed as refuge habitats that may be less affected by climate change and human impacts compared to their shallow counterparts. However, MCEs are often distinct from shallow reefs, and studies assessing how marine biodiversity changes along the depth gradient and what factors can influence marine communities in MCEs are still scarce. Here, we conducted underwater visual censuses to evaluate how fish assemblages change among islands and environmental characteristics across the shallow to mesophotic depth gradient within the Cabo Verde Archipelago. Our results show that the beta diversity of reef fish assemblages was mainly driven by depth and environmental factors such as temperature and benthic variables. A consistent trend of increasing beta diversity from the shallow to the lower mesophotic zone was observed among the islands, with the lowest variation in species composition observed between the shallow (5–30 m) and upper (31–60 m) mesophotic depths. Lower species richness and higher turnover was observed within lower MCEs (61–85 m), suggesting saturation in fish richness at small scales, possibly a result of changes in microhabitat heterogeneity. Furthermore, the effect of geography was negligible, and local-scale environment characteristics were the main drivers of differences in species assemblages. Evidence suggests that increased fishing pressure on the most populated island may reduce the biogeographic influence on fish assemblages across the archipelago.

**KEY WORDS:** Mesophotic coral ecosystems · Nestedness · Turnover · Fish assemblages · Marine biogeography · Cabo Verde · Eastern Atlantic

## 1. INTRODUCTION

The global anthropogenic impacts on coral reefs are widely acknowledged (Wilkinson 1999, Hughes

et al. 2003, Bellwood et al. 2004, Burke et al. 2011, Andrello et al. 2022). Over the past 4 decades, human-induced disturbances have imposed significant stress on coral reef ecosystems, primarily attributable to

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local factors such as pollution, sedimentation, and overfishing (Norse 1993, Maragos et al. 1996, Spalding et al. 2001), as well as global stressors like climate change (Hughes et al. 2003, Brandl et al. 2020, Nagelkerken et al. 2023) and plastic pollution (Pinheiro et al. 2023a). The effects of climate change and habitat degradation have been most extensively investigated in more accessible shallow coral reefs, primarily those above 30 m. However, technological advancements have enabled exploration beyond shallow reefs, providing a better understanding of the patterns and processes in reef ecosystems ranging from 30 to 150 m in depth, known as mesophotic coral ecosystems (MCEs) (Laverick et al. 2018, Rocha et al. 2018, Pyle et al. 2019, Pyle & Copus 2019, Slattery et al. 2024).

The structure of these deeper reef communities is mainly driven by temperature, topography, and light irradiance (Lesser et al. 2009, Turner et al. 2017, Kahng et al. 2019). As temperature and light decrease along the depth gradient (Lesser et al. 2009), there is a corresponding shift in the community assemblage (Lesser et al. 2009, Kahng et al. 2019, Pyle & Copus 2019, Pinheiro et al. 2023b, Slattery et al. 2024). For instance, in tropical latitudes, the benthic composition undergoes a shift from the prevalence of scleractinian corals in shallow-water reefs (Spalding et al. 2001) towards a community dominated by heterotrophic corals, macroalgae, and sponges in MCEs (Slattery et al. 2024).

The species richness of fish, which are one of the most studied taxonomic groups in MCEs (Rocha et al. 2018, Pyle & Copus 2019), generally peaks above 30 m and then declines with increasing depths (Brokovich et al. 2008, Pyle et al. 2019, Pinheiro et al. 2023b). Some similarity in fish species composition has been observed between shallow areas and upper MCEs (30–60 m) (Semmler et al. 2017, Lesser et al. 2019), while the lower zone (60–150 m) harbors more unique assemblages (Pinheiro et al. 2016, Kahng et al. 2017, Rocha et al. 2018). Therefore, some species have shown to be depth generalists and can be found throughout a depth gradient, while others are depth specialists, confined to a particular depth stratum (Rocha et al. 2018, Pyle & Copus 2019, Bosch et al. 2023).

Deep reefs have traditionally been regarded as less affected by climate change and other anthropogenic disturbances when compared to their shallow counterparts. Consequently, some studies have speculated on the potential role of mesophotic reefs as refuges for shallow reef species, giving rise to the 'deep reef refuge hypothesis' (Bongaerts et al. 2010, Laverick et al. 2018, Bongaerts & Smith 2019, Pyle & Copus

2019). Some studies have shown that depth might provide some protection against the thermal bleaching of corals and the effects of marine heat waves (Pérez-Rosales et al. 2021, Bramanti et al. 2023). However, deeper reefs are not spared from natural disturbances (Bongaerts et al. 2013, Rocha et al. 2018), human-induced pressure (e.g. pollution, fishing, and mining) (Olavo et al. 2011, Etnoyer et al. 2016, Rocha et al. 2018, Pinheiro et al. 2023a), and even widespread bleaching (Diaz et al. 2023). Coral reefs exhibiting the most pristine conditions are typically found in locations far removed from human-populated areas, encompassing both shallow and deep coral reef ecosystems (Rocha et al. 2018). Particularly, oceanic islands serve as havens for some of the last remaining near-pristine ecosystems and fish assemblages, due to their isolation (Bruneel et al. 2021), and these often serve as natural laboratories for ecological, biogeographic, and evolutionary studies (Dawson 2016).

A growing body of research has sought to explore the factors influencing the distribution of fish assemblages, both among oceanic islands (Wienerroither et al. 2009, Quimbayo et al. 2019, Bosch et al. 2023) and across the spectrum of shallow and deep reef environments (Pinheiro et al. 2016, Bosch et al. 2023). Beta diversity analyses serve as an essential tool for understanding the impact of diverse habitats and environmental factors on species diversity and distribution. This valuable approach can contribute significantly to conservation planning and management in these vulnerable ecosystems (Harborne et al. 2006, Roff & Zacharias 2011, Baselga & Orme 2012, Maxwell et al. 2022). By integrating beta diversity measurements with environmental or geographical factors, researchers can unveil the underlying processes that drive species distributions and biodiversity patterns within a given region (Harborne et al. 2006, Baselga & Orme 2012, Socolar et al. 2016). Partitioning beta diversity into its components, namely turnover (species replacement) and nestedness (species loss or gain), enhances our understanding of the underlying processes influencing community variation (Baselga 2010, Socolar et al. 2016).

This study represents the first *in situ* investigation conducted in the Cabo Verde Islands across the shallow to mesophotic depth gradient (5–85 m), aiming at understanding the drivers of fish species variability and addressing research gaps pertaining to mesophotic reefs in understudied regions of an Eastern Tropical Atlantic oceanic archipelago. In this study, we assessed the impact of geographic distance and ecological factors on the beta diversity of reef fish assemblages. We aimed to answer the following ques-

tions: (1) What are the main drivers influencing beta diversity; and between depth and geographic distance, which one plays a more significant role in driving beta diversity? (2) Is there a relation between species richness and beta diversity? (3) Is there evidence for human impacts affecting the beta diversity patterns?

As fish assemblages of other oceanic islands in the Atlantic are structured by stepping-stone processes (Mazzei et al. 2021), our hypothesis posits that islands in closer proximity would be more similar to each other (lower beta diversity) compared to more isolated ones. In addition, building upon findings from prior studies as mentioned above (Pinheiro et al. 2016, Semmler et al. 2017, Rocha et al. 2018, Lesser et al. 2019), we would expect that the species assemblages in the shallow and upper zones will be more similar to each other, and distinct from those in the lower mesophotic zone. Lastly, the selective removal of fish species by fishing activities could affect species composition through a subtractive homogenization process (Socolar et al. 2016), which would increase beta diversity, especially the importance of its nestedness component.

## 2. MATERIALS AND METHODS

### 2.1. Study area

The study was carried out in August 2022 in 3 islands of the Cabo Verde Archipelago: Santiago ( $14^{\circ} 54' 31.5''$  N,  $23^{\circ} 36' 18.2''$  W), Fogo ( $14^{\circ} 50' 40.7''$  N,  $24^{\circ} 26' 51.6''$  W), and Santo Antão ( $16^{\circ} 56' 38.6''$  N,  $25^{\circ} 19' 09.4''$  W) (Fig. 1) during the DISCOVER scientific cruise onboard RV 'Antea' (Fauvelot et al. 2022). Cabo Verde Archipelago is located in the north-eastern Atlantic, spanning latitudes between  $14^{\circ}$  and  $17^{\circ}$  N and longitudes from  $21^{\circ}$  to  $25^{\circ}$  W, about 450–600 km off the coast of Senegal, West Africa (Fig. 1). The 10 islands and 8 islets that compose the archipelago are arranged in a west-facing horseshoe shape and can be further divided into a windward group (Santo Antão, Sao Vicente, Santa Luzia, Sao Nicolau, Sal Boa Vista) and a leeward group (Maio, Santiago, Fogo, and Brava) (Ramalho 2011). Santiago is the largest island ( $991 \text{ km}^2$ ), followed by Santo Antão ( $779 \text{ km}^2$ ), with estimated geological ages of 10 and 8 million years, respectively (Ramalho 2011). These 2 islands, separated by 293 km, are in an early post-erosional stage and dis-

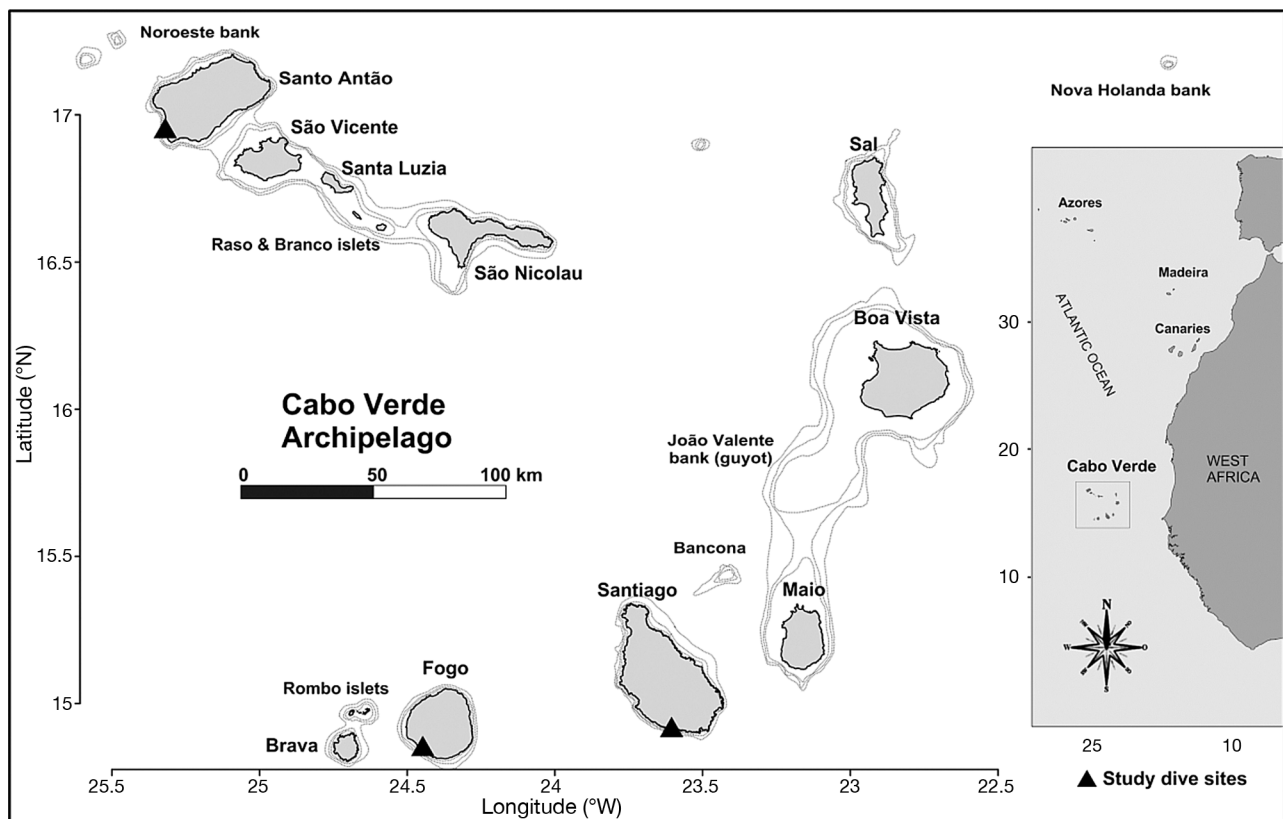


Fig. 1. Cabo Verde archipelago and its location in the Atlantic Ocean. Bathymetric contour lines around the islands represent underwater depth variations, ranging from 0 to 500 m on the shelf

play an overall shield morphology. The youngest island of the archipelago is Fogo, an active stratovolcano with a preserved morphology and an area of 476 km<sup>2</sup> (Ramalho 2011). This island is located 91 km from Santiago and 252 km from Santo Antão. The selection of sampling sites was determined by the presence of steep slopes and considerations related to logistical constraints.

Scleractinian corals are common in the shallow areas of Cabo Verde (van der Land 1993, Moses et al. 2003), notably Atlantic siderastreids (Monteiro et al. 2013). Although mature coral communities can be found in Cabo Verde, true coral reefs and larger reef structures are scarce (Spalding et al. 2001), likely attributable in part to the cold water brought by the Canary Current (Laborel 1974). Nonetheless, rocky reefs in Cabo Verde harbor numerous reef organisms such as sponges, corals, and algae (van der Land 1993). The upper and lower mesophotic areas of the 3 explored islands are characterized by the presence of black coral forests (*sensu* Rossi et al. 2017) which give 3D complexity to the substrate. Forest composition differs between the depth zones, with the upper zone mainly composed of *Antipathella*, *Tanacetipathes*, and *Stichopathes* spp. and the lower zone dominated by *Tanacetipathes* spp. Compared to other island groups in the eastern Atlantic, the Cabo Verde islands exhibit a significantly higher coastal fish endemism (Wirtz et al. 2013, Freitas et al. 2019), and the archipelago has been classified as a global marine biodiversity hotspot (Roberts et al. 2002).

Over the past 70 yr, Cabo Verde has experienced human population growth from less than 200 000 to around 590 000 inhabitants. Santiago is the most populated island, with about half of the population of the entire archipelago (269 300 inhabitants), and the majority of the residents are located in the capital Praia (142 000 inhabitants). Conversely, both Fogo (33 500 inhabitants) and Santo Antão (36 600 inhabitants) have faced a slight decrease in their population in the past 2 decades (City Population 2021, Worldometer 2023). With the expanding population, unregulated fishing, pollution, and tourism stand as the foremost threats to the marine environment in Cabo Verde (Failler et al. 2020).

## 2.2. Sampling methods

Fish species were visually identified and counted *in situ* by H.T.P. and L.A.R. to the lowest taxonomic level possible, and their body size was estimated by eye. The surveys were carried out on reefs ranging from 5 to 85 m

in depth, using underwater visual censuses (UVCs) conducted with mixed-gas closed-circuit rebreathers, covering a 40 m<sup>2</sup> area (20 m × 2 m). Transect locations were randomly chosen but aimed to cover the diversity of microhabitats and 3 depth zones: shallow (5–30 m), upper mesophotic (31–60 m), and lower mesophotic (below 61 m) (Kahng et al. 2017, Soares et al. 2019). The number of replicates for each depth category and island varied between 2 and 10 transects (Table S1 in the Supplement at [www.int-res.com/articles/suppl/m752p021\\_supp.pdf](http://www.int-res.com/articles/suppl/m752p021_supp.pdf)). Biotic and abiotic environmental parameters, such as benthic species cover (e.g. algae and corals), and habitat complexity, were visually assessed for each surveyed transect. Benthic coverage percentage estimation was recorded by a diver swimming along the transect (Jokiel et al. 2015). Habitat complexity was classified as low, medium-low, medium, medium-high, or high (adapted from Pinheiro et al. 2013). Low complexity indicates a bare substratum with an absence of holes and crevices; medium indicates a 50% hard substratum with holes and crevices; and high demonstrates a 100% hard substratum with holes and crevices larger than 1 m (Pinheiro et al. 2013). The temperature at each depth zone was measured and recorded using diving computers. Additionally, anthropogenic debris larger than 5 cm was recorded by the divers along the transects.

## 2.3. Data analysis

A species accumulation curve (Fig. 2), estimated using the function 'specaccum' in the R package 'vegan' (Oksanen et al. 2024), was used to verify if the sampling effort was sufficient to capture most of the fish assemblages within each depth zone.

For the beta diversity analyses, the abundance data of fish species were transformed into presence/absence data, and the sites were grouped into 9 different groups according to geographic and bathymetric criteria, with 3 depth zones (shallow, upper, and lower) for each of the 3 islands: Fogo, Santo Antão, and Santiago. Due to the unequal sampling effort, the sample size was standardized to a minimal sampled area (MSA) (Quimbayo et al. 2019, Dubuc et al. 2023, Silva et al. 2023), defined as the area of the site with the lowest sampled area in the data set (lower Santo Antão). Sampled areas of all other sites were then reduced to this MSA (80 m<sup>2</sup>). For each site, we randomly sub-sampled individual UVCs. The procedure was repeated 1000 times to include multiple combinations of UVCs of each MSA per site. At each simulation step, we calculated the taxonomic beta diversity

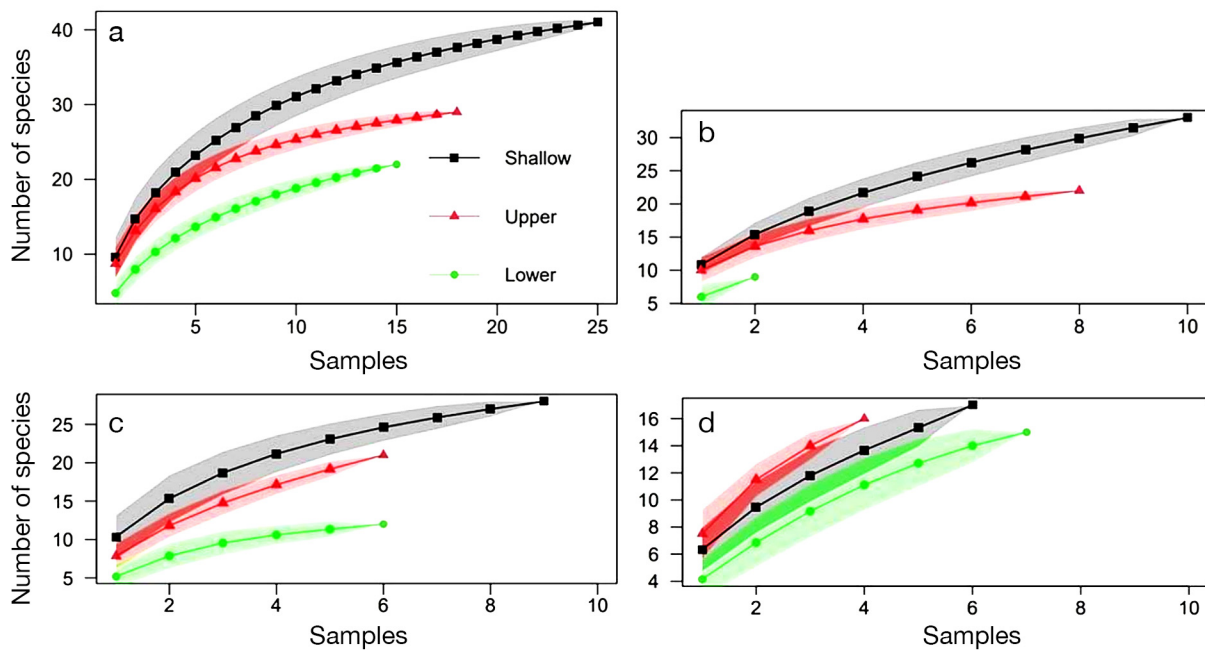


Fig. 2. Species accumulation curve displaying the number of species recorded per transect from each depth zone, with the shaded outline representing the 95% confidence interval for (a) all surveyed islands, (b) Santo Antão, (c) Fogo, and (d) Santiago

between sites using Sorensen's dissimilarity index ( $\beta_{sor}$ ) and its turnover ( $\beta_{sim}$ ) and nestedness ( $\beta_{sne}$ ) components through the 'beta pairwise' function in the R package 'betapart' (Baselga 2010, Baselga & Orme 2012). These measures are robust to small or unequal sample sizes (Koleff et al. 2003, Barwell et al. 2015, Pinheiro et al. 2019). The mean values of the beta Sorensen's, turnover, and nestedness from the 1000 simulations were used to estimate the dissimilarity between the reef fish assemblages. Furthermore, the aforementioned process was iterated for a more expansive MSA, omitting lower Santo Antão and expanding the MSA to 160 m<sup>2</sup>. This expansion aimed to investigate whether the smaller dimensions of the surveyed transects led to heightened variability when compared to the larger dimensions (Arias-González et al. 2008).

To investigate the within-depth zone (shallow, upper, and lower) species variation for each island, we calculated pairwise dissimilarities at the transect level with the same previous methods of Baselga (2010) and Baselga & Orme (2012). Additionally, we used the average linkage of the beta Sorensen's component at the transect level of species dissimilarity between the sites to create a clustering plot (Baselga & Orme 2012). This approach aimed to identify groups that exhibited clustering patterns.

To address our primary research question, i.e. what are the main drivers influencing beta diversity, we

constructed a generalized linear model (GLM) with a beta regression distribution and a log link function. The 'betareg' function in the 'betareg' R package (Cribari-Neto & Zeileis 2010) was employed for building the model. Beta diversity values, obtained from pairwise dissimilarity calculations (Baselga 2010, Baselga & Orme 2012) at the transect level, were set as the dependent variable, as they are well suited for the beta regression model (Cribari-Neto & Zeileis 2010). The beta regression model assumes that the response variable follows a beta distribution, with values ranging between 0 and 1 on the standard unit interval, and can be used for both fixed and variable dispersion beta regressions, and therefore provides more flexibility than the binomial GLM (Cribari-Neto & Zeileis 2010). In cases where the variable  $y$  took the extreme values of 1 (13% of the cases), a transformation was employed as  $(y \times (n - 1) + 0.5)/n$ , where  $n$  represents the sample size (Smithson & Verkuilen 2006, Cribari-Neto & Zeileis 2010).

The aim was to investigate which factor, namely depth or geographic distance, plays a more significant role in driving beta diversity, and to explore the additional impact of ecological variables on beta diversity. The model considered the variation between transects in terms of the depth gradient and geographic distance, alongside abiotic factors such as temperature differences and island size, as well as biotic factors like algae cover, coral cover, het-

erotrophic coral cover, and habitat complexity, all treated as independent variables. The absolute differences in these variables between each pair of samples were calculated and used as predictors in the model. These differences were then connected to the pairwise beta diversity values between the specific samples.

The 'dredge' function in the 'MuMIn' R package (Barton 2023) was run to obtain a complete set of models with possible combinations of the independent variables and determined the best fit model based on the lowest Akaike's information criterion (AIC) value and the highest pseudo R-square. To confirm that the independent variables were not correlated with each other, we estimated the variance inflation factor (VIF) with the function 'VIF' in the 'car' package (Fox et al. 2019). All of the factors had a VIF value <3 and therefore all variables were retained in our model. In addition, we performed a non-metric multidimensional scaling (nMDS) analysis using the Bray-Curtis dissimilarity index (via the 'vegdist' function) to visualize the variation in fish assemblages across different islands and depth zones, and the 'envfit' function to assess the influence of environmental variables (benthic coverage, temperature, depth, island area, and habitat complexity) on beta diversity, both implemented in the 'vegan' R package (Oksanen et al. 2024). The anthropogenic debris recorded along the transects was analyzed using a Tukey honestly significant difference (HSD) test to compare means and determine significant differences among islands.

### 3. RESULTS

#### 3.1. Species richness

Overall, a total of 5516 individual fish, belonging to 57 species and 23 families, were sighted in the surveys (Table S1). Specifically, we observed 42 species in Fogo (28 in the shallow, 21 in the upper, 12 in the lower), 30 in Santiago (17 in the shallow, 16 in the upper, 15 in the lower), and 42 in Santo Antão (33 in the shallow, 22 in the upper, 9 in the lower). The species accumulation curve (Fig. 2a) showed that the sampling captured most of the fish assemblages within each depth zone and revealed that the shallower zones harbor more species than the lower ones. However, when investigating each island separately, the number of species per transect in Santiago was higher in the upper zone than in the shallow one (Fig. 2b–d).

#### 3.2. Beta diversity trends

Beta diversity among islands ranged from 0.41 to 0.58, and most of the dissimilarity was due to species turnover (Fig. 3a). The greatest variation in species composition was observed between the lower depth zones of Santiago and the 2 other islands (Fogo and Santo Antão). When examining the depth profiles of each island (Fig. 3b; Fig. S1), a consistent trend of increasing beta diversity from the shallow to the lower mesophotic zones was observed among the islands (Fig. 3b; Fig. S1). The lowest variation in species composition was observed between the shallow and upper mesophotic zones. Larger MSAs showed similar trends, but with lower beta diversity values (Fig. S2).

The cluster analysis (Fig. 3c) revealed that the lower zones of all islands (Santo Antão: AL; Fogo: FL; Santiago: SL) formed a single cluster. However, we observed variations between islands in terms of the clustering of the shallow and upper mesophotic zones. Specifically, the shallow zone of Santiago (SS) clustered together with its upper mesophotic zone (SU), while the shallow zones of Fogo (FS) and Santo Antão (AS) clustered together, and their respective upper mesophotic zones (FU, AU) formed another distinct cluster (Fig. 3c). The nMDS plot showed similar patterns, i.e. all lower zones within the archipelago were separated from the shallow and upper zones (Fig. S3a).

When investigating intra-site beta diversity within depth zones (Fig. 3d), an increase with depth was observed. Specifically, the lower zone of Santiago displayed the highest species variation (Fig. S4a). On the other hand, the island of Santo Antão presented the lowest beta diversity values in its upper zone (Fig. S4b). Notably, the island of Fogo showed the most similar beta diversity values across all depth zones (Fig. S4c).

#### 3.3. Environmental and geographical drivers

The model (Table 1) showed that while depth remains a significant factor, geographic distance, which was excluded from the best model according to AIC criteria, showed no significant influence on beta diversity. All other variables, such as heterotrophic coral, habitat complexity, depth, algae, coral, area, and temperature, were significant drivers of beta diversity. This model indicated that approximately 41% of the variation in species composition could be explained by these variables, suggesting that factors related to microhabitats were more important in driving local assemblages compared to geographic distance. Particularly, variations in temperature, habitat complexity,

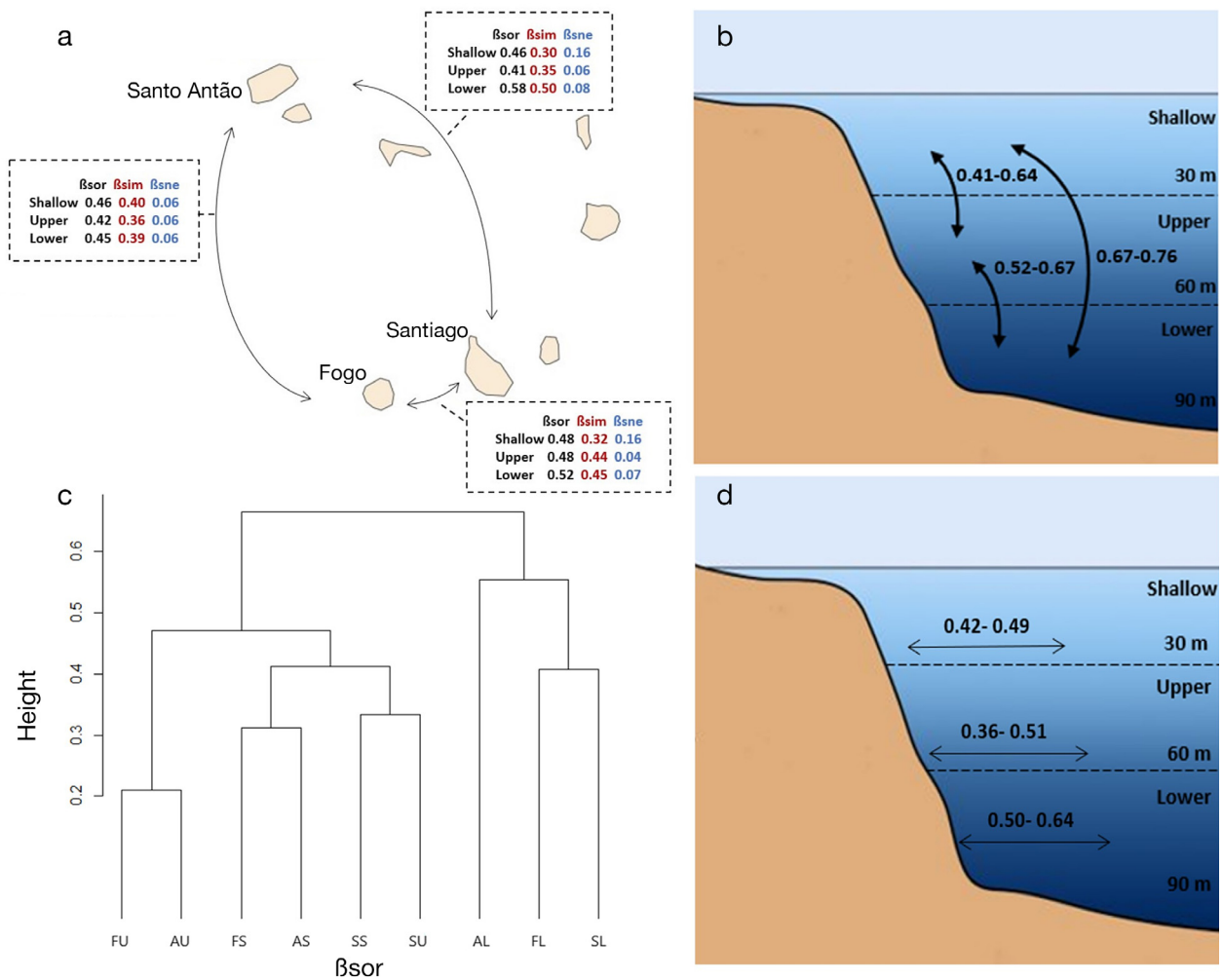


Fig. 3. (a) Sorensen's pairwise dissimilarity ( $\beta_{sor}$ ) and its components (turnover,  $\beta_{sim}$ ; nestedness,  $\beta_{sne}$ ) between the surveyed islands and their depth zones. (b) Sorensen's pairwise dissimilarity between shallow reef fish assemblages and mesophotic depth zones of each island. (c) Cluster analysis showing the average linkage of  $\beta_{sor}$  between the surveyed sites. FU: Fogo upper; AU: Santo Antão upper; FS: Fogo shallow; AS: Santo Antão shallow; SS: Santiago shallow; SU: Santiago upper; AL: Santo Antão lower; FL: Fogo lower; SL: Santiago lower. (d) Intra-site beta diversity using Sorensen's pairwise dissimilarity within each depth zone

Table 1. Results of the best-fitting beta regression log-linear generalized linear model analyzing drivers of beta diversity, along with their corresponding variance inflation factor (VIF). Most significant variables are displayed in **bold**

Variable	Estimate	SE	Z	Pr(> Z )	VIF
Intercept	-0.210	0.055	-3.795	<0.001	
<b>Temperature</b>	<b>0.113</b>	0.012	9.389	<0.0001	2.948
<b>Complexity</b>	<b>0.083</b>	0.023	3.693	<0.001	1.012
<b>Depth</b>	<b>0.033</b>	0.002	19.232	<0.0001	2.669
Algae	-0.015	0.001	-12.962	<0.0001	1.825
Coral	-0.020	0.003	-6.330	<0.0001	1.019
Area	0.001	0.0001	9.820	<0.0001	1.047
Heterotrophic coral	-0.003	0.001	-2.966	0.003	1.231
Pseudo R <sup>2</sup>	0.4125				

and depth appeared to exert the most significant influence on increasing beta diversity.

### 3.4. Fishing debris

Debris was observed on all studied islands, with the majority consisting of debris from the fishing industry (Fig. 4). Among the 3 studied islands, a significantly higher concentration of fishing debris was observed in Santiago compared to the other 2 islands

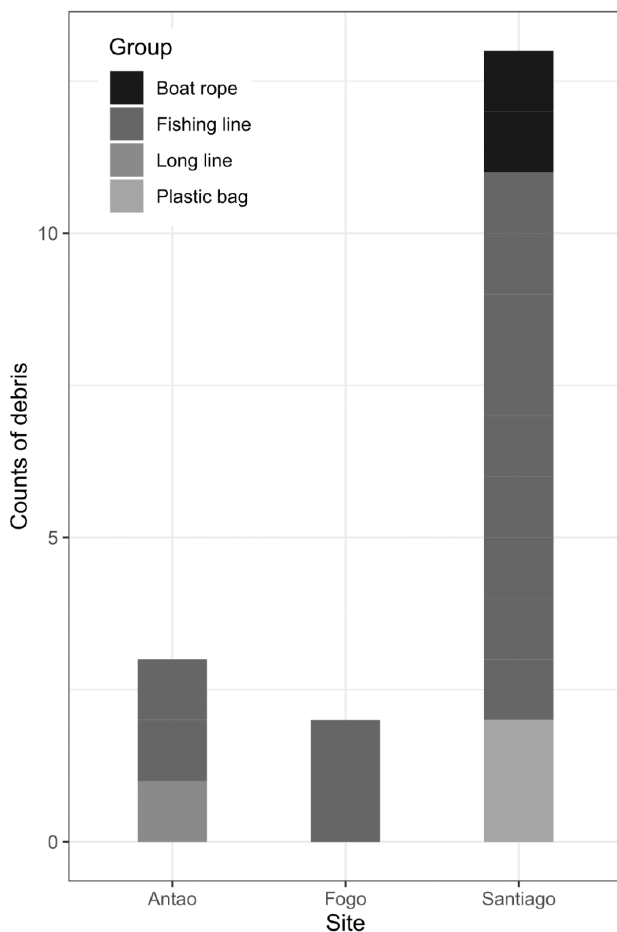


Fig. 4. Count of debris observed at the surveyed islands revealed significant differences between Santiago and the other islands (Tukey HSD test: Santiago–Fogo  $p_{\text{adj}} = 0.001$ ; Santiago–Antão  $p_{\text{adj}} = 0.002$ ; Fogo–Antão  $p_{\text{adj}} = 0.925$ )

(Tukey HSD test: Santiago–Fogo  $p_{\text{adj}} = 0.001$ ; Santiago–Santo Antão  $p_{\text{adj}} = 0.002$ ; Fogo–Santo Antão  $p_{\text{adj}} = 0.925$ ) (Fig. 4).

#### 4. DISCUSSION

This study is the first empirical evaluation of fish assemblage patterns across shallow and mesophotic zones aiming to determine the role of ecological and biogeographical factors in shaping beta diversity. During the examination of beta diversity components, we consistently observed that turnover was dominant over nestedness in all analyses. This pattern aligns with findings from other studies, such as the meta-analysis conducted by Soininen et al. (2018), which suggested a high species turnover in marine organisms potentially influenced by dispersal vari-

ability and environmental heterogeneity among sites. Maxwell et al. (2022) also observed a large-scale pattern of turnover as the dominant component in the taxonomic diversity of reef fishes within the Atlantic realm. Therefore, it seems that turnover is the main beta diversity component in fish assemblages from small (meters) to large (ocean basins) scales.

#### 4.1. Depth vs. geography

As expected, across all the surveyed islands, the proximity of depth zones resulted in a greater similarity between adjacent ones, such as between the shallow and upper mesophotic zones, contrasted with the differences observed between the shallow and lower mesophotic zones, in agreement with previous studies (Slattery et al. 2011, Baldwin et al. 2018, Laverick et al. 2018, Rocha et al. 2018). Further, Lesser et al. (2019) acknowledged a significant loss of shallow water taxa between the upper and lower mesophotic zones. For instance, in our study, 10 species were recorded on shallow and upper mesophotic reefs but were absent from the lower zone, which presented 8 exclusive species (Table S1).

Depth has been broadly acknowledged as the foremost driver of the abundance and distribution of reef fishes (Pinheiro et al. 2015, 2016, 2023b, Rosa et al. 2016, Semmler et al. 2017, Rocha et al. 2018) due to its impact on various factors, such as light availability, water temperature, marine current patterns, food resources, and levels of fishing activity (Lesser et al. 2009). Such changes may explain the increasing beta diversity along the depth gradient in Cabo Verde, as several studies have demonstrated the impact of depth on these aspects (Ferreira et al. 2004, Brokovich et al. 2008, Olavo et al. 2011). Some species seem to have a stronger association with specific depth zones (Baldwin et al. 2018, Silva et al. 2021, Bosch et al. 2023). Others may be more adapted to the environmental conditions, habitat structure, and food availability found within a particular depth range (Medina et al. 2007).

Geographic distance is a well-known driver of species turnover, whereas adjacent sites commonly display higher species similarity than distant ones (Caley & Schluter 1997, Medina et al. 2007). Cabo Verde presents unique characteristics that suggest the importance of geography for assemblage structure. For instance, while Santo Antão benefits from the proximity of seamounts, which have been shown to enhance species abundance (Pinheiro et al. 2015, Kaiser et al. 2020), Fogo's active volcano suggests a geologically



recent disturbance regime that may impact the local fish assemblages (Syms & Jones 2000). Wienerroither et al. (2009) observed that topographic and mesoscale hydrographic features proved to be the most influential factors for fish species distribution in Eastern Atlantic islands of volcanic origin. Similarly, Medina et al. (2008) suggested that the hydrodynamic patterns across the different seasons might be impacting the ecological isolation of Cabo Verde. Interestingly, when the depth zones within the archipelago were compared, they exhibited similar beta diversity values regardless of the geographic distance. Indeed, contrary to our expectations, the islands of Fogo and Santiago, which are closer geographically, did not show the lowest beta diversity values. The lack of a pattern regarding geographic distance may imply that each island harbors, to a certain degree, components of fish assemblages driven mostly by a combination of environmental characteristics rather than by isolation. Notably, for fishes, there have been observations of faunal breaks associated with thermoclines, which appear to influence changes in fish species composition (Pyle & Copus 2019). Our results also confirm that temperature is an important driver of variation in fish species assemblages.

Therefore, the variation in reef fish species composition among the islands within the archipelago may reflect local-scale processes such as inter-site variability in abiotic conditions, biological interactions, habitat heterogeneity, and stochastic recruitment processes (Witman et al. 2004). Of particular note, alongside temperature, habitat heterogeneity emerges as a crucial factor influencing both the similarity and richness of fish communities on oceanic islands, outweighing the impact of geographic isolation (Mazzei et al. 2021).

#### 4.2. Importance of microhabitats

Our study shows that the addition of small-scale environmental factors in the model decreases the importance of the geographic distance to explain beta diversity patterns in our system. In coral reefs, small-scale environmental variables have an important role in determining community patterns (Dornelas et al. 2006), as the existence of microhabitats increases beta diversity (Syms & Jones 2000). Taxonomic groups such as corals, gorgonians, algae, and seagrass are important drivers of beta diversity patterns (Harborne et al. 2006), which was also noted in our study. Differences in benthic cover and habitat complexity are significant drivers of beta diversity, indicating that benthic envi-

ronmental variables are determinants for fish species composition across sites and depth gradients. Zooxanthellate corals and algae dominated shallow and upper zones, whereas heterotrophic corals increased in mesophotic zones. The upper and lower mesophotic of the 3 islands examined are characterized by the presence of black coral forests (*Antipthella*, *Stichopathes*, and *Tanacetipathes* spp.). Prior research has shown that the presence of black coral forests can affect the degree of similarity in fish assemblage structure between depth strata (Rosa et al. 2016, Bosch et al. 2023). Therefore, the high beta diversity observed here may be attributed to species-specific variations in habitat selection (Syms & Jones 2000, Pinheiro et al. 2018). This could be explained by the fact that certain species exhibit a preference for specific microhabitats, indicating their specialization (Srinivasan 2003). An illustrative example is endemic species being habitat specialists (Pinheiro et al. 2018). In our study, we recorded several endemic species, such as *Gobius tetrophthalmus* (Table S1), which inhabits shallow waters with benthic substrates like coralline algae, open sand, and rock (Froese & Pauly 2024). Given the high rate of endemism in Cabo Verde (Freitas et al. 2019), particularly among cryptobenthic species such as blennioids and gobiids (Wirtz et al. 2013), endemic species are likely integral components of local fish assemblages.

We also observed a slight increase in beta diversity within depth zones along the depth gradient. This was rather surprising, since we would expect the shallow and the upper zones to have higher species variation in comparison with the lower zone due to higher species richness. This difference might be caused by the lower zones having less diverse microhabitats. For instance, we found that algae and coral coverage were completely absent from the transects in the lower zones across all of the surveyed islands and were composed solely of heterotrophic coral coverage. With less microenvironment diversity, these areas would offer fewer niches and would consequently be species-saturated, allowing fewer species to coexist at the transect scale (small scale). This would indicate that there are possibly assembly rules on the species distribution that avoid redundancy and maximize the available resources (Pinheiro et al. 2023b) within the lower zones. Consequently, the limitation in niche availability may result in higher beta diversity, as different transects may support distinct subsets of species due to the saturation effect. Studies have shown that the mesophotic zones have less redundancy in terms of functional roles and a greater proportion of species performing fewer common functions compared to shallow reefs (Pinheiro et al. 2023b). Species

with extreme traits create distinct spaces for each community, resulting in higher functional turnover (Villéger et al. 2013). Furthermore, the lower MCEs are known to harbor rare species (Pinheiro et al. 2016). The occasional presence of rare species might also drive the beta diversity up in the lower zones (Socolar et al. 2016). For instance, *Lappanella fasciata*, considered naturally rare by the International Union for Conservation of Nature and Natural Resources, is associated with black coral forests on deep reefs due to their refuge and nursery effects (Bosch et al. 2023).

### 4.3. Conservation

Beta diversity does not only depend on ecological patterns but also on human-induced pressure (Arias-González et al. 2008). Damaging anthropogenic actions can affect local fish communities (Socolar et al. 2016). Among the 3 studied islands, a significantly higher concentration of fishing debris was observed in Santiago compared to the other 2 islands (Tukey HSD test:  $p_{\text{adj}} < 0.001$ ; Fig. 4).

The higher levels of fishing debris, which can be used as an indicator of human pressure (Bruneel et al. 2021, Pinheiro et al. 2023a), most likely affected the observed patterns. Accordingly, beta diversity comparisons with Santiago and the other islands (Fig. 3a) showed the highest nestedness values, despite geographic distance, which could be associated with the selective removal of fish species by fishing. In addition, the shallow and upper MCE zones of Santiago clustered together and had lower species richness, contrasting with the other islands. This observation may be indicative of fishing activities targeting specific species in the shallow and upper zones (Lindfield et al. 2016). For example, the family Carangidae was completely absent from the surveys in Santiago, and the species *Cephalopholis taeniops* (Epinephelidae) was observed in lower frequencies in comparison to Santo Antão and Fogo. Both Carangidae and *C. taeniops* are known to have high economic value; *C. taeniops* is the most commercially caught fish in Cabo Verde (Tariche et al. 2015), and the family of jacks is known to be overfished in some regions (Lino et al. 2011, Silva et al. 2021). Previous studies have also shown the negative impact of anthropogenic pressures on fish assemblages of tropical islands (Bruneel et al. 2021).

Shallow reefs are known to be targets for overfishing; however, depth does not provide absolute shelter from fishing activities. Signs of higher fishing pressure

have also been observed at mesophotic depths (Rocha et al. 2018, Ho et al. 2020, Pinheiro et al. 2023a) as well as the presence of marine debris (Angiolillo et al. 2015). MCEs are known to harbor rare species with narrow distributions (Pyle et al. 2019), making them particularly vulnerable to human impacts such as fishing. Such impacts can reduce beta diversity through the complete disappearance of rare species, a process known as subtractive homogenization (Socolar et al. 2016).

Rocha et al. (2018) highlighted that regardless of depth, the distance to human activities seems to be the main driver of the fish community status. Thus, as for shallow waters (Cinner et al. 2013), remote reefs less exposed to coastal population impacts tend to have higher biodiversity and healthier ecosystems, approaching pristine conditions. Conversely, MCEs that are directly adjacent to shore are more likely to be locally impacted by overfishing and sedimentation from runoff than MCEs that are further away (Frade et al. 2019, Pyle & Copus 2019, Spalding et al. 2019, Pinheiro et al. 2023a). Local stressors might have a higher impact on MCEs than on shallow reefs because in general, deeper reefs have lower diversity and less functional redundancy (Pinheiro et al. 2023b) and are closer to the limit of photosynthetically viable light levels, presenting higher sensitivity and slower recovery with changes in water clarity (Pyle & Copus 2019).

Understanding the contribution of each component to beta diversity is crucial for effective conservation management (Socolar et al. 2016). For sites with high turnover along environmental gradients, conservation efforts should focus on protecting multiple locations to maintain biodiversity; however, for sites with high nestedness, prioritizing larger areas of biodiverse locations would be a more effective approach (Socolar et al. 2016), since the species-poor sites are a subset of them (Baselga 2010). While not many ecological studies have specifically investigated beta diversity patterns in MCEs, recent research suggests that turnover is the dominant component along the depth gradient (Rocha et al. 2018). Thus, instead of presenting a high overlap with the large biodiversity pool found in shallow waters, species composition of MCEs is mostly different, a pattern driven by independent assembly rules acting over evolutionary time scales (Pinheiro et al. 2023b). Since our results corroborate previous findings showing that turnover is the dominant component of beta diversity between shallow reefs and MCEs in Cabo Verde, it would be crucial for conservation efforts to extend reef protection vertically to encompass these deeper ecosystems. How-

ever, while our study focused on taxonomic differences, it is worth noting that anthropogenic factors can also impact functional diversity of reef fishes (Friedlander & DeMartini 2002, Quimbayo et al. 2019, Dubuc et al. 2023). Therefore, future studies could consider integrating functional diversity analysis to gain a more comprehensive understanding of reef fish communities.

## 5. CONCLUSION

Here, we show that beta diversity within the Cabo Verde archipelago was mainly driven by depth and environmental variables such as temperature, habitat complexity, and benthic coverage. The shift in depth concurrently influences habitat structure and temperature regime, resulting in an increase in beta diversity in reef fish assemblages with increasing depth. Notably, higher species richness does not necessarily result in higher beta diversity within zones. Our results suggest that the higher beta diversity within the poorer lower MCE assemblages appears to be a result of saturation, likely due to reduced microhabitat heterogeneity at smaller scales. Furthermore, the effect of geographic distance is reduced within the archipelago of Cabo Verde since the combination of environmental characteristics within depth zones contributes most to promoting differences in species assemblages.

Determining the extent of species decline in the ecosystem resulting from destructive activities is challenging when the initial baseline of abundance and diversity is unknown. To protect mesophotic reefs, it is essential to take initial steps that involve conducting fundamental research on habitat and species richness in these understudied locations (Hughes et al. 2017, Turner et al. 2019). This should be prioritized before granting approvals for destructive activities. As with shallow reefs (Hughes et al. 2017), implementing local measures to protect deep reefs from overfishing and pollution should enhance the resilience of reef ecosystems and their capacity of buffering the impacts of climate change.

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