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Environmental and geographical drivers of reef fish beta diversity across a depth gradient in an oceanic archipelago of the eastern Atlantic Ocean.

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Environmental and geographical drivers of reef fish beta diversity across a depth gradient in an oceanic archipelago of the eastern Atlantic Ocean.

Mestrado em Biologia Marinha

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Declaração de autoria de trabalho

Environmental and geographical drivers of reef fish beta diversity across a depth gradient in an oceanic archipelago of the Atlantic Ocean.

Declaro ser a autora deste trabalho, que é original e inédito. Autores e trabalhos consultados estão devidamente citados no texto e constam da listagem de referências incluída.

I hereby declare to be the author of this work, which is original and unpublished. Authors and works consulted are properly cited in the text and included in the reference list.

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Resumo

O impacto mundial das pressões antropogénicas nos recifes de coral é cada vez mais agravante. As perturbações induzidas pelo homem nas últimas décadas causadas maioritariamente pela poluição, sedimentação e pesca excessiva causam um stress significativo nos ecossistemas recifais. As consequências das alterações climáticas e da degradação do habitat têm sido investigadas intensivamente nos recifes pouco profundos, principalmente acima dos 30 metros, pela sua maior acessibilidade. No entanto, avanços tecnológicos recentes têm permitido a investigação em recifes mais profundos entre 30 e 150 metros, uma zona conhecida como "Ecossistemas de Corais Mesofóticos" (MCEs).

Geralmente considera-se que os recifes mais profundos têm sido menos afetados pelas alterações climáticas e outras perturbações antropomórficas quando comparados aos seus homólogos menos profundos. Os recifes que apresentam condições menos alteradas são naturalmente aqueles que estão mais distantes dos locais habitados por humanos. As ilhas oceânicas remotas abrigam alguns desses últimos ecossistemas devido ao seu isolamento, e são consideradas laboratórios naturais para estudos ecológicos, biogeográficos e evolutivos.

Um número crescente de estudos tem tentado investigar os fatores relacionados com a distribuição e composição de espécies de peixes entre ilhas oceânicas ou as diferenças entre recifes rasos e profundos. As análises de diversidade beta fornecem uma ferramenta essencial para compreender como diferentes habitats e fatores ambientais influenciam a diversidade e distribuição de espécies. Ao medir a taxa de mudança na composição das espécies entre habitats ou comunidades, os índices de diversidade beta podem identificar fatores ambientais ou geográficos que influenciam os padrões de variação das espécies numa região. Fragmentar a diversidade beta nos seus componentes, turnover (substituição de espécies) e aninhamento (perda ou ganho de espécies), ajuda-nos a compreender melhor os processos subjacentes às variações da comunidade.

Este estudo marca o primeiro estudo in situ a ser realizado em Cabo Verde envolvendo um gradiente de profundidade (recifes rasos a mesofóticos,10-90 m). A investigação tem como objetivo identificar os fatores que impulsionam a diversidade beta das comunidades de peixes de recife no arquipélago e determinar a relevância de fatores ecológicos ou biogeográficos na formação da diversidade beta. A amostragem foi realizada por mergulhadores em recifes com profundidades a variar dos 5 aos 90 metros, realizando censos visuais subaquáticos (UVCs) ao longo de três zonas de profundidade: superficial (0-30m), mesofótica superior (31-60), mesofótica inferior (61-90m). Parâmetros ambientais como cobertura de algas, cobertura de corais, cobertura de corais heterotróficos, complexidade do habitat e temperatura foram avaliados para cada transecto analisado.

Os dados de abundância de peixes recolhidos foram transformados em dados de presença-ausência, categorizados por ilhas e zonas de profundidade. O esforço de amostragem desigual foi abordado usando uma área de amostragem mínima (MSA) para padronizar os dados. A diversidade beta taxonómica foi medida com o índice de Sorensen e os seus componentes, usando 1000 simulações que forneceram informações sobre a dissimilaridade entre as comunidades de peixes de recife. Para analisar a variação de espécies dentro de cada zona, foram calculadas dissimilaridades entre pares de espécies, usando a média dos componentes Sorensen beta para cada transecto (com profundidades variáveis) com o objetivo de identificar padrões nos vários grupos. Além disso, usaram-se dois Modelos Lineares Gerais (GLMs) utilizando a distribuição de regressão Beta e uma função de ligação (log) para investigar os fatores promotores da diversidade beta. O primeiro modelo procurou analisar qual dos dois fatores, profundidade e distância geográfica, é mais determinante para a diversidade beta. O segundo modelo teve como objetivo explorar o impacto adicional das variáveis ecológicas na diversidade beta.

Os nossos resultados mostraram que a composição das comunidades de peixes de recife varia entre as ilhas e a maior parte da dissimilaridade resulta do turnover, substituição de espécies. A maior variação na composição de espécies foi observada na zona de menor profundidade entre a ilha de Santiago e as outras duas ilhas (Antão e Fogo). Os perfis de profundidade de cada ilha mostraram uma tendência consistente de aumento da diversidade beta da zona rasa para a zona mesofótica inferior, com a menor variação na composição de espécies observada entre a zona mesofótica rasa e superior. A análise de cluster revelou que todas as zonas inferiores formavam um único cluster. No entanto, foram observadas variações entre ilhas em termos de agrupamento das zonas mesofóticas rasas e superiores, onde Santiago se agrupou com a sua zona mesofótica superior, enquanto as zonas rasas do Fogo e Antão se agruparam, com as suas respectivas zonas mesofóticas superiores formando outra zona distinta.

Ao investigar as diferenças da diversidade beta entre zonas com diferentes profundidades no arquipélago de Cabo Verde, constatou-se um ligeiro aumento da variação do número de espécies com a profundidade. Especificamente, a zona mais profunda da ilha de Santiago apresentou a maior variação no número de espécies comparativamente a zonas mais superficiais.

Aqui mostramos que a diversidade beta no arquipélago de Cabo Verde foi impulsionada principalmente pelo gradiente de profundidade e pelas variáveis ambientais. O primeiro modelo mostrou que tanto a profundidade quanto a distância geográfica têm influências significativas na variação de espécies entre locais. Por outro lado, o segundo modelo que inclui todas as outras variáveis ambientais, mostrou que a distância geográfica não influi na diversidade beta, sugerindo que outros fatores relacionados com o microhabitat foram mais importantes na variação da composição das comunidades de peixes de recife.

O aumento da profundidade influencia a estrutura do habitat e a temperatura, o que se traduz numa redução da similaridade da composição das comunidades de peixes de recife, entre as zonas superficiais e mais profundas. Notoriamente, uma maior riqueza de espécies não resulta necessariamente numa maior diversidade beta. Os nossos resultados sugerem que o MCE mais profundo parece estar saturado como resultado da menor heterogeneidade do microhabitat, o que leva a uma diminuição do número de nichos e consequentemente menos riqueza específica, mas maior rotatividade das espécies que têm que se adaptar a condições mais extremas de luminosidade e temperatura. O efeito da geografia é reduzido dentro do arquipélago de Cabo Verde, uma vez que cada ilha parece ter características únicas em pequena escala que contribuem para gerar diferenças na composição das comunidades de espécies. A elevada pressão de pesca evidente na ilha mais populosa parece aumentar o aninhamento da comunidade através da remoção de espécies-alvo, um indicativo de que a pressão humana pode estar afetando os padrões ecológicos e biogeográficos.

Abstract

The worldwide impact of anthropogenic pressures on coral reefs is not surprising. The deeper reefs between -30 to -150 meters, a zone known as "Mesophotic Coral Ecosystems" (MCEs), have been commonly considered to be less affected by climate change and human impacts compared to their shallow counterparts. However, they still face natural and anthropogenic pressures. Reefs that have shown the most pristine conditions are the ones that are furthest away from human-populated locations. Oceanic islands harbour some of the last remaining pristine ecosystems and fish assemblages. An increasing number of studies have attempted to investigate the factors related to the distribution of fish species assemblages between oceanic islands or across the depth gradient. By measuring the rate of change in species composition across habitats or communities, beta diversity analyses provide an essential tool to identify environmental or geographical factors that influence patterns of species variation in a region.

This study marks the first *in situ* study to be conducted in Cape Verde across the shallow to mesophotic depth gradient (-10 to -90 m). Here we aim to identify the factors driving beta diversity for reef fish assemblages within the archipelago and determine whether ecological or biogeographical factors have a more prominent role in shaping beta diversity. Our results show that beta diversity within the Cape Verde archipelago is mainly driven by the depth gradient and environmental 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 (-0 to -30 m) and upper (-31 to -60 m) mesophotic zones. Our results suggest that the lower MCE seems to be species saturated as a result of lower microhabitat heterogeneity, showing lower richness but higher species turnover. Furthermore, the effect of geography is reduced within the archipelago of Cape Verde since each island seems to have unique characteristics that contribute to differences in species assemblages. High fishing pressure, more evident in the most populated island, seems to increase the community nestedness through the removal of target species, indicative that human pressure may be affecting the ecological and biogeographic patterns.

Keywords: Mesophotic Coral Ecosystems, Reef Fishes, Beta Diversity, Marine Biogeography, Cape Verde.

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List of Abbreviations, Acronyms and Symbols

AIC (Akaike information criterion)

ßsor (Beta Sorensen)

ßsim (Beta simpson)

ßsne (Beta nestedness)

GLM (General linear model)

MCE (Mesophotic coral ecosystem)

MSA (Minimal sampling area)

UVCs (Underwater visual censuses)

VIF (Variance inflation factor)

General Introduction

1. Coral reefs and Mesophotic Coral ecosystems

Coral reefs are one of the most astonishing ecosystems in the world and provide a wide variety of ecosystem services. In addition, these ecosystems harbour more species per unit area than any other habitat on our planet and are, therefore, highly important as biodiversity hotspots (Maragos et al., 1996; Spalding et al., 2001). Unfortunately, the past decades of human-induced disturbances have led to a significant level of stress on coral reef ecosystems, mainly due to pollution, sedimentation, and overfishing (Norse, 1993; Maragos et al., 1996; Spalding et al., 2001). The effects of climate change and habitat degradation have been extensively studied on coral reefs in the last decades. The research has mainly focused on reefs above 30 meters, which are the most accessible. However, as technology evolved, an increasing number of studies is shifting their focus to deeper reefs, on the so-called "Mesophotic Coral Ecosystems" (MCEs) (Laverick et al., 2018; Pyle et al., 2019; Pyle & Copus, 2019)

1.1. Structure of reef communities along the depth gradient

On a global scale, MCEs are found wherever shallow coral reefs exist (Lesser et al., 2009; Kahng et al., 2016; Pyle & Copus, 2019) and are considered an extension of their shallow counterparts (Kahng et al., 2017; Lesser et al., 2019). Fish and scleractinian corals are well-studied taxonomic groups at MCEs. Most fishes inhabiting these depths belong to families and genera frequently found on shallow coral reefs (Pyle et al., 2019). There are, however, some discrepancies, with some species being depth specialists and confined to a particular depth stratum, while others are depth generalists and can be found throughout a depth gradient (Rocha et al., 2018; Pyle & Copus, 2019). Top predators such as groupers, snappers, and sharks usually show a wider depth range (Papastamatiou et al., 2015).

The structure of MCE communities is mainly driven by abiotic factors such as temperature, topography, and light attenuation (Lesser et al., 2009; Turner et al., 2017; Kahng et al., 2019). While shallow tropical coral reefs are characterized by warm and clear water, there is a decrease in the temperature and light towards the MCEs. Yet, in tropical zones, the temperature difference between shallow and upper mesophotic zones is usually less than 5°C, which has a low impact on the community structure along the depth gradient (Lesser et al., 2009). However, some taxonomic groups, such as fishes, show a pattern of faunal breaks associated with major thermoclines (Pyle & Copus, 2019). Light attenuation also plays an enormous role in controlling the productivity of corals, and coral communities from deeper zones have shown adaptations to adjust to the low light environment through mixotrophy or change in shape and light-harvesting pigment systems (Lesser et al., 2009; Kahng et al., 2019). Other factors, such as the steepness and direction of the reef slopes, ancient shorelines, and water movement patterns, may also shape benthic communities at MCEs (Pyle & Copus, 2019).

MCEs low-light adapted coral communities are typically found within a boundary depth from -30 to -150 meters (Lesser et al., 2009; Kahng et al., 2017; Pyle & Copus, 2019). The species richness of fish and scleractinian corals usually peaks at 30 meters and then declines with increasing depths (Brokowich et al., 2008; Pyle et al., 2019; Pinheiro et al., 2023a). Recent studies have proposed a community break and a distinct change in species composition at approximately -60 meters, with a significant loss of shallow-water taxa (Lesser et al., 2019). The fish assemblage structure changes gradually with increasing depths (Brokowich et al., 2008; Pinheiro et al., 2023a). There is a shift in the trophic guilds of fish between the depth gradient, with macro carnivores, invertebrate feeders and planktivores being more diverse and abundant in deeper reefs (Pinheiro et al., 2023a). In contrast, territorial herbivores are almost exclusively associated with shallow-water reefs (Pereira et al., 2018).

Scleractinian corals are the predominant reef-building organisms in shallow-water reefs (Spalding et al., 2001), but they also play a crucial role in deep-water reefs (Pyle & Copus, 2019). However, in the MCEs, they are not the primary habitat-forming benthic organisms. Instead, Octocorallia, Anthipatharia, macroalgae, and sponges are much more abundant (Pyle & Copus, 2019), with sponge diversity increasing with depth (Lesser et al., 2009; Kahng et al., 2017). The same pattern has been observed for the octocorals and antipatharians, possibly due to the reduced competition for space among phototrophic taxa. The benthic macroalgae also provide critical ecological functions to the MCEs through nutrient recycling and primary production (Kahng et al., 2017).

1.2. Stressors on the reef

The deeper reefs have been commonly considered to be less impacted by climate change and other anthropogenic disturbances than their shallow counterparts. As a result, some studies have suggested that mesophotic reefs could potentially serve as a refugee for their shallow reef species which has led to the "Deep reef refugee hypothesis" (Lesser et al., 2009; Bongaerts et al., 2010; Laverick et al., 2018; Bongaerts & Smith, 2019).

The deeper reefs seem to provide some protection against the thermal bleaching of corals (Pérez-Rosales et al., 2021). However, MCEs are closer to the limit of photosynthetically viable light levels and may be more sensitive to minor changes in water clarity than shallow-water reefs (Pyle & Copus, 2019). In addition, natural disturbances such as tropical storms and hurricanes may also cause damage towards the MCEs. Previous studies in the Bahamas (Rocha et al., 2018; Pinheiro et al., 2019) and Great Barrier Reef (Bongaerts et al., 2013) have observed deeper coral reefs buried by sedimentation after major storms.

The deeper reefs have not been spared from human-induced disturbances. Plastic pollution and fishing debris have been observed in the same high frequencies in the deeper reefs as in the shallower ones (Rocha et al., 2018; Pinheiro et al., 2023b). The coral reefs that have shown the most pristine condition are the ones that are furthest away from human-populated locations, for both shallow and deep coral reefs (Rocha et al., 2018). However, these more isolated reefs are not free from degradation. Pollution, destructive fishing (Olavo et al., 2011; Etnoyer et al., 2016), and mining increasingly impact MCE reefs. It is imperative to extend the focus beyond the shallow zones and consider the mesophotic zone to ensure the conservation of the coral reefs. Although shallow coral reefs have received most of the attention in conservation efforts, neglecting the deeper reefs is problematic, as they are also vulnerable to disturbances and may require longer recovery time (Rocha et al., 2018)

2. Biodiversity indices

The conservation of marine biodiversity is a critical issue, and understanding the ecological and environmental drivers that influence communities in the environment is essential for effective planning (Roff & Zacharias, 2011). However, there is currently a lack of comprehensive records of marine biodiversity at the global, provincial, and ecoregional levels. To better understand the distribution of species diversity, it is crucial to inventory and comprehend how the different communities are structured and what processes affect marine biodiversity, making it a top priority (Roff & Zacharias, 2011).

2.1. Alpha diversity

There are various ways to measure biodiversity at both the species and community level. For example, alpha diversity or species richness, is the taxonomic diversity of a specific area, habitat, or community. However, measuring species richness may lead to biases based on the sample size and sampled area, and the number of species should only be compared among alike and similar habitats (Rolf and Zacharias, 2011).

Besides richness, the evenness of abundance across species tells us how evenly distributed the individuals of each species are in a sample. Species richness and evenness can vary greatly depending on the size of the sampled area. Standardized measurements across a spatial scale are crucial to ensure that comparisons are made consistently across different areas (Whittaker et al., 2001). Statistical methods can correct for sample size, allowing for more comparable values. Standard indices for alpha diversity are Simpson and Shannon, which measure species diversity per individual rather than per unit area (Rolf and Zacharias, 2011). On the other hand, gamma diversity measures the total biodiversity over a more extensive area or region. It explains the species richness in a range of habitats in a geographic area. Gamma diversity is the sum of alpha and beta diversity. However, it is crucial to acknowledge that overall measures of gamma diversity depend on how we define the boundaries of a region (Rolf and Zacharias, 2011).

2.2. Beta diversity and its components

Beta diversity measures the variation in species composition between different habitats, ecosystems or along environmental gradients on temporal or spatial scales. This term was first used by Whittaker (1960) and defined by the equation beta = gamma/alpha, where alpha represents species richness at a specific site, gamma represents total species richness over a region, and beta represents the difference in species richness between sites (Whittaker, 1960). This measure can compare species diversity between habitats or communities by assessing the unique or shared species present. In addition, by measuring the rate of change in species composition across habitats or communities, beta diversity indices can reveal the processes driving species distributions and biodiversity and may serve as a proxy for the latter (Harborne et al., 2006; Baselga & Orme, 2012).

Two commonly used beta diversity indices are the Sorensen and Jaccard pairwise similarity indices, which are monotonic transformations of gamma/alfa (Baselga & Orme, 2012). Both are based on qualitative presence-absence data, and their value ranges from 0 to 1. A value of 1 indicates the same species composition at both sites, and a value of 0 indicates that all species differ between the sites (Chao et al., 2005). Dissimilarity indices are the opposite: a value of 0 shows total overlap, while 1 indicates that species do not overlap (Baselga, 2013). The pairwise beta diversity explains the average dissimilarity in species composition between all possible pairs of sites within a specific region. Moreover, they can be utilized to identify environmental or geographical factors that influence patterns of the beta diversity in the region. The sites with larger compositional dissimilarities are also more likely to have more significant difference in environmental or geographic features. By analysing these relationships helps us to understand what factors shapes the distribution and composition of species across different sites (Socolar et al., 2016). Another beta diversity index based on abundance data is the Bray-Curtis index, a modified Sorensen index. The Bray-Curtis index is the method for detecting gradients in species abundances (Chao et al., 2005). Abundance-based indices place lower importance on rare species by giving them less weight in the calculations. Therefore, they might be preferred in analyses where the sites are dominated by common species (Socolar et al., 2016).

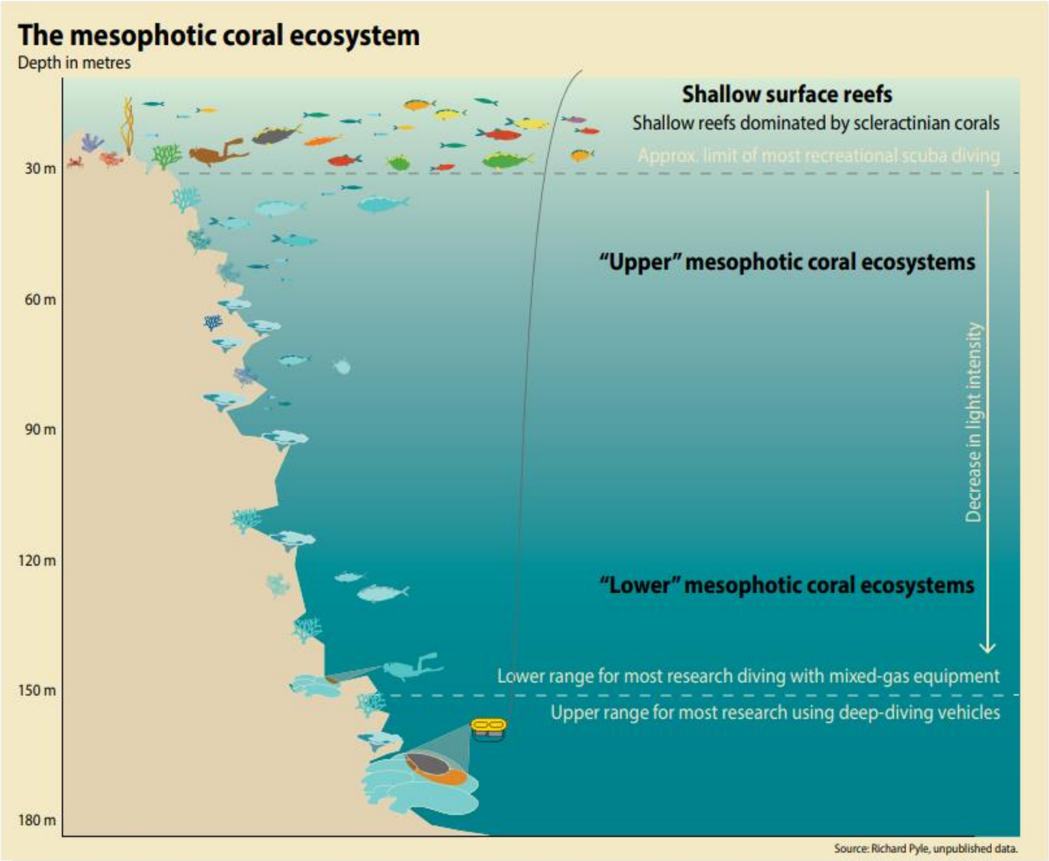
Recently, Baselga (2010) proposed disentangling the beta diversity in two components. The first is species replacement, also known as turnover, which is species replacement along a spatial or ecological gradient. Turnover occurs when species found in one site are not present in another site, but are substituted by other species absent from the initial site. The second is nestedness, which indicates the removal or addition of species from one of the sites, where species are not necessarily replaced by additional species. This result in the poorest community assemblage being a subset of the richest site (Baselga & Orme, 2012; Socolar et al., 2016). Separating these two components can help with a better understanding of the underlying processes behind beta diversity and identifying the factors contributing to beta diversity (Baselga, 2010). Legendre et al. (2014) has acknowledged an additional component of beta diversity, difference in richness, which refers to that one community may include a larger number of species than another. Richness difference may reflect the diversity of available niches at different locations along the sampling area causing nestedness (Legendre, 2014). Regarding conservation management, higher rates of turnover would imply that conservation should target multiple sites, whereas higher rates of nestedness would target the species richest sites (Socolar et al., 2016).

Different indices can be used to estimate these two components, however, some dissimilarity measurements view them as equivalent, such as Whittaker's (1960) beta diversity measure and Sorensen and Jaccard indices. The Simpson index (bsim) only takes turnover into account and is a widely recommended presence/absence measurement due to its insensitiveness towards the sample size. The bsim is especially adapted to identify where turnover of rare species occurs along a spatial and environmental gradient (Socolar et al., 2016). Therefore, choosing dissimilarity indices can have a different impact on the beta diversity analysis (Baselga & Orme, 2012; Bevilacqua & Terlizzi, 2020).

Overall, beta diversity provides an essential tool for understanding how different habitats and environmental factors influence species diversity and distribution and can aid in conservation planning and management (Harborne et al., 2006; Rolf and Zacharias, 2011; Baselga & Orme, 2012).

2.3. Gaps in the research

A few studies aimed to measure the beta diversity across shallow and the mesophotic reefs, mainly between the shallow and the upper zone. Their results have shown that the reef fish and coral assemblages gradually changes with increasing depth (Bosch et al., 2023; Brokovich et al., 2008; Lesser et al., 2019) and that the “Deep Reef Refugee Hypothesis” might not be as adequate as thought, at least not for entire communities (García-Hernández et al., 2018; Medeiros et al., 2021; Morais & Santos, 2018; Rocha et al., 2018; Semmler et al., 2017). Lesser et al. (2009), Pyle & Copus (2019) have pointed out that there is a lack of research on the lower MCEs due to the difficulty of accessing deeper areas of the reef. However, recent technological advancements have made research in deeper reefs more accessible and cost-effective. Technical diving has been particularly efficient in discovering cryptic species (Pyle, 2019; Pyle & Copus, 2019). Using the same research methods in shallow and deep reefs allows for a direct comparison between surveyed sites (Brokovich et al., 2008).



Source: Richard Pyle, unpublished data.

Figure 1. Illustration of typical research methods conducted along the depth gradient of coral reefs. Image source: (Baker et al., 2015).

However, research on MCEs has been unevenly distributed geographically, performed mainly in the Atlantic Ocean and with only one-third conducted in the Pacific (Kahng et al., 2017; Pyle & Copus, 2019). The research on MCEs is still in its early phase, recording species, diversity, biogeographic patterns, and processes, which will provide fundamental information on the ecological characteristics and how to proceed with conservation (Pyle & Copus, 2019).

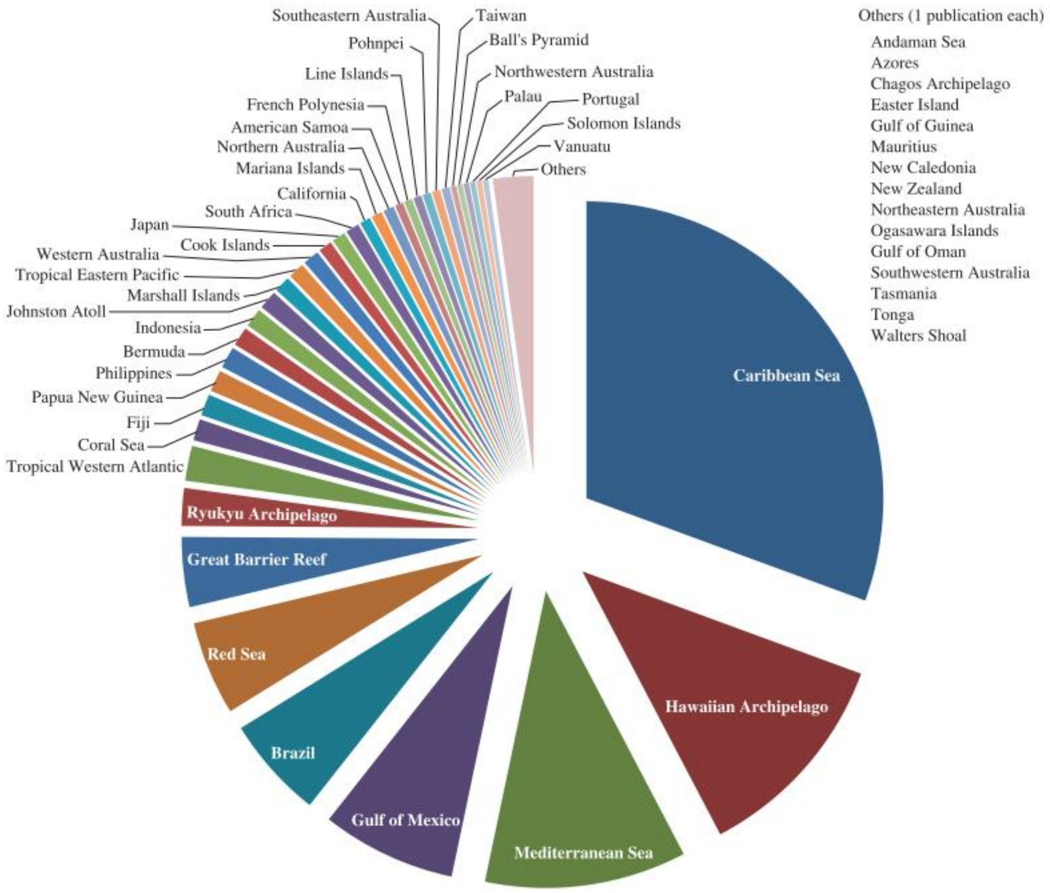


Figure 2. Illustration of geographic distribution of scientific publications of MCE habitats between 1960-2017. Image source: (Pyle & Copus, 2019).

3. The Cape Verde archipelago

The Atlantic Ocean is the youngest ocean in the world and the second largest after the Pacific (Spalding et al., 2001). Half of all the conducted MCE research has taken place there. The main focus has been on the Caribbean, which is the main centre of marine biodiversity in the Atlantic Ocean (Spalding et al., 2001; Pinheiro et al., 2018). Some studies have suggested that peripheral provinces may also harbour centres of biodiversity through the overlap of tropical and subtropical species (Pinheiro et al., 2018). However, still lacks research on deeper reefs in the rest of the Atlantic (Pyle & Copus, 2019).

The Cape Verde archipelago, located in the north-eastern Atlantic, spans from latitudes 14° to 17° N and longitudes 21° to 25° W, and is situated parallel to Senegal, between 450 and 600 km off the Western coast of Africa (Ramalho, 2011). The ten islands and eight islets that make up the archipelago are arranged in a west-facing horseshoe shape and can be divided into a northern chain (Santo Antao, Sao Vicente, Santa Luzia, Sao Nicolau) and a southern chain (Sal, Boa Vista, Maio, Santiago, Fogo, and Brava) (Ramalho, 2011). This archipelago has been traditionally grouped in the Macaronesia biogeographic region, with Canary Islands, Azores, Selvagens and Madeira (Spalding et al., 2007). However, a recent study suggested that Cape Verde should be considered part of the West African transition zone, and classified it as a subprovince within that region (Freitas, et al., 2019b), as it's community structure of marine coastal fishes differs significantly from the other archipelagos in Macaronesia (Santos et al., 1995; Wirtz et al., 2013). The Cape Verde Front flowing North of the Cape Verde archipelago, serves as an important oceanic biogeographic barrier, isolating Cape Verde from the rest of the Macaronesia islands. Studies have shown a clear separation between Cape Verde and the rest of Macaronesia, and whereas Cape Verde being one of the most diverse archipelagos regarding coastal fish species with a high number of endemic species (Freitas, et al., 2019b). Cape Verde has shown higher affinity regarding coastal fishes towards Sao Tome and the Tropical West Africa (Freitas, et al., 2019b), which is shown by the high number of shared species with the African sub-region (P. Monteiro et al., 2008). Moreover, some of the islands in Cape Verde, such as Santiago, have shown similar structure of fish community compared to islands in the Caribbean (Zander., 2011).

3.1. Community composition of the mesophotic zone of the Cape Verde Islands

In Cape Verde, our understanding of mesophotic reefs is limited, with a lack of in situ research conducted on deeper reefs below 30 meters (Baker et al., 2016). The coral community structure in Cape Verde is influenced by the depth and substrate type, wherein the local coral species demonstrate preference to specific type of surface and depth strata (J. Monteiro et al., 2008). Moreover, the archipelago's landscape naturally exhibits heterogeneity and fragmentation (Medina et al., 2007). These communities are further affected by temperature variations and the wind regime, which contribute to significant dust depositions from the Sahara (J. Monteiro et al., 2008).

Although mature coral communities can be found in Cape Verde, true coral reefs and larger reef structures are scarce (Spalding et al., 2001), probably due to the cold waterfront of the Canary Current (Laborel, 1974). The most abundant scleractinian coral contributing to reef frameworks in Cape Verde is the Atlantic siderastreids. *Siderastrea radians*, a slow-growing species, has shown adaptation to local environmental conditions and can thrive at different depths (Monteiro et al., 2013). In Cape Verde, whip corals are common from 10 meters downwards (Wirtz & d'Udekem-d'Acoz, 2001). These anthipatharians dominate the vertical and sub-vertical facies, where scleractinian corals are scarce (J. Monteiro et al., 2008). The most common anthipatharians species found in Cape Verde are the larger ones *Anthipathes subpinnata* and the smaller ones *Anthipathes spinescens* (Wirtz & d'Udekem-d'Acoz, 2001). In the mesophotic reefs of West Africa, specifically in Sao Tome, black coral forests dominate, while scleractinian corals and coralline algae are prevalent in shallow reefs up to 30 meters. Here as well the presence of antipatharians increases towards the deeper reefs (Morais & Maia, 2017).

The anthipatharians have been found to play a significant role in the mesophotic fish assemblage, indicating that black coral forests promote specialization of reef fishes (Bosch et al., 2023). Previous studies conducted in Lanzarote in the Eastern Atlantic have shown that fish assemblage changes across the depth gradient, with a decrease in species richness and shifts in species composition. Their results showed that shallow fish assemblages were mainly characterized by damsel fishes (*Chromis limbata* and *Similiparma lurida*), wrasses (*Thalassoma pavo*), rockfish (*Scorpaena maderensis*) and seabream (*Lithognathus mormyrus*) and the mesophotic fish assemblage of barracuda (*Sphyraena viridensis*), hogfish (*Bodianus scrofa*), seaperch (*Anthias anthias*), comber (*Serranus cabrilla*) and rainbow wrasse (*Coris julis*) (Bosch et al., 2023). In the Western African mesophotic reefs of Sao Tome, the most abundant reef fish species includes *Paranthias furcifer*, *Clepticus africanus* and *Lutjanus fulgens*, which have been shown to seek shelter in the canopies of black coral forests (Morais & Maia, 2017).

The reef fish assemblage in Cape Verde consists mainly of species from the amphi-Atlantic, tropical West Africa, Eastern Atlantic, and endemic species of Cape Verde and Macaronesia (Freitas et al., 2019b). Compared to other island groups in the eastern Atlantic, the Cape Verde Islands exhibit a significantly higher degree of coastal fish endemism (Freitas, et al., 2019b; Wirtz et al., 2013), especially smaller size endemic species such as blennioids and gobiids (Wirtz et al., 2013). As previously stated, there has not been conducted any in situ research on mesophotic reefs in Cape Verde. However, research conducted in the shallow parts of Santa Luzia in Cape Verde has shown that the genus Chromis (*Chromis multilineata* and *Chromis lubbocki*) is highly abundant around the island (Freitas, et al., 2019a). These species are also predominant in the Northwest Bank (close to Santo Antao) and abundant in Joao Valente Bank (close to BoaVista) (P. Monteiro et al., 2008). The endemic species of Cape Verde (*C. lubbocki*) mostly occurs in large schools (Freitas, et al., 2019a; P. Monteiro et al., 2008.) Plankton feeders have been shown to be abundant as well in the island of Santiago (Zander, 2011). Carnivorous fish species such as *Cephalopholis taeniops*, of the family Serranidae, and *Caranx lugubris* and *Caranx crysos*, family of Carangidae, are frequently recorded species within the archipelago (Medina et al., 2008; P. Monteiro et al., 2008). The grouper *C. taeniops,* that can occur between the depth range of 20-200 m, is one of the most important commercial demersal species in Cape Verde (Lino et al., 2011)

The significant levels of endemism observed among reef fishes and gastropods in Cape Verde can be partially attributed due to the archipelago's location in the lower latitude, which during the glacial periods acted as a protective buffer along with its biogeographical isolation from the western African shores. This resulted in the fostering of ancient species, and as a result, Cape Verde is now home to a remarkable array of endemic species (Freitas, et al., 2019a).

Regarding the West African coral communities, their origin has been the subject of various theories. Some propose that they originated from the Caribbean and dispersed over long distances using Bermuda, Azores, or Brazil as stepping stones. Others suggest an origin from the ancient Mediterranean-Tethys Sea (Spalding et al., 2001). Most likely the closure of Tethys Sea has had an impact on the evolution of Atlantic reef biota. Soft barriers such as Benguela and mid-Atlantic current, and Amazon plume have restricted the species dispersal and promoted development of new species in the Atlantic (Floeter et al., 2008). It is highly likely that there are undiscovered significant and diverse coral communities in various locations that have not yet been discovered in the Eastern Atlantic (Spalding et al., 2001). To gain a comprehensive understanding of these ecosystems and their importance, it is crucial to prioritize and stabilize geographical research on mesophotic coral ecosystems (Pyle & Copus, 2019).

References

Baker, E., Thygesen, K., Harris, P., Andradi-Brown, D., Appeldoorn, R. S., Ballantine, D., Bejarano, I., Bridge, T. L., Colin, P. L., Eyal, G., , Holstein, D., Jones, R., Kahng, S. E., Laverick, J., Loya, Y., Pochon, X., Pomponi, S. A., Puglise, K. A., Pyle, R. L., Reaka, M. L., Ruiz, J. H., Sealover, N., Semmler, R. F., Schizas, N., Schmidt, W., Sherman, C., Sinniger, F., Slattery, M., Spalding, H. L., Villalobos, S. G., Weil, E., & Wood, E. (2016). Mesophotic coral ecosystems: a lifeboat for coral reefs? UN Environment, GRID-Arendal.

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global ecology and biogeography*, *19*(1), 134-143.

Baselga, A. (2013). Separating the two components of abundance-based dissimilarity: Balanced changes in abundance vs. abundance gradients. *Methods in Ecology and Evolution*, *4*(6), 552–557. https://doi.org/10.1111/2041-210X.12029

Baselga, A., & Orme, C. D. L. (2012). betapart: an R package for the study of beta diversity. *Methods in ecology and evolution*, *3*(5), 808-812.

Bevilacqua, S., & Terlizzi, A. (2020). Nestedness and turnover unveil inverse spatial patterns of compositional and functional β-diversity at varying depth in marine benthos. *Diversity and Distributions*, *26*(6), 743-757.

Bongaerts, P., Muir, P., Englebert, N., Bridge, T. C. L., & Hoegh-Guldberg, O. (2013). Cyclone damage at mesophotic depths on Myrmidon Reef (GBR). *Coral Reefs*, *32*, 935-935.

Bongaerts, P., Ridgway, T., Sampayo, E. M., & Hoegh-Guldberg, O. (2010). Assessing the 'deep reef refugia'hypothesis: focus on Caribbean reefs. *Coral reefs*, *29*, 309-327.

Bongaerts, P., & Smith, T. B. (2019). Beyond the "Deep Reef Refuge" hypothesis: a conceptual framework to characterize persistence at depth. *Mesophotic coral ecosystems*, 881-895.

Bosch, N. E., Espino, F., Tuya, F., Haroun, R., Bramanti, L., & Otero-Ferrer, F. (2023). Black coral forests enhance taxonomic and functional distinctiveness of mesophotic fishes in an oceanic island: implications for biodiversity conservation. *Scientific Reports*, *13*(1). https://doi.org/10.1038/s41598-023-32138-x

Brokovich, E., Einbinder, S., Shashar, N., Kiflawi, M., & Kark, S. (2008). Descending to the twilight-zone: Changes in coral reef fish assemblages along a depth gradient down to 65 m. *Marine Ecology Progress Series*, *371*, 253–262. https://doi.org/10.3354/meps07591

Chao, A., Chazdon, R. L., Colwell, R. K., & Shen, T. J. (2005). A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecology letters*, *8*(2), 148-159.

Etnoyer, P. J., Wickes, L. N., Silva, M., Dubick, J. D., Balthis, L., Salgado, E., & MacDonald, I. R. (2016). Decline in condition of gorgonian octocorals on mesophotic reefs in the northern Gulf of Mexico: before and after the Deep-water Horizon oil spill. *Coral Reefs*, *35*, 77-90.

Floeter, S. R., Rocha, L. A., Robertson, D. R., Joyeux, J. C., Smith-Vaniz, W. F., Wirtz, P., Edwards, A. J., Barreiros, J. P., Ferreira, C. E. L., Gasparini, J. L., Brito, A., Falcón, J. M., Bowen, B. W., & Bernardi, G. (2008). Atlantic reef fish biogeography and evolution. *Journal of Biogeography*, *35*(1), 22–47. https://doi.org/10.1111/j.1365-2699.2007.01790.x

Freitas, R., Mendes, T. C., Almeida, C., Melo, T., Villaça, R. C., Noguchi, R., Floeter, S. R., Rangel, C. A. & Ferreira, C. E. L. (2019a). Reef fish and benthic community structures of the Santa Luzia Marine Reserve in the Cabo Verde islands, eastern central Atlantic Ocean. *African Journal of Marine Science*, *41*(2), 177-190.

Freitas, R., Romeiras, M., Silva, L., Cordeiro, R., Madeira, P., González, J. A., Wirtz, P., Falcón, J. M., Brito, A., Floeter, S. R., Afonso, P., Porteiro, F., Viera-Rodríguez, M. A., Neto, A. I., Haroun, R., Farminhão, J. N. M., Rebelo, A. C., Baptista, L., Melo, C. S., Martinez, A., Núñez, J., Berning, B., Johnson, M. E. & Ávila, S. P. (2019b). Restructuring of the 'Macaronesia' biogeographic unit: A marine multi-taxon biogeographical approach. *Scientific Reports*, *9*(1). https://doi.org/10.1038/s41598-019-51786-6

García-Hernández, J. E., Sanchez, P. J., Hammerman, N. M., & Schizas, N. V. (2018). Fish, coral, and sponge assemblages associated with altiphotic and mesophotic reefs along the Guánica biosphere reserve continental shelf edge, Southwest Puerto Rico. *Frontiers in Marine Science*, *5*(SEP). https://doi.org/10.3389/fmars.2018.00303

Harborne, A. R., Mumby, P. J., ZŻychaluk, K., Hedley, J. D., & Blackwell, P. G. (2006). Modeling the beta diversity of coral reefs. *Ecology*, *87*(11), 2871-2881.

Kahng, S., Copus, J. M., & Wagner, D. (2017). Mesophotic Coral Ecosystems. *Marine Animal Forests*, 1–22. Springer International Publishing. https://doi.org/10.1007/978-3-319-17001-5_4-1

Kahng, S. E., Akkaynak, D., Shlesinger, T., Hochberg, E. J., Wiedenmann, J., Tamir, R., & Tchernov, D. (2019). Light, temperature, photosynthesis, heterotrophy, and the lower depth limits of mesophotic coral ecosystems. *Mesophotic coral ecosystems*, 801-828. Springer International Publishing.

Laborel, J., 1974. West African reef corals: an hypothesis on their origin. *Proceedings of the Second International Coral Reef Symposium 1*, 425-443

Laverick, J. H., Piango, S., Andradi-Brown, D. A., Exton, D. A., Bongaerts, P., Bridge, T. C. L., Lesser, M. P., Pyle, R. L., Slattery, M., Wagner, D., & Rogers, A. D. (2018). To what extent do mesophotic coral ecosystems and shallow reefs share species of conservation interest? A systematic review. In *Environmental Evidence, 7*(1). BioMed Central Ltd. https://doi.org/10.1186/s13750-018-0127-1

Legendre, P. (2014). Interpreting the replacement and richness difference components of beta diversity. *Global Ecology and Biogeography*, *23*(11), 1324–1334. https://doi.org/10.1111/geb.12207

Lesser, M. P., Slattery, M., Laverick, J. H., Macartney, K. J., & Bridge, T. C. (2019). Global community breaks at 60 m on mesophotic coral reefs. *Global Ecology and Biogeography*, *28*(10), 1403–1416. https://doi.org/10.1111/geb.12940

Lesser, M. P., Slattery, M., & Leichter, J. J. (2009). Ecology of mesophotic coral reefs. In *Journal of Experimental Marine Biology and Ecology*, *375*(1–2), 1–8. https://doi.org/10.1016/j.jembe.2009.05.009

Lino, P. G., Bentes, L., Oliveira, M. T., Erzini, K., & Santos, M. N. (2011). THE AFRICAN HIND'S (Cephalopholis taeniops, SERRANIDAE) USE OF ARTIFICIAL REEFS OFF SAL ISLAND (CAPE VERDE): A PRELIMINARY STUDY BASED ON ACOUSTIC TELEMETRY*. In *BRAZILIAN JOURNAL OF OCEANOGRAPHY* (Vol. 59).

Maragos, J. E., Crosby, M. P., & McManus, J. W. (1996). Coral reefs and biodiversity: a critical and threatened relationship. *Oceanography, 9(1),* 83-99.

Medeiros, A. P. M., Ferreira, B. P., Alvarado, F., Betancur-R, R., Soares, M. O., & Santos, B. A. (2021). Deep reefs are not refugium for shallow-water fish communities in the southwestern Atlantic. *Ecology and Evolution*, *11*(9), 4413–4427. https://doi.org/10.1002/ece3.7336

Medina, A., Brêthes, J. C., & Sévigny, J. M. (2008). Habitat fragmentation and body-shape variation of African hind Cephalopholis taeniops (Valenciennes) in an archipelago system (Cape

Verde, eastern Atlantic Ocean). *Journal of Fish Biology*, *73*(4), 902–925. https://doi.org/10.1111/j.1095-8649.2008.01986.x

Medina, A., Brêthes, J. C., Sévigny, J. M., & Zakardjian, B. (2007). How geographic distance and depth drive ecological variability and isolation of demersal fish communities in an archipelago system (Cape Verde, Eastern Atlantic Ocean). *Marine Ecology*, *28*(3), 404–417. https://doi.org/10.1111/j.1439-0485.2007.00163.x

Monteiro, J., Almeida, C., Freitas, R., Delgado, A., Porteiro, F., & Santos, R. (2008). Coral assemblages of Cabo Verde: preliminary assessment and description. In *Proceedings of the 11th International Coral Reef Symposium, Fort Lauderdale, Florida, 7*(11), 1416-19.

Monteiro, J. G., Costa, C. F., Gorlach-Lira, K., Fitt, W. K., Stefanni, S. S., Sassi, R., Santos, R. S & LaJeunesse, T. C. (2013). Ecological and biogeographic implications of Siderastrea symbiotic relationship with Symbiodinium sp. C46 in Sal Island (Cape Verde, East Atlantic Ocean). *Marine Biodiversity, 43,* 261-272.

Monteiro, P., Ribeiro, D., Silva, J. A., Bispo, J., & Gonçalves, J. M. (2008). Ichthyofauna assemblages from two unexplored Atlantic seamounts: Northwest Bank and João Valente Bank (Cape Verde archipelago). *Scientia Marina*, *72*(1), 133-143.

Morais, J., & Santos, B. A. (2018). Limited potential of deep reefs to serve as refuges for tropical Southwestern Atlantic corals. *Ecosphere*, *9*(7). https://doi.org/10.1002/ecs2.2281

Morais, R. A., & Maia, H. A. (2017). Lush underwater forests in mesophotic reefs of the Gulf of Guinea. *Coral Reefs*, *36*(1), 95. https://doi.org/10.1007/s00338-016-1523-z

Norse, E. A. (Ed.). (1993). *Global marine biological diversity: a strategy for building Conservation into decision making*, *2*. Island Press.

Olavo, G., Costa, P. A., Martins, A. S., & Ferreira, B. P. (2011). Shelf-edge reefs as priority areas for Conservation of reef fish diversity in the tropical Atlantic. *Aquatic Conservation: marine and freshwater ecosystems*, *21*(2), 199-209.

Papastamatiou, Y. P., Meyer, C. G., Kosaki, R. K., Wallsgrove, N. J., & Popp, B. N. (2015). Movements and foraging of predators associated with mesophotic coral reefs and their potential for linking ecological habitats. *Marine Ecology Progress Series*, *521*, 155-170.

Pereira, P. H. C., Macedo, C. H., Nunes, J. de A. C. C., Marangoni, L. F. de B., & Bianchini, A. (2018). Effects of depth on reef fish communities: Insights of a "deep refuge hypothesis" from Southwestern Atlantic reefs. *PLoS ONE*, *13*(9). https://doi.org/10.1371/journal.pone.0203072

Pérez-Rosales, G., Rouzé, H., Torda, G., Bongaerts, P., Pichon, M., Parravicini, V., & Hédouin, L. (2021). Mesophotic coral communities escape thermal coral bleaching in French Polynesia. *Royal Society Open Science*, *8*(11). https://doi.org/10.1098/rsos.210139

Pinheiro, H. T., MacDonald, C., Quimbayo, J. P., Shepherd, B., Phelps, T. A., Loss, A. C., Teixeira, J. B., & Rocha, L. A. (2023a). Assembly rules of coral reef fish communities along the depth gradient. *Current Biology*, *33*(8), 1421-1430.e4. https://doi.org/10.1016/j.cub.2023.02.040

Pinheiro, H. T., MacDonald, C., Santos, R. G., Ali, R., Bobat, A., Cresswell, B. J., Francini-Filho, R., Freitas, R., Galbraith, G. F., Musembi, P., Phelps, T. A., Quimbayo, J. P., Quiros, T. E. A. L., Shepherd, B., Stefanoudis, P. V., Talma, S., Teixeira, J. B., Woodall, L. C., & Rocha, L. A. (2023b). Plastic pollution on the world's coral reefs. *Nature*, *619*(7969), 311–316. https://doi.org/10.1038/s41586-023-06113-5

Pinheiro, H. T., Rocha, L. A., Macieira, R. M., Carvalho-Filho, A., Anderson, A. B., Bender, M. G., Di Dario, F., Ferreira, C. E. L., Figueiredo-Filho, J., Francini-Filho, R., Gasparini, J. L., Joyeux, J. C., Luiz, O. J., Mincarone, M. M., Moura, R. L., Nunes, J. de A. C. C., Quimbayo, J. P., Rosa, R. S., Sampaio, C. L. S., Sazima, I., Simon, T., Vila-Nova, D. A. & Floeter, S. R.

(2018). South-western Atlantic reef fishes: Zoogeographical patterns and ecological drivers reveal a secondary biodiversity centre in the Atlantic Ocean. *Diversity and Distributions*, *24*(7), 951–965. https://doi.org/10.1111/ddi.12729

Pinheiro, H. T., Eyal, G., Shepherd, B., & Rocha, L. A. (2019). Ecological insights from environmental disturbances in mesophotic coral ecosystems. *Ecosphere*, *10*(4), e02666.

Pyle, R. L., & Copus, J. M. (2019). *Mesophotic Coral Ecosystems: Introduction and Overview* (pp. 3–27). https://doi.org/10.1007/978-3-319-92735-0_1

Pyle, R. L., Kosaki, R. K., Pinheiro, H. T., Rocha, L. A., Whitton, R. K., & Copus, J. M. (2019). *Fishes: Biodiversity* (pp. 749–777). https://doi.org/10.1007/978-3-319-92735-0_40

Ramalho, R. A. dos S. (2011). The Cape Verde Archipelago. In *Building the Cape Verde Islands* (pp. 13–26). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-19103-9_2

Rocha, L. A., Pinheiro, H. T., Shepherd, B., Papastamatiou, Y. P., Luiz, O. J., Pyle, R. L., & Bongaerts, P. (2018). *Mesophotic coral ecosystems are threatened and ecologically distinct from shallow water reefs*. http://science.sciencemag.org/

Roff, J. C., Zacharias, M., & Day, J. (2011). Marine conservation ecology. London, UK: *Earthscan*, 158-161.

Santos, R. S., Hawkins, S., Monteiro, L. R., Alves, M., & Isidro, E. J. (1995). Marine research, resources and Conservation in the Azores. *Aquatic Conservation: marine and freshwater ecosystems*, *5*(4), 311-354.

Semmler, R. F., Hoot, W. C., & Reaka, M. L. (2017). Are mesophotic coral ecosystems distinct communities and can they serve as refugia for shallow reefs? *Coral Reefs*, *36*(2), 433–444. https://doi.org/10.1007/s00338-016-1530-0

Socolar, J. B., Gilroy, J. J., Kunin, W. E., & Edwards, D. P. (2016). How Should Beta-Diversity Inform Biodiversity Conservation? In *Trends in Ecology and Evolution* (Vol. 31, Issue 1, pp. 67–80). Elsevier Ltd. https://doi.org/10.1016/j.tree.2015.11.005

Spalding, M., Spalding, M. D., Ravilious, C., & Green, E. P. (2001). *World atlas of coral reefs*. Univ of California Press.

Spalding, M. D., Fox, H. E., Allen, G. R., Davidson, N., Ferdaña, Z. A., Finlayson, M., Halpern, B. S., Jorge, M. A., Lombana, A., Lourie, S. A., Martin, K. D., McManus, E., Molnar, J., Recchia, C. A., & Robertson, J. (2007). Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *BioScience*, *57*(7), 573-583.

Turner, J. A., Babcock, R. C., Hovey, R., & Kendrick, G. A. (2017). Deep thinking: A systematic review of mesophotic coral ecosystems. *Journal of Marine Science 74* (9), 2309–2320. Oxford University Press. https://doi.org/10.1093/icesjms/fsx085

Whittaker, R. H. (1960). Vegetation of the Siskiyou mountains, Oregon and California. *Ecological monographs*, *30*(3), 279-338.

Whittaker, R. J., Willis, K. J., & Field, R. (2001). Scale and species richness: Towards a general, hierarchical theory of species diversity. *Journal of Biogeography*, *28*(4), 453–470. https://doi.org/10.1046/j.1365-2699.2001.00563.x

Wirtz, P., Brito, A., Falcon, J. M., Freitas, R., Fricke, R., Monteiro, V., Reiner, F., & Tariche, O. (2013). The coastal fishes of the Cape Verde Islands–new records and an annotated check-list. *Spixiana*, *36*(1), 113-142.

Wirtz, P., & d’Udekem-d’Acoz, C. (2001). Decapoda from Antipatharia, Gorgonaria and Bivalvia at the Cape Verde Islands. *Helgoland Marine Research*, *55*(2), 112–115. https://doi.org/10.1007/s101520100073

Zander, C. D. (2011). Zoogeographical and ecological comparison of reef fishes of Tobago (Caribbean) and Cape Verde (tropical eastern Atlantic). *Bulletin of Fish Biology*, *13*, 77-82.

Environmental and geographical drivers of reef fish beta diversity across a depth gradient in an oceanic archipelago of the eastern Atlantic Ocean.

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Abstract

The worldwide impact of anthropogenic pressures on coral reefs is not surprising. The deeper reefs between -30 to -150 meters, a zone known as "Mesophotic Coral Ecosystems" (MCEs), have been commonly considered to be less affected by climate change and human impacts compared to their shallow counterparts. However, they still face natural and anthropogenic pressures. Reefs that have shown the most pristine conditions are the ones that are furthest away from human-populated locations. Oceanic islands harbour some of the last remaining pristine ecosystems and fish assemblages.

An increasing number of studies have attempted to investigate the factors related to the distribution of fish species assemblages between oceanic islands or across the depth gradient. By measuring the rate of change in species composition across habitats or communities, beta diversity analyses provide an essential tool to identify environmental or geographical factors that influence patterns of species variation in a region.

This study marks the first *in situ* study to be conducted in Cape Verde across the shallow to mesophotic depth gradient (-10 to -90 m). Here we aim to identify the factors driving beta diversity for reef fish assemblages within the archipelago and determine whether ecological or biogeographical factors have a more prominent role in shaping beta diversity. Our results show that beta diversity within the Cape Verde archipelago is mainly driven by the depth gradient and environmental 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 (-0 to -30 m) and upper (-31 to -60 m) mesophotic zones. Our results suggest that the lower MCE seems to be species saturated as a result of lower microhabitat heterogeneity, showing lower richness but higher species turnover.

Furthermore, the effect of geography is reduced within the archipelago of Cape Verde since each island seems to have unique characteristics that contribute to differences in species assemblages. High fishing pressure, more evident in the most populated island, seems to increase the community nestedness through the removal of target species, indicative that human pressure may be affecting the ecological and biogeographic patterns.

1. Introduction

The worldwide impact of anthropogenic pressures on coral reefs is not surprising (Wilkinson, 1999; Bellwood et al., 2004; Hughes et al., 2003). Human-induced disturbances over the past decades have inflicted significant stress on coral reef ecosystems, primarily caused by pollution, sedimentation, and overfishing (Norse, 1993; Maragos et al., 1996; Spalding et al., 2001). The effects of climate change and habitat degradation have been extensively investigated in shallow coral reefs, primarily those above 30 meters, as they are more accessible for research. However, advancements in technology have woken up curiosity about the extensions of the shallow reefs, facilitating studies on the deeper reefs between -30 to 150 meters, a zone known as "Mesophotic Coral Ecosystems" (MCEs) (Laveric et al., 2018; Pyle et al., 2019; Pyle & Copus, 2019).

The structure of these low-light adapted coral communities is mainly driven by temperature, topography, and light attenuation (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), the community assemblage also changes (Pyle & Copus, 2019; Lesser et al., 2009; Kahng et al., 2019; Pinheiro et al., 2023a). The benthic composition changes from the dominant Scleractinian corals in the shallow-water reefs (Spalding et al., 2001) towards heterotrophic corals, macroalgae, and sponges in the MCEs (Pyle & Copus, 2019).

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

The deeper reefs have been commonly considered to be less impacted by climate change and other anthropogenic disturbances than their shallow counterparts. As a result, some studies have been speculating if these mesophotic reefs could potentially serve as a refugee for their shallow reef species, which has led to the "Deep reef refugee hypothesis" (Lesser et al., 2009; Bongaerts et al., 2010; Laverick et al., 2018; Bongaerts & Smith, 2019). The deeper reefs seem to provide some protection against the thermal bleaching of corals (Pérez-Rosales et al., 2021). However, natural disturbances (Bongaerts et al., 2013; Rocha et al., 2018) and pollution, fishing and mining also impact these deeper reefs (Olavo et al., 2011; Etnoyer et al., 2016; Rocha et al., 2018; Pinheiro et al., 2023b). The reefs that have shown the most pristine conditions are the ones that are located furthest away from human-populated locations, for both shallow and deep coral reefs (Rocha et al., 2018). Especially oceanic islands, which harbour some of the last remaining pristine ecosystems and fish assemblages due to their isolation (Bruneel et al., 2021), and are considered natural laboratories for ecological, biogeographic and evolutionary studies (Dawson, 2016).

An increasing number of studies have attempted to investigate the factors related to the distribution of fish species assemblages between oceanic islands (Quimbayo et al., 2019; Wienerroither et al., 2009) or across the shallow and deeper reefs (Pinheiro et al., 2016; Bosch et al., 2023). Beta diversity analyses provide an essential tool for understanding how different habitats and environmental factors influence species diversity and distribution and can aid in conservation planning and management in these vulnerable ecosystems (Harborne et al., 2006; Rolf and Zacharias, 2011; Baselga & Orme, 2012). By measuring the rate of change in species composition across habitats or communities, beta diversity indices may reveal the processes driving species distributions and biodiversity (Harborne et al., 2006; Baselga & Orme, 2012). They can identify environmental or geographical factors that influence patterns of species variation in a region (Socolar et al., 2016). Partitioning beta diversity into its components, turnover (species replacement) and nestedness (species loss or gain), helps us further understand the underlying processes behind community variation (Baselga, 2010; Socolar et al., 2016).

Here, in this study we assessed how biogeographic and ecological factors affect the beta diversity of reef fish assemblages within an oceanic archipelago, assessing shallow and mesophotic reefs of Cape Verde, Eastern Atlantic. We aim to answer the following questions: (A) What are the main drivers influencing beta diversity? (B) Which factor, depth or geographic distance, plays a more significant role in driving beta diversity within Cape Verde? (C) Is there a relation between species richness and beta diversity?

(D) Is there evidence for human impacts affecting the beta diversity within the archipelago?

As fish assemblages of other oceanic islands in the Atlantic are structured by stepping stone processes (Mazzei et al., 2021), we hypothesize that the islands closer to each other would have a lower beta diversity than the more isolated islands. In addition, and according to previous studies mentioned above, we hypothesize that the shallow and upper zones should display a more similar species assemblage and distinct from the lower mesophotic zone. Lastly, the removal of fish species by fishing activities could affect species composition and increase beta diversity, especially the importance of the nestedness component. This study marks the first *in situ* study to be conducted in Cape Verde across the shallow to mesophotic depth gradient (10- 90 m). With this study, we aim to understand what are the drivers for fish species variation and fill research gaps about the mesophotic reefs in understudied areas of an Eastern Atlantic oceanic archipelago.

2. Material & Methods

2.1. Study Area

The study was carried out between the 6th to 16th of August 2022 in three islands of the Cape Verde Archipelago: Santiago (14°54'31.5"N 23°36'18.2"W), Fogo (14°50'40.7"N 24°26'51.6"W) and Santo Antão (16°56'38.6"N 25°19'09.4"W) (Fig. 2.1). Santiago and Fogo are the closest to each other (91 km), and Santo Antão is located at 293 km from Santiago and 252 km from Fogo. All sites were previously visited by researchers and chosen due to the presence of steeper slopes and logistical reasons.

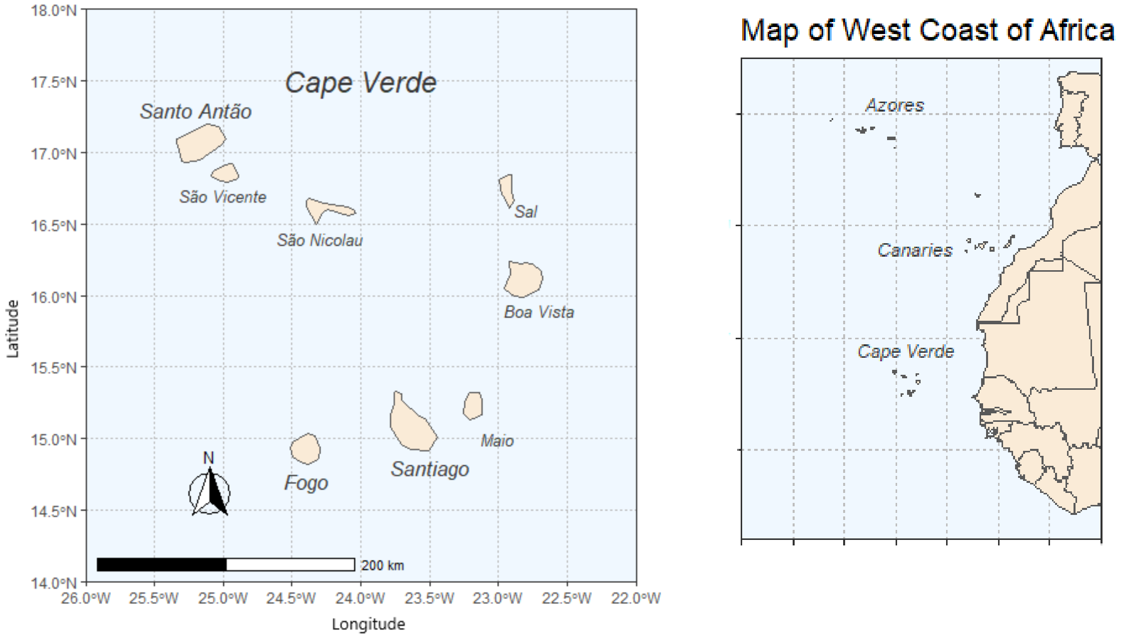

Figure 2.1. Map of Cape Verde archipelago and its location in the Atlantic Ocean.

The Cape Verde islands are located in the north-eastern Atlantic, spanning from latitudes between 14° to 17° N and longitudes from 21° to 25° W. The archipelago is located between 450 and 600 km off Senegal in the Western coast of Africa (Fig. 1). The ten islands and eight islets that compose the archipelago are arranged in a west-facing horseshoe shape, and can be divided further into a northern (Santo Antão, Sao Vicente, Santa Luzia, Sao Nicolau) and southern (Sal, Boa Vista, Maio, Santiago, Fogo, and Brava) chains (Ramalho, 2011).

Cape Verde has a tropical oceanic climate, with annual temperatures ranging from 19 to 29°C. The archipelago is of volcanic origin and is located on top of the Cape Verde Rise, which is one of the largest bathymetric anomalies in the world (Ramalho. 2011; Ramalho & Ramalho, 2011). The archipelago is characterized by the presence of several seamounts near the main islands, whereas the most significant ones are Senghor Seamount (100 km of Sal), the Boa Vista and Cabo Verde Seamounts (ESE of Boa Vista), the Maio Seamount (S of Maio), the Cadamosto Seamount (WSW of Brava), and the Nola Seamount (WNW of Santo Antão) (Ramalho, 2011).
Santiago is the largest island with 991 km^2, followed by Santo Antão with 779 km2, with estimated geological ages of 10 and 8 million years (Ma), respectively (Ramalho, 2011). Both islands are in an early post-erosional stage and display an overall shield

morphology. The youngest island of the archipelago is Fogo with an area of 476 km^2 and an active stratovolcano with a preserved morphology (Ramalho, 2011).

Hermatypic corals (van der Land 1993) and hard corals are common in the shallow areas of Cape Verde (Moses et al., 2003). However, due to the cold water front of the Canary Current, no true coral reefs can form (Laborel, 1974). Nonetheless, rocky reefs in Cape Verde comprise numerous reef organisms such as sponges, corals and algae (van der Land, 1993).

Over the past 70 years, Cape Verde has experienced a population growth from less than 200,000 to around 590,000 people individuals. Santiago represents the most populated island, with more than half of the population (269,300 inhabitants), whereas 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 two decades (City Population, 2021; Worldometers, 2023). With the expanding population, unregulated fishing, pollution, and tourism stands as the foremost threat to the marine environment in Cape Verde (Failler et al., 2021).

2.2 Sampling methods

The fish species were visually identified and counted *in situ* by divers to the lowest taxonomic level possible, alongside their body size, on reefs ranging from 5 to 85 meters in depth. Underwater visual censuses (UVCs) were performed along 20 m transect lines, encompassing 1 m on either side of the line for a total survey area of 40 m2. Transect locations were randomly chosen, but aimed to cover the diversity of habitats and three depth zones: shallow (0 to -30m), upper mesophotic (-31 to -60 m), lower mesophotic (-61 to -90m) (Kahng et al., 2017; Soares et al., 2019). The number of replicates for each depth category and island varied between two to ten transects: 20 in Santo Antão (ten on shallow reefs; eight on upper mesophotic reefs; two on lower mesophotic reefs), 21 in Fogo (nine on shallow reefs; six on upper mesophotic reefs; six on lower mesophotic reefs) and 17 in Santiago (six on shallow reefs; four on upper mesophotic reefs; seven on lower mesophotic reefs). A species accumulation curve (Fig. 3.1), computed using the function *rarefy* from the R (Oksanen et al., 2013) *Vegan* package, was used to examine if the sampling effort was sufficient to capture most of the community within each depth zone. Environmental parameters such as algae, coral and heterotrophic coral cover, and habitat complexity were visually assessed for each surveyed transect. Additionally, temperature across each depth zone was measured using diving computers. Habitat complexity was classified between Low, Medium-Low, Medium, Medium-High and High (adapted from Pinheiro et al., 2013). Accordingly, 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).

2.3. Data analysis

2.3.2. Pairwise dissimilarity

The abundance data of fish species were transformed into presence-absence data and the sites were grouped into nine different groups based on the islands and their depth zones: Fogo: shallow, upper and lower; Antão: shallow, upper, and lower; Santiago: shallow, upper and lower. Due to the unequal sampling effort, a minimal sampled area (MSA) was used to standardize the sample size among sites (Quimbayo et al., 2019). We identified the site with the lowest sampled area in the dataset (lower Santo Antão) and restricted the sampled area in all other sites to this area limit (80m^2). 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 between sites using Sorensen's dissimilarity index and its turnover and nestedness components through the beta pairwise function from R *betapart* package by Baselga (2010) and Baselga & Orme (2012). The mean value of the beta Sorensen's, turnover and nestedness from the 1000 simulations was used to estimate the dissimilarity between the reef fish assemblages. Furthermore, the aforementioned process was iterated for a more expansive MSA, omitting the lower Santo Antão and expanding the MSA to 160m^2. This expansion aimed to investigate whether the smaller dimensions of the surveyed transects lead to heightened variability when compared to the larger dimensions (Arias-González et al., 2008).

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

2.3.3. General Linear Model

To investigate the drivers of beta diversity, we constructed two General Linear Models (GLMs) utilizing the Beta regression distribution and a link-function (log). The *betareg* function from the *betareg* R package (Cribari-Neto & Zeileis, 2010) was employed for building the models. 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. 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 binominal GLM (Cribari-Neto & Zeileis, 2010). In cases where the variable y took the extreme values of 0 and 1, a transformation was employed as $(y \cdot (n - 1) + 0.5)/n$, where n represents the sample size (Smithson and Verkuilen, 2006; Cribari-Neto & Zeileis, 2010).

In our first model, our objective was to address the primary research question: Which factor, depth or geographic distance, plays a more significant role in driving beta diversity? The model considered the variation between transects in terms of the depth gradient and geographic distance as independent variables. Previous research conducted by Harbourne et al. (2006) has demonstrated that beta diversity can be effectively modelled using just two variables. For the second model, we aimed to explore the additional impact of ecological variables on beta diversity. The independent variables in this model were defined as the disparities between transects concerning abiotic factors such as differences in temperature, depth, geographic distance, area size, and biotic factors like algae cover, coral cover, heterotrophic coral cover, and habitat complexity.

Further on, the “dredge” function from the *MuMln* R package (Barton & Barton, 2015) was run to get a complete set of models with possible combinations of the independent variables and determined the best fit of the model based on the lowest Akaike information criterion (AIC) value and the highest pseudo R-square. To ensure that the independent variables were not correlated with each other, we estimated the variance inflation factor (VIF) with the function VIF from the car package (Fox et al., 2012). All of the factors had a VIF value < 3 and therefore maintained all the variables in our model.

3. Results

3.1. Species Richness

The Cape Verde surveys rendered a total of 5516 individuals from 57 species and 23 families (Table 1), from which 42 species were recorded 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. 3.1A) shows that the sampling was enough to capture most of the community within each depth zone and revealed that the shallower zones harbour more species than the lower depths. However, when investigating each island separately, Santiago's upper zone displayed a higher number of species per transect than its shallow zone (Fig. 3.1D).

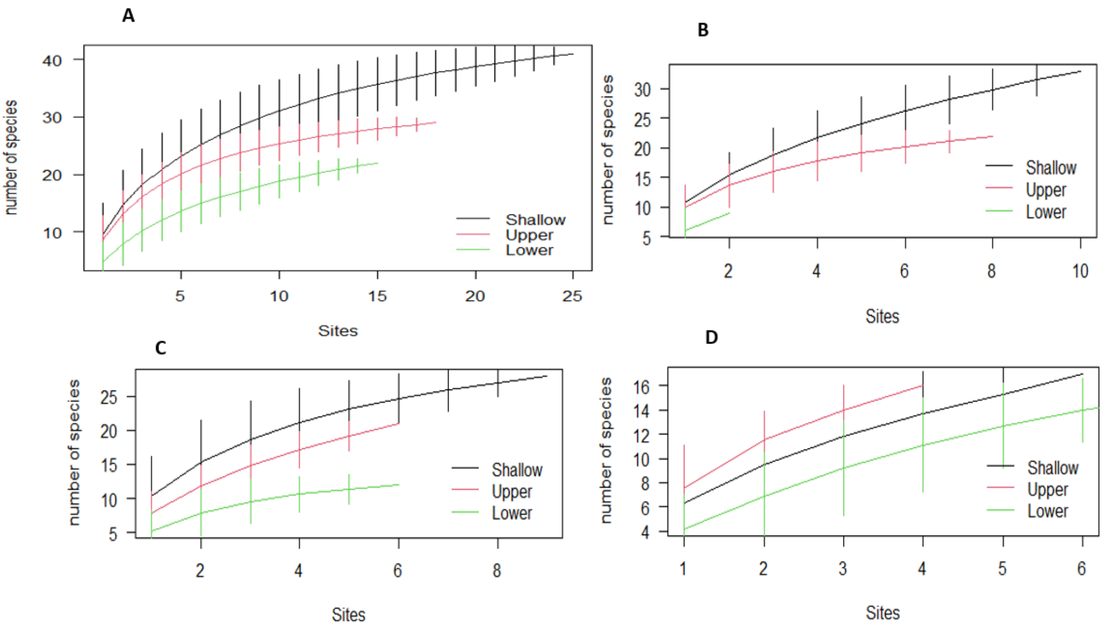

Figure 3.1. Species accumulation curve displaying the number of species recorded per transect from each depth zone of **(A)** all surveyed islands **(B)** Santo Antão **(C)** Fogo **(D)** Santiago.

Table 1. Abundance of fish species recorded in Cape Verde Archipelago.

Families Species	Shallow	Upper	Lower	Shallow	Upper	Lower	Shallow	Upper	Lower
Acanthuridae	**8**	**2**	**2**	**2**	**14**	**4**	**53**	**23**	
Acanthurus monroviae	8	2	2	2	14	4	53	23	
Aulostomidae	**5**	**11**		**17**	**9**	**3**	**14**	**16**	**1**
Aulostomus strigosus	5	11		17	9	3	14	16	1
Balistidae	**5**	**1**		**1**			**10**	**4**	
Balistes punctatus	5			1					
Canthidermis sufflamen		1					10	4	
Carangidae		**6**					**2**	**8**	
Caranx crysos							2		
Caranx lugubris								1	
Seriola rivoliana		6						7	
Chaetodontidae	**4**	**1**	**7**		**4**	**27**	**1**	**4**	**3**
Chaetodon robustus	4	1			2		1	4	
Prognathodes marcellae			7		2	27			3
Diodontidae				**1**					
Diodon holocanthus				1					
Girellidae							**31**		
Girella stuebeli							31		
Gobiidae	**3**						**3**		
Gnatholepis thompsoni	3						1		
Gobius tetrophthalmus							2		
Haemulidae		**10**			**3**		**1**	**57**	
Parapristipoma humile		10			3		1	57	
Holocentridae	**25**	**15**	**5**	**16**	**12**	**9**	**39**	**61**	**1**
Corniger spinosus						3			
Myripristis jacobus	22	14		13	10	6	39	41	
Sargocentron hastatum	3	1	5	3	2			20	1
Labridae	**100**	**3**	**1**	**28**	**21**	**1**	**111**	**1**	
Bodianus speciosus	10	1	1						
Coris atlantica	10			1	1				
Lappanella aff fasciata						1			
Scarus hoefleri	4						1		
Sparisoma choati	5			2	7		16		
Sparisoma cretense	4	2		22	13		8	1	
Sparisoma frondosum	1			1			2		
Sparisoma spp	1						5		
Thalassoma pavo	65			2			79		
Lethrinidae	**70**								
Lethrinus atlanticus	70								
Lutjanidae	**5**	**37**				**3**	**9**	**2**	
Apsilus fuscus	5						6		
Lutjanus fulgens		37				3	1	2	
Lutjanus goreensis							2		
Monacanthidae		**1**					**1**		
Alupterus scriptus		1					1		
Mullidae	**38**	**13**		**1**	**7**		**20**	**7**	
Mulloidichthys martinicus	33	13		1	5		12	6	
Pseudupeneus prayensis	5				2		8	1	
Muraenidae	**2**						**1**		**1**
Gymnothorax vicinus	1								
Muraena helena									1
Muraena melanotis	1						1		
Pomacanthidae		**3**							
Holacanthus africanus		3							
Pomacentridae	**588**	**807**	**73**	**220**	**69**	**250**	**1040**	**899**	**64**
Abudefduf hoefleri	77								
Abudefduf saxatilis							2		
Chromis lubocki	122	805	71		50	250	867	720	64
Chromis multilineata	310			190	19		159	175	
Similiparma hermani		2	2					4	
Stegastes imbricatus	79			30			12		
Scorpaenidae						**1**			
Scorpaena maderensis						1			
Serranidae	**33**	**17**	**76**	**5**	**8**	**17**	**32**	**19**	**6**
Anthias spp			60			9			
Cephalopholis taeniops	32	16	11	5	8	1	29	14	1
Liopropoma emanueli			4			5			2
Mycteroperca fusca		1						1	1
Rypticus saponaceus	1						3	4	2
Serranus atricauda			1			2			
Sparidae		**7**	**2**	**30**			**115**	**16**	
Diplodus fasciatus		7	2				3	8	
Diplodus lineatus							15		
Diplodus prayensis								8	
Spicara melanurus				30			97		
Sphyraenidae		**30**							
Sphyraena viridensis		30							
Tetraodontidae	**3**	**3**	**4**	**4**	**11**	**4**	**7**	**5**	
Canthigaster capistrata	3	3	4	4	11	3	7	5	
Sphoeroides marmoratus						1			

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. 3.2A). The greatest variation in species composition was observed between the lower depth zones of Santiago and the two other islands (Fogo and Santo Antão). When examining the depth profiles of each island (Fig. 3.2B), a consistent trend of increasing beta diversity from the shallow to the lower mesophotic zones was observed among the islands (Fig. 3.2B). The lowest variation in species composition was observed between the shallow and upper mesophotic zones. Larger MSAs showed similar trends, but with average lower beta diversity values (Supplementary Fig. 1).

The cluster analysis (Fig. 3.2C) revealed that all the lower zones (AL, FL, SL) formed a single cluster. However, there were variations observed between islands in terms of the clustering of the shallow and upper mesophotic zones. Specifically, the shallow zone (SS) of Santiago clustered together with its upper mesophotic zone (SU), while the shallow zones of Fogo (FS) and Santo Antão (AS) clustered together, with their respective upper mesophotic zones (FU, AU) forming another distinct cluster.

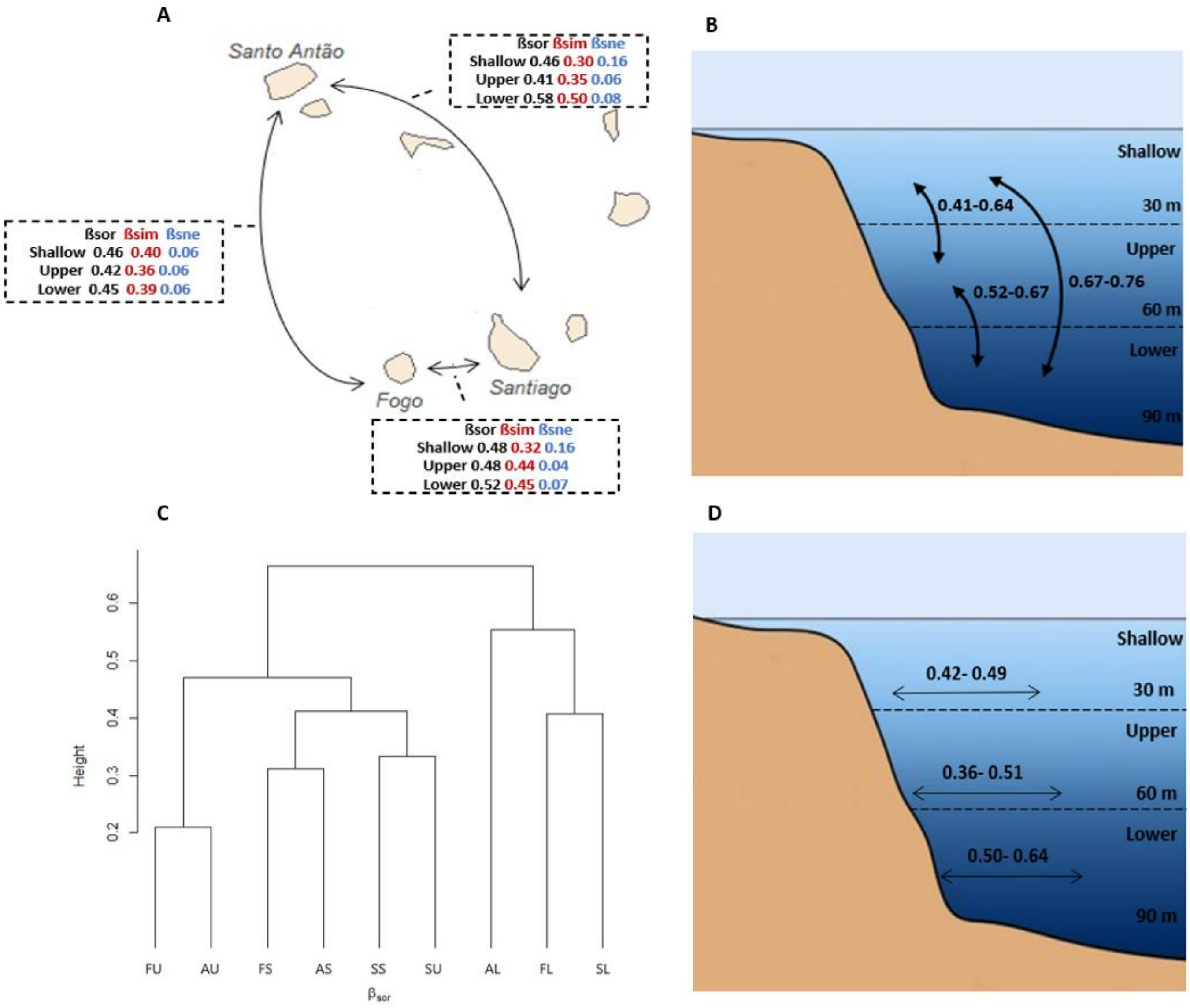

Figure 3.2. (A) Sorensen's pairwise dissimilarity and its components turnover and nestedness between the surveyed islands and their depth zones. **(B)** Sorensen's pairwise dissimilarity between shallow reef fish communities and mesophotic depth zones of each island. **(C)** Cluster analysis showing the average linkage of ßsor of species dissimilarity 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 beta diversity using Sorensen's pairwise dissimilarity within each depth zone.

When investigating intra-site beta diversity within depth zones (Fig. 3.2D), it was found an average increase with depth. Specifically, the lower zone of Santiago displayed the highest species variation (Supplementary Fig. 2A). On the contrary, the island of Santo Antão presented the lowest beta diversity values in its upper zone (Supplementary Fig.

2B). Notably, the island of Fogo showed the most similar beta diversity values across all depth zones (Supplementary Fig. 2C).

3.3. Environmental and geographical drivers

The initial model showed that both depth and geographic distances have significant influence on species variation between sites (Table 2). This model indicated that approximately 30% of the variation in species composition could be explained by these two variables. However, a second model (Table 3), which included all other environmental variables, showed a lack of influence of the geographic distance on the beta diversity, which was excluded from the best model (according to “dredge” and the AIC information). The pseudo R^2 value for this model was 0.41, suggesting that factors related to microhabitat were more important in driving local assemblages compared to geographic distance.

Table 2. Results from beta regression log-linear GLM (General Linear Models) of beta diversity and difference in depth and geographic distance.

	Estimate	SE	z value	Pr(>|z|)	VIF
Intercept	-0.1059299	0.0462635	-2.290	0.02204	
Depth	0.0344498	0.0011615	29.660	2e-16	1.088356
Geographic distance	0.0005983	0.0001838	3.255	0.00113	1.001301
Pseudo R^2	0.3037				

Table 3. Results from the most adequate model with all the environmental parameters included.

	Estimate	SE	z value	Pr(>|z|)	VIF
Intercept	-0.2096839	0.0552594	-3.795	0.000148	
Heterotrophic coral	-0.0025594	0.0008628	-2.966	0.003013	1.230674
Complexity	0.0834696	0.0225991	3.693	0.000221	1.011767
Depth	0.0330615	0.0017191	19.232	2e-16	2.669158
Algae	-0.0145839	0.0011251	-12.962	2e-16	1.825306
Coral	-0.0200295	0.0031643	-6.330	2.46e-10	1.018901
Area	0.0009908	0.0001009	9.820	2e-16	1.047459
Temperature	0.1132080	0.0120570	9.389	2e-16	2.947634
Pseudo R^2	0.4125				

4. Discussion

This study is the first empirical evaluation of fish assemblage patterns and beta diversity across shallow and mesophotic zones in the Cape Verde archipelago. The research aimed to identify the factors driving beta diversity within the archipelago and determine if ecological or biogeographical factors have a more prominent role in shaping beta diversity. During the examination of beta diversity components, it was consistently found 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). Their analyses suggest that high species turnover in marine organisms is potentially influenced by dispersal potential variability and environmental heterogeneity among sites. Furthermore, 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 communities from small (meters) to large (ocean basins) scales.

4.1. Depth vs geography

As expected, adjacent depth zones displayed higher similarity between each other in comparison to the shallow and lower mesophotic zones across all the surveyed islands. This pattern of higher similarity between the shallow and upper mesophotic zone found here aligns with previous studies that observed similar species composition between these two depth zones (Baldwin et al., 2018; Laverick et al., 2018; Slattery et al., 2011). Further, Lesser et al. (2019) acknowledge a significant loss of shallow water taxa between the upper and lower mesophotic zones.

Depth has been broadly acknowledged as the foremost driver of the abundance and distribution of reef fishes (Pinheiro et al., 2015; 2016; 2023a; Rosa et al., 2016; Semmler et al., 2017). The depth gradient is attributed to simultaneous changes in various factors, such as light availability, water temperature, marine current patterns, food resources, and level of fishing activity (Lesser et al., 2009). Such changes may explain the increasing beta diversity along the depth gradient in Cape 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 have been observed to have a stronger association with specific depth zones (Baldwin et al., 2018; Silva et al., 2021; Bosch et al., 2023). Certain species may be more adapted to the environmental conditions, habitat structures, and food availability found within a particular depth range (Medina et al., 2007).

On the other hand, geographic distance is a well-known driver of species turnover, whereas adjacent sites commonly display higher similarity of species than distant ones (Caley & Schluter, 1997; Medina et al., 2007). Interestingly, when the depth zones within the Cape Verde archipelago were compared, they exhibited higher beta diversity than the geographic distance. 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 pattern implies that each island harbours, to a certain degree, unique components of fish assemblages, which could be further driven by local environmental characteristics rather than by isolation, as each island displays differences in life history and morphology. For instance, while Santo Antão benefits from the proximity of seamounts, which have been shown to enhance species abundance (Kaiser et al., 2020; Pinheiro et al., 2015), 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 Cape Verde.

Therefore, the variation in species composition of the reef fishes among the islands within Cape Verde 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, 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

Not only the depth gradient and geography affect the species composition (Pinheiro et al., 2016) but also environmental variables and microhabitat differences play an important role in structuring the community composition (Srinivasan, 2003; Syms & Jones, 2000). 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 coral reefs, small-scale environmental variables have an important role in determining community patterns (Dornelas et al., 2006), as the existence of microhabitats increases the 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 could be also noted in this study. The difference in benthic cover and habitat complexity showed to be significant drivers of beta diversity, indicating that the benthic environmental variables are determinants for fish species composition across sites and depth gradients. The zooxanthella corals and algae dominated shallow and upper zones while the heterotrophic corals increased in the mesophotic zones. Previous studies have shown that the presence of black coral forests affects the degree of similarity in fish assemblage structure between the depth strata (Bosch et al., 2023; Rosa et al., 2016). Therefore, the high beta diversity observed in the study may be attributed to species-specific variations in habitat selection (Pinheiro et al., 2018; Syms & Jones, 2000). This can be explained by the fact that certain species exhibit a preference for specific microhabitats, indicating their specialization (Srinivasan, 2003). An illustrative example is the fact that endemic species are known to be habitat specialists (Pinheiro et al., 2018).

In addition, we observed within depth zones a slight increase in beta diversity with depth. 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 could be due to that the lower zones microhabitats are less heterogeneous resulting in less available niches, thus they are species saturated. This would indicate that there are assembly rules on the species distribution to avoid redundancy and maximize the available resources (Pinheiro et al., 2023a). Furthermore, the lower MCE are known to harbour 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).

Here we show that the beta diversity within the Cape Verde archipelago was mainly driven by the depth gradient and environmental variables. The shift in the depth has a concurrent influence on the habitat structure and temperature regime resulting in the similarity of reef fish species composition decreasing with increasing depth. Notably higher species richness does not necessarily result in higher beta diversity. Our results suggest that the lower MCE seems to be saturated as a result of lower microhabitat heterogeneity that drives niche reduction in the lower zones, therefore, showing lower richness but higher species turnover. Furthermore, the effect of geography is reduced within the archipelago of Cape Verde since each island seems to have unique characteristics that contribute to promote differences in species assemblages.

4.3. Conservation

Beta diversity does not only depend on ecological patterns but also on human-induced pressure (Magurran, 2004; Arias-González et al., 2008). Damaging anthropogenic actions change local communities (Socolar et al., 2016). Among the three studied islands, a higher concentration of fishing debris was observed on Santiago compared to the other two islands (Fig. 4.1).

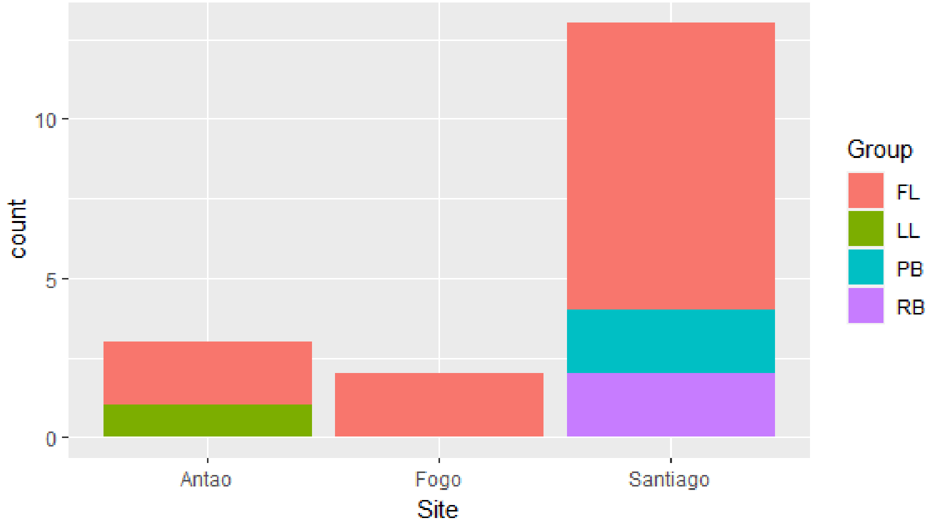

Figure 4.1. Count of trash observed at the surveyed islands. FL= Fishing line, LL= Long line, PB= Plastic bag, RB=Boat rope.

The higher levels of fishing debris, which is an indicator of human pressure (Bruneel et al., 2021; Pinheiro et al., 2023b) most likely affect the ecological and biogeographic patterns found. As expected, beta diversity comparisons with Santiago and the other islands (Fig. 3.2A) showed the highest nestedness values, despite geographic distance, what could be associated with the removal of fish species by fishing. In addition, the shallow and upper MCE zones of Santiago clustered together and harbour lower species richness, differently from the other islands. This observation may be indicative of fishing activities targeting the shallow and upper zones (Lindfield et al., 2016). For example, the family Carangidae was completely absent 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 fishing value, whereas *C. taeniops* is the most commercially caught fish in Cape Verde, and the family of Jacks are known to be overfished in some regions (Lino et al., 2011; Silva et al., 2021). Previous studies have confirmed the negative effects of anthropogenic pressures on fish assemblages of tropical islands (Bruneel et al., 2021).

Determining the extent of species loss in the ecosystem resulting from destructive activities is challenging when the initial baseline of species 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 by companies. Implementing local measures to protect reefs from overfishing and pollution can enhance the resilience of reef ecosystems to withstand the impacts of climate change (Hughes et al., 2017).

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References

Arias-González, J. E., Legendre, P., & Rodríguez-Zaragoza, F. A. (2008). Scaling up beta diversity on Caribbean coral reefs. *Journal of Experimental Marine Biology and Ecology*, *366*(1-2), 28-36.

Baldwin, C. C., Tornabene, L., & Robertson, D. R. (2018). Below the mesophotic. *Scientific reports*, *8*(1), 4920.

Barton, K., & Barton, M. K. (2015). Package 'mumin'. *Version*, *1*(18), 439.

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global ecology and biogeography*, *19*(1), 134-143.

Baselga, A., & Orme, C. D. L. (2012). betapart: an R package for the study of beta diversity. *Methods in ecology and evolution*, *3*(5), 808-812.

Bellwood, D. R., Hughes, T. P., Folke, C. & Nystrom, M. (2004). Confronting the coral reef crisis. *Nature, 429,* 827–833. https:// doi. org/ 10.1038/ natur e02691

Bongaerts, P., Muir, P., Englebert, N., Bridge, T. C. L., & Hoegh-Guldberg, O. (2013). Cyclone damage at mesophotic depths on Myrmidon Reef (GBR). *Coral Reefs*, *32*, 935-935.

Bongaerts, P., Ridgway, T., Sampayo, E. M., & Hoegh-Guldberg, O. (2010). Assessing the 'deep reef refugia'hypothesis: focus on Caribbean reefs. *Coral reefs*, *29*, 309-327.

Bongaerts, P., & Smith, T. B. (2019). Beyond the "deep reef refuge" hypothesis: a conceptual framework to characterize persistence at depth. *Mesophotic coral ecosystems*, 881-895.

Bosch, N. E., Espino, F., Tuya, F., Haroun, R., Bramanti, L., & Otero-Ferrer, F. (2023). Black coral forests enhance taxonomic and functional distinctiveness of mesophotic fishes in an oceanic island: implications for biodiversity conservation. *Scientific Reports*, *13*(1). https://doi.org/10.1038/s41598-023-32138-x

Bruneel, S., Van Echelpoel, W., Ho, L., Raat, H., Schoeters, A., De Troyer, N., Sor, R., Ponton-Cevallos, J., Vandeputte, R., Van der heyden, C., De Sayer, N., Forio, M. A. E., Bermudez, R., Dominguez-Granda, L., Luca, S., Moens, T. & Goethals, P. (2021). Assessing the drivers behind the structure and diversity of fish assemblages associated with rocky shores in the Galapagos Archipelago. *Journal of Marine Science and Engineering*, *9*(4), 375.

Brokovich, E., Einbinder, S., Shashar, N., Kiflawi, M., & Kark, S. (2008). Descending to the twilight-zone: changes in coral reef fish assemblages along a depth gradient down to 65 m. *Marine Ecology Progress Series*, *371*, 253-262. https://doi.org/10.3354/meps07591

Caley, M. J., & Schluter, D. (1997). The relationship between local and regional diversity. *Ecology*, *78*(1), 70-80.

City Population (2021, August 27). Population statistics for countries, administrative divisions. Cities, urban areas and agglomerations. http://www.citypopulation.de/en/capeverde/

Cribari-Neto, F., & Zeileis, A. (2010). Beta regression in R. *Journal of statistical software*, *34*, 1-24.

Dawson, M. N. (2016). Island and island-like marine environments. *Global Ecology and Biogeography*, *25*(7), 831–846. https://doi.org/10.1111/geb.12314

Dornelas, M., Sean, R.C., Hughes, T., (2006). Coral reef diversity refutes the neutral theory of biodiversity. *Nature 440,* 80–82.

Etnoyer, P. J., Wickes, L. N., Silva, M., Dubick, J. D., Balthis, L., Salgado, E., & MacDonald, I. R. (2016). Decline in condition of gorgonian octocorals on mesophotic reefs in the northern Gulf of Mexico: before and after the Deep-water Horizon oil spill. *Coral Reefs*, *35*, 77-90.

Failler, P., Touron-Gardic, G., Drakeford, B., Sadio, O., & Traoré, M. S. (2020). Perception of threats and related management measures: The case of 32 marine protected areas in West Africa. *Marine Policy*, *117*. https://doi.org/10.1016/j.marpol.2020.103936

Ferreira, C.E.L., Floeter, S.R., Gasparini, L.L., Joyeux, J.C., Ferreira, P.B., (2004). Trophic structure patterns of Brazilian reef fishes: a latitudinal comparison. *Journal of Biogeography, 31* (7), 1093–1106. https://doi.org/10.1111/j.1365-2699.2004.01044.x.

Fox, J., Weisberg, S., Adler, D., Bates, D., Baud-Bovy, G., Ellison, S., Firth, D, Friendly, M., Gorjanc, G., & Graves, S. (2012). Package 'car'. *Vienna: R Foundation for Statistical Computing*, *16*.

Harborne, A. R., Mumby, P. J., ZŻychaluk, K., Hedley, J. D., & Blackwell, P. G. (2006). Modeling the beta diversity of coral reefs. *Ecology*, *87*(11), 2871-2881.

Hughes, T. P., Baird, A. H., Bellwood, D. R., Card, M., Connolly, S. R., Folke, C., Grosberg, R., Hoegh-Guldberg, O., Jackson, J. B. C., Kleypas, J., Lough, J. M., Marshall, P., Nyström, M., Palumbi, S. R., Pandolfi, S. R., Rosen, B., & Roughgarden, J. (2003). Climate change, human impacts, and the resilience of coral reefs. *science*, *301*(5635), 929-933.

Hughes, T. P., Barnes, M. L., Bellwood, D. R., Cinner, J. E., Cumming, G. S., Jackson, J. B. C., Kleypas, J., Van De Leemput, I. A., Lough, J. M., Morrison, T. H., Palumbi, S. R., Van Nes, E. H., & Scheffer, M. (2017). Coral reefs in the Anthropocene. *Nature, 546*(7656), 82–90. Nature Publishing Group. https://doi.org/10.1038/nature22901

Kahng, S. E., Akkaynak, D., Shlesinger, T., Hochberg, E. J., Wiedenmann, J., Tamir, R., & Tchernov, D. (2019). Light, temperature, photosynthesis, heterotrophy, and the lower depth limits of mesophotic coral ecosystems. *Mesophotic coral ecosystems*, 801-828. Springer International Publishing.

Kahng, S., Copus, J. M., & Wagner, D. (2017). Mesophotic coral ecosystems. *Marine animal forests*, *10*, 1–22. Springer International Publishing. https://doi.org/10.1007/978-3-319-17001-5_4-1.

Kaiser, M. J., Attrill, M. J., Jennings, S., Thomas, D. N., Barnes, D. K., Brierley, A. S., Graham, N. A. J., Hiddink, J. G., Howell, K., & Kaartokallio, H. (2020). Marine Ecology: Processes, Systems, and Impacts.

Laborel, J., 1974. West African reef corals: an hypothesis on their origin. *Proceedings of the Second International Coral Reef Symposium 1*, 425-443.

Laverick, J. H., Piango, S., Andradi-Brown, D. A., Exton, D. A., Bongaerts, P., Bridge, T. C. L., Lesser, M. P., Pyle, R. L., Slattery, M., Wagner, D., & Rogers, A. D. (2018). To what extent do mesophotic coral ecosystems and shallow reefs share species of conservation interest? A systematic review. *Environmental Evidence*, *7*(1). BioMed Central Ltd. https://doi.org/10.1186/s13750-018-0127-1

Lesser, M. P., Slattery, M., Laverick, J. H., Macartney, K. J., & Bridge, T. C. (2019). Global community breaks at 60 m on mesophotic coral reefs. *Global Ecology and Biogeography*, *28*(10), 1403-1416.

Lesser, M. P., Slattery, M., & Leichter, J. J. (2009). Ecology of mesophotic coral reefs. *Journal of experimental marine biology and ecology*, *375*(1-2), 1-8.

Lindfield, S. J., Harvey, E. S., Halford, A. R., & McIlwain, J. L. (2016). Mesophotic depths as refuge areas for fishery-targeted species on coral reefs. *Coral Reefs*, *35*(1), 125–137. https://doi.org/10.1007/s00338-015-1386-8

Lino, P. G., Bentes, L., Oliveira, M. T., Erzini, K., & Santos, M. N. (2011). The African hind's (Cephalopholis taeniops, serranidae) use of artificial reefs off sal island (Cape Verde): a preliminary study based on acoustic telemetry. *Brazilian Journal of Oceanography*, *59*, 69-76.

Magurran, A.E., (2004). Measuring Biological Diversity. Blackwell Publishing, United Kingdom

Maragos, J. E., Crosby, M. P., & McManus, J. W. (1996). Coral reefs and biodiversity: a critical and threatened relationship. *Oceanography, 9(1),* 83-99.

Maxwell, M. F., Leprieur, F., Quimbayo, J. P., Floeter, S. R., & Bender, M. G. (2022). Global patterns and drivers of beta diversity facets of reef fish faunas. *Journal of Biogeography*, *49*(5), 954-967.

Mazzei, E. F., Pinheiro, H. T., Simon, T., Moura, R. L., Macieira, R. M., Pimentel, C. R., Teixeira, J. B., Floeter, S. R., Ferreira, C. E. L., Ghisolfi, R. D., Francini-Filho, R. B., Quimbayo, J. P., Rocha, L. A., Gasparini, J. L., & Joyeux, J. C. (2021). Mechanisms of dispersal and establishment drive a stepping stone community assembly on seamounts and oceanic islands. *Marine Biology*, *168*(7). https://doi.org/10.1007/s00227-021-03919-7

Medina, A., Brêthes, J. C., & Sévigny, J. M. (2008). Habitat fragmentation and body-shape variation of African hind Cephalopholis taeniops (Valenciennes) in an archipelago system (Cape Verde, eastern Atlantic Ocean). *Journal of Fish Biology*, *73*(4), 902–925. https://doi.org/10.1111/j.1095-8649.2008.01986.x

Medina, A., Brêthes, J. C., Sévigny, J. M., & Zakardjian, B. (2007). How geographic distance and depth drive ecological variability and isolation of demersal fish communities in an archipelago system (Cape Verde, Eastern Atlantic Ocean). *Marine Ecology*, *28*(3), 404–417. https://doi.org/10.1111/j.1439-0485.2007.00163.x

Moses, C.S., K.P. Helmle, P.K. Swart, R.E. Dodge & S.E. Merino, 2003. Pavements of *Siderastrea radians* on Cape Verde reefs. *Coral Reefs, 22,* 506-506.

Norse, E. A. (Ed.). (1993). *Global marine biological diversity: a strategy for building Conservation into decision making* (Vol. 2). Island Press.

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H., Wagner, H., & Oksanen, M. J. (2013). Package 'vegan'. *Community ecology package, version, 2*(9), 1-295.

Olavo, G., Costa, P.A.S., Martins, A.S., Ferreira, B.P., 2011. Shelf-edge reefs as priority areas for conservation of reef fish diversity in the tropical Atlantic. *Aquatic conservation: marine and freshwater ecosystems, 21* (2), 199–209. https://doi.org/10.1002/aqc.1174.

Pérez-Rosales, G., Rouzé, H., Torda, G., Bongaerts, P., Pichon, M., Parravicini, V., & Hédouin, L. (2021). Mesophotic coral communities escape thermal coral bleaching in French Polynesia. *Royal Society Open Science*, *8*(11). https://doi.org/10.1098/rsos.210139

Pinheiro, H.T., Mazzei, E., Moura, R.L., Amado-Filho, G.M., Carvalho-Filho, A., Braga, A. C., Costa, P.A.S., Ferreira, B.P., Ferreira, C.E.L., Floeter, S.R., Francini-Filho, R.B., Gasparini, J.L., Macieira, R.M., Martins, A.S., Olavo, G., Pimentel, C.R., Rocha, L.A., Sazima, I., Simon, T., Teixeira, J.B., Xavier, L.B., Joyeux, J.C., (2015). Fish biodiversity of the vitoria-trindade ´ seamount chain, southwestern atlantic: an updated database. PloS One 10 (3), e0118180. https://doi.org/10.1371/journal. pone.0118180.

Pinheiro, H. T., MacDonald, C., Quimbayo, J. P., Shepherd, B., Phelps, T. A., Loss, A. C., Teixeira, J. B., & Rocha, L. A. (2023a). Assembly rules of coral reef fish communities along the depth gradient. *Current Biology*, *33*(8), 1421-1430.e4. https://doi.org/10.1016/j.cub.2023.02.040

Pinheiro, H. T., MacDonald, C., Santos, R. G., Ali, R., Bobat, A., Cresswell, B. J., Francini-Filho, R., Freitas, R., Galbraith, G. F., Musembi, P., Phelps, T. A., Quimbayo, J. P., Quiros, T. E. A. L., Shepherd, B., Stefanoudis, P. V., Talma, S., Teixeira, J. B., Woodall, L. C., & Rocha, L. A. (2023b). Plastic pollution on the world's coral reefs. *Nature*, *619*(7969), 311–316. https://doi.org/10.1038/s41586-023-06113-5

Pinheiro, H. T., Martins, A. S., & Joyeux, J. C. (2013). The importance of small-scale environment factors to community structure patterns of tropical rocky reef fish. *Journal of the Marine Biological Association of the United Kingdom*, *93*(5), 1175–1185. https://doi.org/10.1017/S0025315412001749

Pinheiro, H. T., Goodbody-Gringley, G., Jessup, M. E., Shepherd, B., Chequer, A. D., & Rocha, L. A. (2016). Upper and lower mesophotic coral reef fish communities evaluated by underwater visual censuses in two Caribbean locations. *Coral Reefs*, *35*(1), 139–151. https://doi.org/10.1007/s00338-015-1381-0

Pinheiro, H. T., Rocha, L. A., Macieira, R. M., Carvalho-Filho, A., Anderson, A. B., Bender, M. G., Di Dario, F., Ferreira, C. E. L., Figueiredo-Filho, J., Francini-Filho, R., Gasparini, J. L., Joyeux, J. C., Luiz, O. J., Mincarone, M. M., Moura, R. L., Nunes, J. de A. C. C., Quimbayo, J. P., Rosa, R. S., Sampaio, C. L. S., Sazima, I., Simos, T., Vila-Nova, D. A., & Floeter, S. R., (2018). South-western Atlantic reef fishes: Zoogeographical patterns and ecological drivers reveal a secondary biodiversity centre in the Atlantic Ocean. *Diversity and Distributions*, *24*(7), 951–965. https://doi.org/10.1111/ddi.12729

Pyle, R. L., & Copus, J. M. (2019). Mesophotic Coral Ecosystems: Introduction and Overview. *Mesophotic coral ecosystems,* 3–27. https://doi.org/10.1007/978-3-319-92735-0_1

Pyle, R. L., Kosaki, R. K., Pinheiro, H. T., Rocha, L. A., Whitton, R. K., & Copus, J. M. (2019). Fishes: Biodiversity. *Mesophotic coral ecosystems,*749–777. https://doi.org/10.1007/978-3-319-92735-0_40

Ramalho, R. A. (2011). *Building the cape verde Islands*. Springer Science & Business Media.

Ramalho, R. A., & Ramalho, R. A. D. S. (2011). Tracers of uplift and subsidence in the Cape Verde Archipelago. *Building the Cape Verde Islands*, 79-138.

Rocha, L. A., Pinheiro, H. T., Shepherd, B., Papastamatiou, Y. P., Luiz, O. J., Pyle, R. L., & Bongaerts, P. (2018.). Mesophotic coral ecosystems are threatened and ecologically distinct from shallow water reefs. *Science, 361*(6399), 281-284. http://science.sciencemag.org/

Rosa, M. R., Alves, A. C., Medeiros, D. V., Coni, E. O. C., Ferreira, C. M., Ferreira, B. P., de Souza Rosa, R., Amado-Filho, G. M., Pereira-Filho, G. H., de Moura, R. L., Thompson, F. L., Sumida, P. Y. G., & Francini-Filho, R. B. (2016). Mesophotic reef fish assemblages of the remote St. Peter and St. Paul's Archipelago, Mid-Atlantic Ridge, Brazil. *Coral Reefs*, *35*(1), 113–123. https://doi.org/10.1007/s00338-015-1368-x

Semmler, R. F., Hoot, W. C., & Reaka, M. L. (2017). Are mesophotic coral ecosystems distinct communities and can they serve as refugia for shallow reefs?. *Coral Reefs, 36*, 433-444.

Silva, M. B., Rosa, R. S., Menezes, R., & Francini-Filho, R. B. (2021). Changes in reef fish assemblages in a cross-shelf euphotic-mesophotic gradient in tropical SW Atlantic. *Estuarine, Coastal and Shelf Science*, *259*, 107465.

Slattery, M., Lesser, M. P., Brazeau, D., Stokes, M. D., & Leichter, J. J. (2011). Connectivity and stability of mesophotic coral reefs. *Journal of Experimental Marine Biology and Ecology*, *408*(1-2), 32-41.

Smithson, M., & Verkuilen, J. (2006). A better lemon squeezer? Maximum-likelihood regression with beta-distributed dependent variables. *Psychological methods*, *11*(1), 54.

Soares, M. D. O., Tavares, T. C. L., & Carneiro, P. B. D. M. (2019). Mesophotic ecosystems: Distribution, impacts and conservation in the South Atlantic. *Diversity and Distributions*, *25*(2), 255-268.

Socolar, J. B., Gilroy, J. J., Kunin, W. E., & Edwards, D. P. (2016). How Should Beta-Diversity Inform Biodiversity Conservation? In *Trends in Ecology and Evolution*, *31*(1), 67–80). Elsevier Ltd. https://doi.org/10.1016/j.tree.2015.11.005

Soininen, J., Heino, J., & Wang, J. (2018). A meta-analysis of nestedness and turnover components of beta diversity across organisms and ecosystems. *Global Ecology and Biogeography*, *27*(1), 96–109. https://doi.org/10.1111/geb.12660

Spalding, M., Ravilious, C., & Green, E. P. (2001). *World atlas of coral reefs*. Univ of California Press.

Srinivasan, M. (2003). Depth distributions of coral reef fishes: The influence of microhabitat structure, settlement, and post-settlement processes. *Oecologia*, *137*(1), 76–84. https://doi.org/10.1007/s00442-003-1320-6

Syms, C., & Jones, G. P. (2000). Disturbance, Habitat Structure, and the Dynamics of a Coral-Reef Fish Community. *Ecology*, *81*(10), 2714-2729.

Turner, J. A., Andradi-Brown, D. A., Gori, A., Bongaerts, P., Burdett, H. L., Ferrier-Pagès, C., Voolstra, C. R., Weinstein, D. K., Bridge, T. C. L., Costantini, F., Gress, E., Laverick, J., Loya, Y., Goodbody-Gringley, G., Rossi, S., Taylor, M. L., Viladrich, N., Voss, J. D., Williams, J., Woodall, L. C., & Eyal, G. (2019). Key Questions for Research and Conservation of Mesophotic Coral Ecosystems and Temperate Mesophotic Ecosystems. *Mesophotic coral ecosystems*, 989–1003. https://doi.org/10.1007/978-3-319-92735-0_52

Turner, J. A., Babcock, R. C., Hovey, R., & Kendrick, G. A. (2017). Deep thinking: A systematic review of mesophotic coral ecosystems. *Journal of Marine Science*, *74*(9) 2309–2320. Oxford University Press. https://doi.org/10.1093/icesjms/fsx085

van der Land J., 1993. Marine biota of the Cape Verde Islands. *Courier Forschungsinstitut Senckenberg*, *159*, 39-44.

Wienerroither, R., Uiblein, F., Bordes, F., & Moreno, T. (2009). Composition, distribution, and diversity of pelagic fishes around the Canary Islands, Eastern Central Atlantic. *Marine Biology Research*, *5*(4), 328-344.

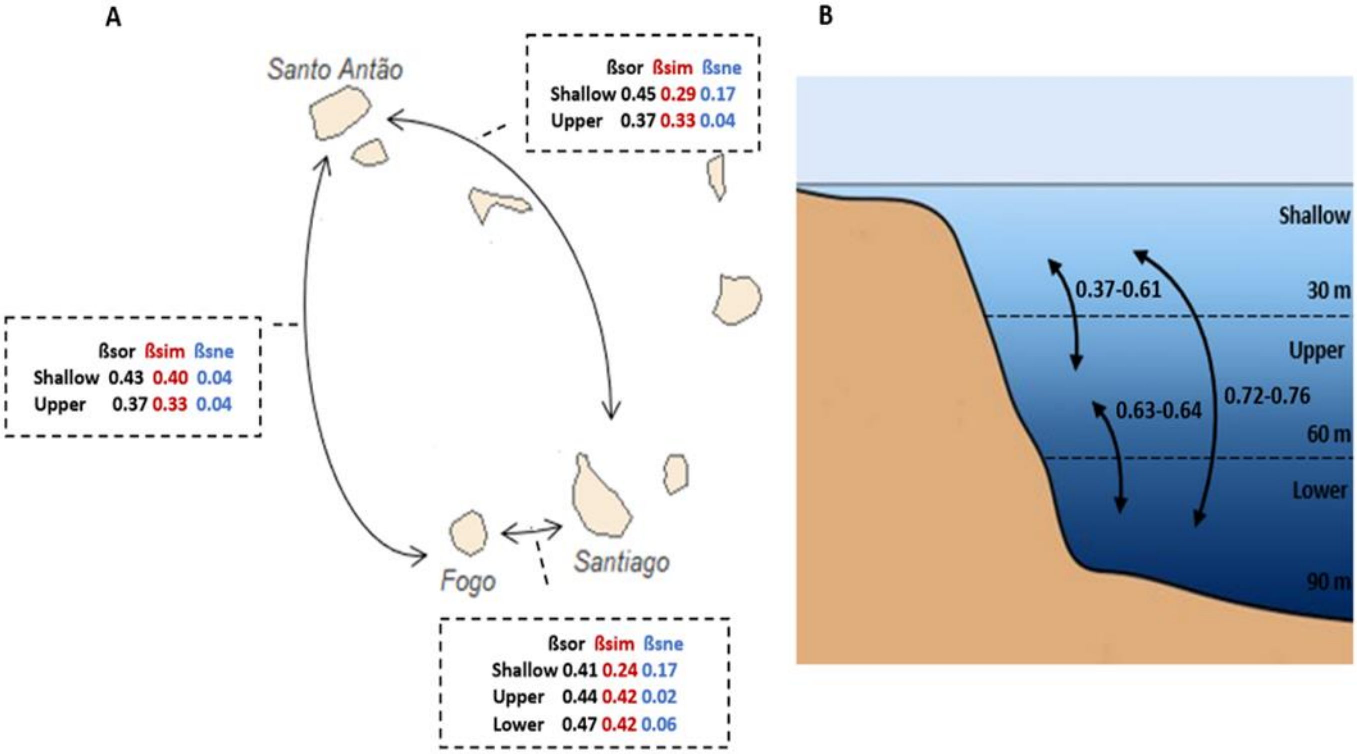
Wilkinson, C. R. Global and local threats to coral reef functioning and existence: review and predictions. *Marine and freshwater research*, *50*(8), 867–878. https:// doi. org/ 10. 1071/ mf991 21 (1999)

Witman, J. D., Etter, R. J., & Smith, F. (2004). The relationship between regional and local species diversity in marine benthic communities: a global perspective. *Proceedings of the National Academy of Sciences*, *101*(44), 15664-15669.

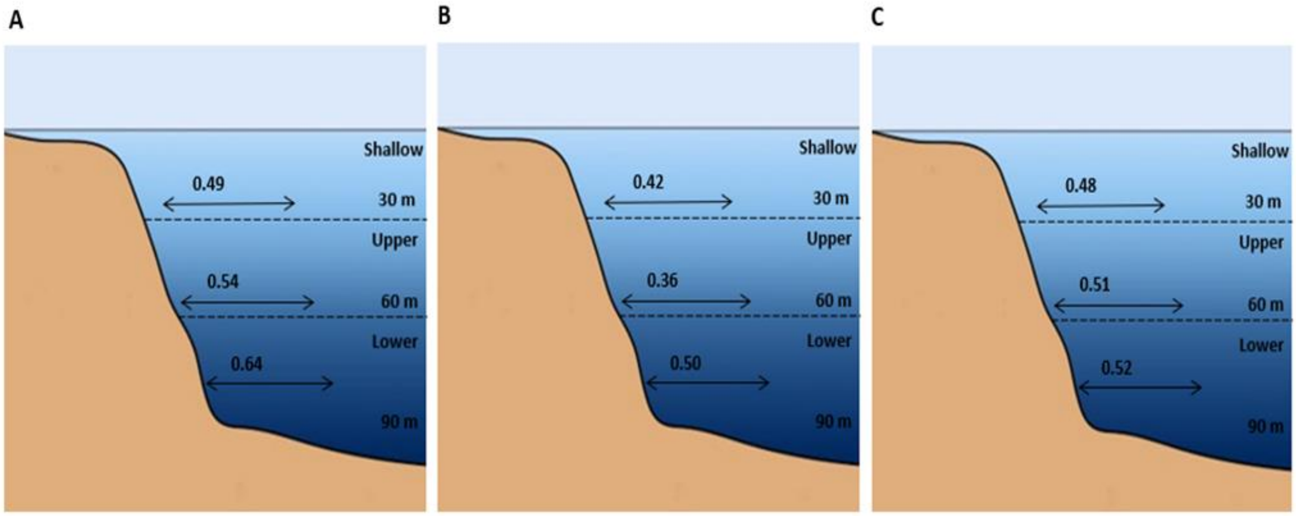
Worldometers (2023, July 16). Cabo Verde Population. https://www.worldometers.info/world-population/cabo-verde-population/

Quimbayo, J. P., Dias, M. S., Kulbicki, M., Mendes, T. C., Lamb, R. W., Johnson, A. F., Aburto-Oropeza, O., Alvarado, J. J., Bocos, A. A., Ferreira, C. E. L., Garcia, E., Luiz, O. J., Mascareñas-Osorio, I., Pinheiro, H. T., Rodriguez-Zaragoza, F., Salas, E., Zapata, F. A., & Floeter, S. R. (2019). Determinants of reef fish assemblages in tropical Oceanic islands. *Ecography*, *42*(1), 77-87.

Appendix



Supplementary Figure 1. MSA 160m^2, excluding lower Santo Antão. (**A)** Sorensen's pairwise dissimilarity and its components turnover and nestedness between the surveyed islands and their depth zones. **(B)** Sorensen's pairwise dissimilarity between shallow reef fish communities and mesophotic depth zones of each island.



Supplementary Figure 2. Intra beta diversity using Sorensen's pair-wise dissimilarity within each depth zone of each surveyed islands: **(A)** Santiago, **(B)** Santo Antão, **(C)** Fogo.