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Fish Diversity in Mangroves of São Tomé Island (Gulf of Guinea)

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Dedicatory

I dedicate this work to my daughter, Kerstin, and my son, Kristoff. May this work be the first step in the construction of a better future for both of you.

Acknowledgments

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Resumo

O valor dos mangais é cada vez mais reconhecido, nomeadamente pelo elevado número de bens e serviços que fornecem não apenas localmente, mas também a nível global. Desempenham um papel importante na regulação do clima através do sequestro de carbono e podem combater a erosão costeira, além de fornecerem diversas matérias-primas. Outro dos principais bens fornecidos é o alimento, destacando-se os recursos pesqueiros. Os mangais têm comunidades de peixes diversas, pois geralmente fazem parte de sistemas complexos, na transição entre o meio terrestre e aquático e entre o meio dulçaquícola e marinho, onde as raízes das árvores de mangue fornecem abrigo para muitas espécies de peixes, especialmente juvenis que frequentemente crescem nestes sistemas. Além da sua importância como viveiro para muitas espécies de água salgada e de água doce, também servem como zona de alimentação para peixes.

Apesar da importância destes sistemas, sabe-se pouco sobre os mangais da ilha de São Tomé ou sobre as suas comunidades piscícolas. Esta tese tem como objetivo compreender como a diversidade de peixes varia entre mangais com características distintas, através do uso de diversos índices de diversidade e comparar o resultado das métricas taxonómicas e funcionais de diversidade. Esta informação é fulcral para assegurar a adequação de planos de gestão.

Este estudo teve lugar durante a estação seca de 2017, amostrando quatro dos 12 sistemas de mangal identificados na ilha, nomeadamente os de: i) Malanza, no sul; ii) Praia das Conchas, no norte; iii) Diogo Nunes, no nordeste; e iv) Angolares no sudeste. Durante a amostragem, os parâmetros ambientais temperatura, salinidade e oxigénio dissolvido foram medidos no perfil vertical da coluna de água, a intervalos de 50 cm. Amostras de água foram também recolhidas à superfície para determinação da concentração de nutrientes e de biomassa fitoplantónica. Adicionalmente, amostras de sedimentos foram obtidas para caracterização da sua granulometria e conteúdo em matéria orgânica. Devido à variedade de condições encontradas nos diferentes mangais, não foi possível fazer uma amostragem padronizada da fauna piscícola e foi aplicada uma estratégia de amostragem multi-habitat, usando todas as artes de pesca disponíveis e utilizáveis, passivas e ativas, em cada um dos mangais, nomeadamente, rede de emalhar, palangre, covos, redinha e pesca à linha. Todos os indivíduos capturados foram medidos, pesados e identificados ao menor nível taxonómico possível.

Para determinar a diversidade das comunidades de peixes, vários índices de diversidade taxonómica foram aplicados, o Índice de Shannon-Wiener, o Índice de Diversidade de Simpson e o Índice de Distinção Taxonómica. Foram ainda usados a equitabilidade de Pielou para avaliar a uniformidade da abundância de espécies em cada local; e a Similaridade de Jaccard para avaliar a similaridade das comunidades dos diferentes mangais. Por fim, a diversidade funcional foi avaliada sob a forma de Riqueza Funcional, Equitabilidade Funcional e Dispersão Funcional, além da Riqueza do Grupo Funcional, a Média Ponderada no Nível da Comunidade e a Redundância Funcional.

Todos os mangais apresentaram diferenças significativas entre si, de acordo com as suas condições ambientais, com maiores semelhanças entre os mangais de maiores dimensões (Malanza e Angolares). As condições ambientais foram mais homogéneas nos mangais mais pequenos (Diogo Nunes e Praia das Conchas), e enquanto as condições ambientais encontradas em Malanza eram heterogéneas mas estáveis entre os eventos de amostragem, em Angolares variaram bastante entre momentos de amostragem. O mangal de Diogo Nunes era o único com ligação direta para o mar, sendo por isso o mais afetado pelas marés. Praia das Conchas foi o mangal com influência dulçaquícola mais forte, não existindo intrusão marinha.

Foram identificadas 22 espécies piscícolas, sendo o mangal de Malanza o que apresentou maior riqueza de espécies. O mangal de Praia das Conchas era o mais pobre, com apenas uma espécie, o que impossibilitou a sua inclusão nas restantes análises de diversidade. Malanza foi o sistema mais diverso, enquanto Angolares e Diogo Nunes apresentavam valores de diversidade semelhantes. As comunidades de Angolares foram as mais equitativas, seguidas pelas de Malanza e Diogo Nunes, que apresentaram valores semelhantes. A distinção taxonómica foi mais alta em Angolares e mais baixa em Malanza indicando que a comunidade de Angolares é composta por espécies menos relacionadas entre si do que em Malanza. A variação na distinção taxonómica foi mais alta em Diogo Nunes e mais baixa em Malanza, assinalando uma sobre-representação de certos grupos taxonómicos em Diogo Nunes enquanto em Malanza os diferentes grupos taxonómicos são mais semelhantes em abundância. Para os índices de diversidade funcional, Malanza apresentou os maiores valores de riqueza, de equitabilidade e dispersão funcional. Angolares apresentou baixa riqueza e dispersão, mas alta uniformidade funcional. Diogo Nunes apresentou valores intermédios de riqueza, baixa equitabilidade e altos valores de dispersão. A redundância funcional foi elevada em Angolares e Malanza e baixa em Diogo Nunes, apontando para uma maior resiliência a perturbações para a manutenção das funções nos dois primeiros sistemas.

Malanza é capaz de manter uma comunidade com uma elevada riqueza especifica e funcional, sem sobre-representar espécies ou grupos de espécies funcionalmente semelhantes. A alta diversidade deste mangal de maiores dimensões deve-se provavelmente à heterogeneidade espacial das condições ambientais, associada a uma estabilidade temporal das mesmas. O mangal de Angolares apresenta uma baixa diversidade, tanto específica como funcional e uma comunidade mais equitativa. Esta baixa diversidade deve-se provavelmente às condições ambientais muito variáveis, devido à ocasional quebra repentina da barreira para o mar, que apenas permitem o estabelecimento de espécies tolerantes. Embora as espécies presentes pertençam a *taxa* muito diferentes, todas desempenham funções semelhantes e, na maioria das vezes, mais do que uma espécie desempenha as mesmas funções. O tamanho e a profundidade reduzidos do mangal de Diogo Nunes provavelmente reduzem a sua diversidade: durante a maré baixa a área alagada é reduzida a um riacho raso, reduzindo o espaço para as espécies residentes, e apenas durante a maré alta é que espécies marinhas entram neste mangal, não sendo capazes de se estabelecer. No entanto, as espécies de peixes que ocorrem no mangal Diogo Nunes são funcionalmente mais diversas do que as de Angolares, provavelmente devido à presença de espécies de peixes marinhos mais diversas no primeiro. Observámos que as espécies pelágicas e marinhas preferiram os mangais maiores e mais profundos de Malanza e Angolares, enquanto as espécies bentónicas e estuarinas foram predominantes no mangal Diogo Nunes. Estes resultados reforçam a importância de avaliar a diversidade funcional para compreender associações ambientais de grupos de espécies.

Os índices de diversidade específica e os de diversidade funcional apresentavam uma correlação positiva, mostrando que a diversidade funcional complementa estes índices comumente usados e adiciona informações valiosas sobre as interações espécie-ambiente. No entanto, equitabilidade funcional e equitabilidade especifica não estavam correlacionadas, mostrando a importância do uso de ambas as métricas de diversidade para adquirir um entendimento mais completo das comunidades de peixes. A diversidade taxonómica e a diversidade funcional estavam negativamente correlacionadas, indicando que grupos taxonómicos diferentes podem desempenhar funções semelhantes, ressalvando mais uma vez a importância de utilizar métricas complementares de diversidade. Do ponto de vista de gestão, esta abordagem permite identificar os sistemas mais importantes para cada grupo de espécies, bem como as comunidades e sistemas mais suscetíveis.

Palavras-chave: Comunidades Ictíicas; Diversidade Funcional; Mangais; São Tomé e Príncipe; Suscetibilidade ecológica.

Abstract

Mangroves are valued for their role in climate regulation, countering coastal erosion and providing raw materials. Mangroves have diverse fish communities, and the roots of mangrove trees provide shelter for fish species, especially juveniles. Little is known about Santomean mangroves, with 12 mangrove systems identified, from which four were included in this study. This thesis aims to comprehend how fish diversity varies between mangroves with different characteristics, using Santomean mangroves as case study.

The environmental conditions found in the smaller systems were more homogeneous than those of the larger systems. Twenty-two species were sampled, with Malanza showing the highest richness and Praia das Conchas the lowest. The functional diversity results suggest that Malanza is more diverse and has a functionally richer community. This higher diversity is probably due to the heterogeneity of environmental conditions and their temporal stability. Angolares had low diversity, with an even but species poor community. Likely due to the environmental variability that only allows tolerant species to establish. The reduced size and depth of Diogo Nunes is probably stunting its diversity. Nevertheless, the fish community of Diogo Nunes is functionally more diverse than that of the larger Angolares system. Pelagic and marine species preferred larger and deeper mangroves, while benthic and estuarine species were predominant in Diogo Nunes.

Species and functional diversity were positively correlated indicating complementarity between them and showing that functional diversity adds information about species-environment interactions. Functional and species evenness were not correlated showcasing the importance of the use of both metrics to acquire a more complete understanding of the communities. Taxonomic and functional diversity were negatively correlated indicating that species from different taxa may perform similar functions. From a management point of view this approach represents an advantage as it can identify which systems are more important for which groups, allowing the prioritizing of systems for conservation and management.

Keywords: Ecological susceptibility; Fish Communities; Functional Diversity, Mangroves; São Tomé e Príncipe.

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1. General Introduction

Fish diversity follows a gradient of increasing species richness towards the Equator (Hillebrand, 2004), which is not equal across regions (Briggs, 1999). The highest diversity is observed in the Indo-West Pacific Ocean, particularly in the area between New Guinea and Queensland (Briggs, 1999; Miller et al., 2018). West Africa has a low species richness compared to other tropical regions, but it is still higher than that of temperate or polar regions (Nelson et al., 2016). The reason for the higher diversity of the New Guinea and Queensland area remains to be fully understood, as well as the factors that promote these global patterns (Miller et al., 2018). Meanwhile, other factors such as increased habitat complexity, providing shelter and substrate especially for juvenile fishes, nutrient rich waters, that stimulate primary production (Cloern et al., 2014; Ford et al., 2017; Stuart-Smith et al., 2013) and higher sea surface temperatures (Tittensor et al., 2010) have been identified as having a positive impact on fish richness and diversity. Fish communities found on islands tend to be poorer than those in continental waters (Lévêque et al., 2008), especially among freshwater species, since these often fail to colonize islands. As a result, most species found on islands are of marine origin (Blaber, 2000). Finally, estuaries tend to concentrate large number of fish species, having conditions favourable for feeding, breeding and migration (Elliot and Hemingway, 2002). Species richness in estuaries is strongly dependent on morphological characteristics of the estuary, such as size and connectivity to the ocean. Larger estuaries that are permanently open tend to support higher species richness (Pasquaud et al., 2015; Vasconcelos et al., 2015). Higher temperatures are also associated with higher richness (Vasconcelos et al., 2015). In this context, it is important to note that tropical estuaries have stable water temperature, above 20 °C throughout the year (Blaber, 2000).

Mangroves are forest systems associated with tropical estuaries (Hogarth, 2015). They are composed of mangrove trees that have a strong impact on the morphology and dynamics of the estuaries as well as on their species assemblages. Mangroves can cover large areas in the deltas of rivers, especially in continental areas. On islands they tend to cover smaller areas (Spalding et al., 1997), but nevertheless can have huge ecological importance (Mumby et al., 2004). Mangrove vegetation increases habitat complexity, forming structures that provide shelter and substrate for a variety of organisms (Hogarth, 2015). There are three main hypotheses to explain why mangroves are so attractive to fish: i) reduced predation by larger predators; ii) increased supply of food and shelter; and iii) greater structural complexity provided by the mangroves roots (Nagelkerken et al., 2008). Mangroves tend to have a positive effect on fish richness and biomass, comparing to equivalent systems without mangroves (Blaber, 2007; Nanjo et al., 2014). This is especially true for juvenile populations, stressing the role of mangroves as nursery grounds. The high species richness and biomass of mangroves stresses the role of these systems as diversity hotspots (Whitfield, 2017).

Species diversity assures ecosystem functioning (Duffy, 2009), therefore being able to quantify and monitor changes in diversity is crucial for ecosystem conservation and resource management. One of the primary components of diversity is species richness and abundance, but these two aspects alone are increasingly recognized as insufficient to characterize the diversity of species assemblages (Daly et al., 2018; Reiss et al., 2009). Functional diversity has gained importance in the characterization of species assemblages, since it considers species traits along with species richness and abundance (Cadotte et al., 2011). Species traits are the attributes and behaviours that influence how species interact with their environment (Costello et al., 2015), ultimately influencing ecosystem functioning. Assemblages with high functional diversity maximize the usage of ecosystems resources, and assure that more ecosystem functions are performed (Cadotte et al., 2011). The shift from prioritizing species richness and abundance to species-environment interactions in conservation will allow a more efficient maintenance of ecosystem functioning and services and ultimately of biodiversity and ecosystem processes (Harvey et al., 2017). The usage of functional diversity to assess mangrove fish diversity has only began recently (Dolbeth et al., 2016; Silva-Júnior et al., 2016). In estuaries, contrary to rivers and lakes where the relation tends to reach an asymptote, species richness and functional diversity have a linear relationship (Teichert et al., 2017a). Hence, species rich estuaries such as estuaries with mangroves should have a high functional diversity.

African fish assemblages are understudied in comparison to those of other continents, especially considering mangrove fish assemblages (Faunce and Serafy, 2006), and the existing literature focusses mainly on east and south African mangroves. The islands in the Gulf of Guinea are known as diversity hotspots considering the terrestrial fauna and flora (Jones, 1994), but the knowledge about the aquatic fauna is reduced. The proximity of São Tomé to the Equator makes it especially interesting to study, since fish diversity tends to peak at this latitude (Mittelbach, 2017). The island also receives nutrient-rich water that has high temperatures and low salinities driven by the convergence of the Guinea Current from the north and the Congo Current from the south, which produces a westward flowing current along the equator (Measey et al., 2007). The combination of these factors creates the potential for the establishment of a diverse ichthyofauna that remains poorly studied. Up to date, 12 mangroves have been identified on São Tomé Island, in São Tome and Príncipe (Afonso, 2019). Despite being part of the African Mangrove Network since 2003, little is known about these ecosystems in this tiny island nation (Bojang et al., 2009). Only the mangroves of Malanza and Praia das Conchas have management plans, and they are also the only ones included in a protected area, the São Tomé Obô Natural Park (Loloum et al., 2015a, 2015b). The degree of environmental degradation varies largely between mangroves, even though all are affected by anthropogenic activities, namely due to the generalized poor perception in São Tomé about the importance of ecosystem services provided by mangroves (Afonso, 2019).

1.1. Main objectives

This work aims to understand how fish assemblage diversity varies between mangroves with differing characteristics, comparing taxonomic and functional community metrics, and using Santomean mangroves as a case study.

Chapter I assesses differences in fish assemblages between mangroves with different environmental settings, through the use of taxonomic alpha and beta diversity indices.

Chapter II evaluates differences between the functions of the fish assemblages in different mangroves, assessing functional diversity. These novel diversity metrics will be compared to traditional methods, to evaluate performance of both, identifying conflicting or complementary results from an environmental management standpoint.

Finally, the combined results will allow a better understanding of the Santomean mangrove fish assemblages as to how different mangrove characteristics influence the fish assemblages and the identification of species-environment interactions, representing an important contribution to the development of management plans of these mangroves.

1.2. Study area

São Tomé Island has 857 km^2 and is 255 km west of the African mainland. It is part of the Cameroon volcanic line, along with the islands of Príncipe, Bioko and Annobón. São Tomé is a relatively young volcanic island, and the landscape mirrors this origin, with a steep morphology carved by many water courses. At 2024 m, Pico de São Tomé, located in the northwest of the island, is the highest peak. The central and southern part of the island have a steeper terrain and are geologically older, contrasting with the gentler slopes found in the younger north (Caldeira et al., 1988).

The predominant southern winds, in combination with the warm Guinea current and the islands morphology shape its climate. Immediately north of the Equator, São Tomé has a tropical humid climate, characterized by warm temperatures throughout the year (Hess and Tasa, 2014; Vaz and Oliveira, 2007). There are two dry seasons, a large one, between June and September, known as “gravana”, and a smaller one, between December and February, known as “gravanito”. At sea level, temperatures are around 25 °C all year round, being a little higher in the north, and lower at higher altitudes, never reaching the freezing point. Annual rainfall reaches a maximum of around 7000 mm in the southwest, decreasing towards the northeast due to the rain shadow caused by the mountains at the centre of the island (Juste and Fa, 1994; Jones et al., 1991).

The mangroves of São Tomé are dominated by red (*Rhizophora mangle* L. (1753) and *R. racemosa* G.Mey (1818)) and black mangroves (*Avicennia germinans* (L.) Stearn (1958)) (Figueiredo et al., 2011). Like elsewhere, Santomean mangroves occur in transitional waters, like estuaries and coastal lagoons, but tend to be smaller due to the geomorphological constraints of the island. Four mangrove systems were sampled (Figure 1.1): Malanza, in the south and Praia das Conchas in the north, both part of the São Tomé Obô Natural Park; Angolares in the southeast; and Diogo Nunes in the northeast.

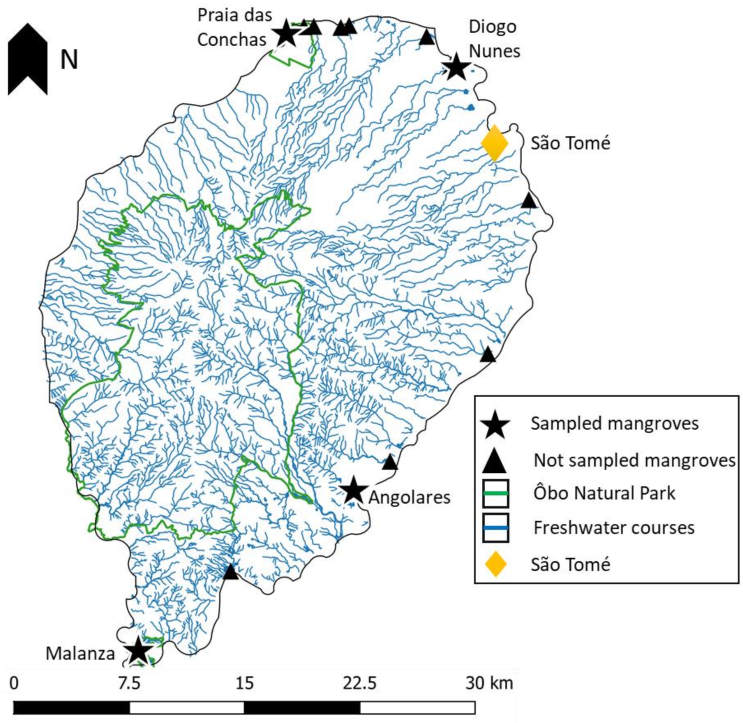

Figure 1.1 *- Map of São Tomé island, showing the location of the sampled mangroves (stars) and the not sampled mangroves (triangles), the Obo Natural Park (green line) the countries freshwater courses (blue lines) and the country’s capital (diamond)*

Malanza is the largest mangrove system of the island, covering around 152 hectares. It is one of the two exclaves of the island's only protected area, the São Tomé Obô Natural Park (Law decree nr. 06/2006). Malanza is located in the southernmost part of the island and is the only mangrove that is commercially exploited for tourism (Pisoni et al., 2015). The downstream area of the system is often used by children to fish, and occasionally by adults (Pisoni et al., 2015). Its hydrographic basin extends over 7.41 km^2, most of which is covered by secondary forest, followed by non-forested areas, including farmland, two small villages and two resorts. The remaining is covered by agroforest. The water course of the system is fed by the drainage of the basin and seawater during high tide (Afonso et al., 2021; Loloum et al., 2015a). The flow of water in the mangrove is constrained by a bridge located downstream and restricted to two sluice-gates (permanently open), which limits the water exchanges with the sea and increases the waterbody upstream of this structure (Félix et al., 2017).

Praia das Conchas is the smallest sampled system, with an area of 1 ha. The system is fed and dominated by a small creek, which has a hydrographic basin that covers 13.31 km^2. Almost half of this area is covered by agroforest, the remaining being covered by farmland and secondary forest. Some villages can be found in the hydrographic basin, as well as the Lobata district landfill. The creek is used for irrigation, personal hygiene, and to wash clothes and vehicles. It is also crossed by a road, resulting in a diminished water inflow from the sea, which happens mostly during spring tides and storms. This system has been drained and heavily deforested (Afonso, 2019; Pisoni et al., 2015).

Angolares mangrove is one of the largest mangroves of the country, covering 13 ha. It is fed by two small rivers on the southeast of the island, one of which bifurcates shortly before the mangrove, resulting in a small river delta. The connection to the sea in the northern portion of this system closes periodically due to sediment accumulation, in the form of a sand barrier, creating an enclosed coastal lagoon. Tidal influence is greater in the northern arm, resulting in a more constant water level in the southern arm. The hydrographic basin covers 7.82 km^2, most of which is covered by agroforest, and only a small portion by secondary forest and non-forested areas, such as villages and a small landfill, located near the southern river arm. The main human activities consist of fishing, mostly by children, and laundry, upstream of the mangrove (Afonso, 2019).

The Diogo Nunes mangrove is located in the northeast of the island, near the country's capital. It has an area of 1 ha and is the only true intertidal mangrove included in this study, being flooded during high tide and dominated by a small creek during the low tide. The hydrographic basin covers 23.35 km^2, with almost two thirds of this area planted with agroforest, and the rest being covered with farmland and constructed areas, including roads, communities, and the country's international airport. Only a residual part of the hydrographic basins is covered by secondary forest, all of which is upstream. The mangrove is under great pressure from human activities, including mangrove deforestation, laundry activities, occasional trash dump and runoff from farms and inhabited areas (Afonso, 2019).

2. General methods

2.1. Sampling design

Fish sampling was carried out from August to September 2017 in the mangroves of Malanza, Praia das Conchas, Angolares and Diogo Nunes. The Praia das Conchas mangrove was sampled once, since the high degradation of the mangrove only allows for the establishment of a freshwater species in the creek that crosses the mangrove. Previous sampling campaigns caught only one species and the first sampling round of the present work confirmed these results. The fish diversity previously reported for this mangrove (Félix et al., 2017) occurred in a saline pool, due to the road that crosses the mangrove the saline pool does not have contact with the sea. Over time conditions in the saline pool worsen and the pool turns progressively hypersaline, the worsening conditions make survival of the colonizing fish community impossible and ultimately lead to their death. Sampling the species found in the hypersaline pool is not viable as they are trapped and do not survive. The remaining mangroves were sampled consecutively (sampling rounds). Malanza was always sampled first, followed by Angolares and finally, Diogo Nunes was sampled last. A two-day interval was set between sampling rounds, *i.e.* between the last sampling day at Diogo Nunes and the first sampling day at Malanza. A total of three sampling rounds were done.

In each mangrove, sampling sites were defined according to mangrove characteristics (*e.g.* size), to represent habitat heterogeneity, and to encompass the salinity gradient. Sampling site selection was constrained by the dense vegetation that limited accessibility and the use of fishing gear in large areas of the mangroves.

Seven sampling sites were established in Malanza (Figure 2.1):

- M1 - in a small shallow lagoon, not exceeding 50 cm of depth, surrounded by shrubs and ferns on one side, and by a sandy beach bordered by coconut trees on the other, which separates the western limits of the Malanza system from the sea.
- M2 - immediately downstream from the bridge, with a depth strongly dependent on tides, and in an area dominated by juvenile mangrove trees.
- M3 – in a lagoon, resulting from the constrained opening to the sea, with large sand banks cut by canals created by water motion and surrounded by adult mangrove trees.
- M4 and M5 - in the upstream mangrove canal, with depths of up to 2 meters and bordered by adult mangrove trees.
- M6 and M7 - at the limit of the mangrove, in a shallow area where mangrove trees grow densely, limiting access.

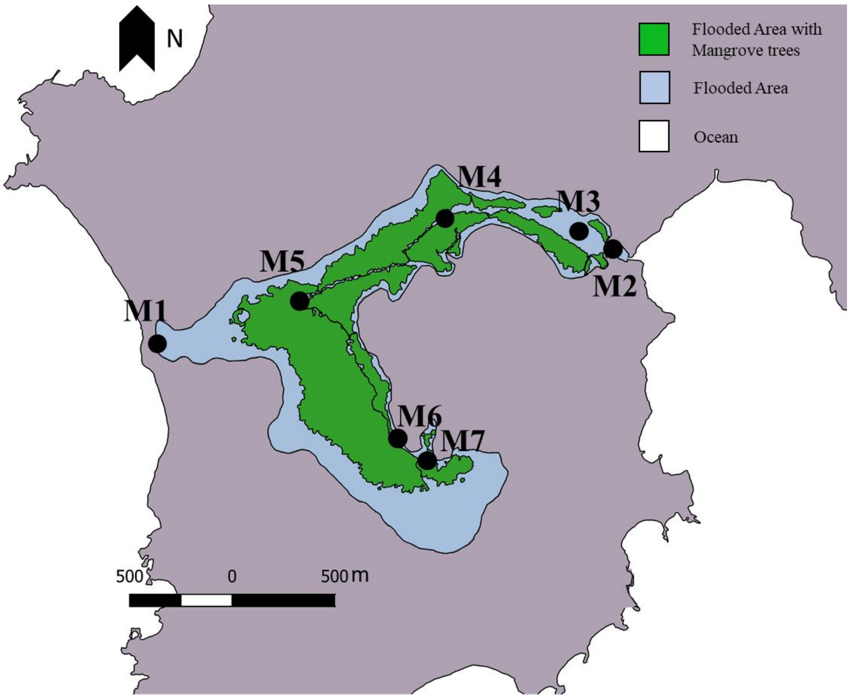

__Figure 2.1__ - Map of the location of the sampling sites in Malanza (black dots)

Three sampling sites were established in Praia das Conchas (Figure 2.2), along the shallow creek where depth never exceeds 50 cm: PC1 downstream, immediately after the bridge, and PC2 and PC3 upstream, with increasing distance from the bridge.

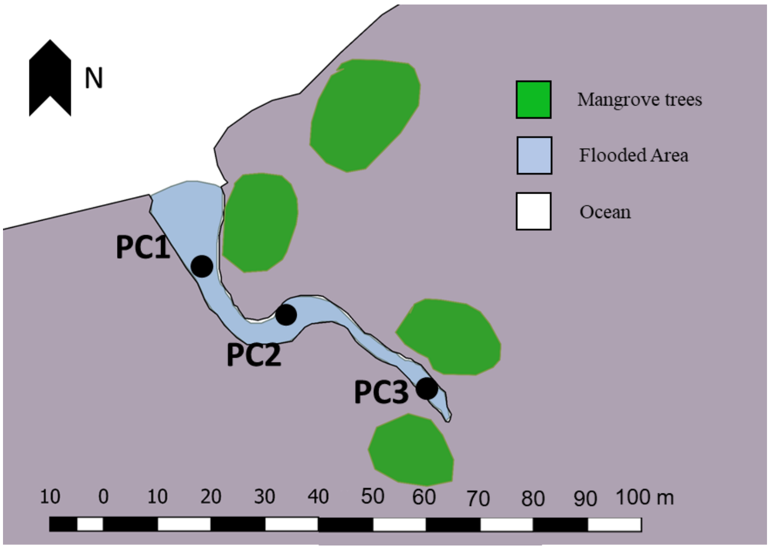

__Figure 2.2__ - Map of the location of the sampling sites in Praia das Conchas (black dots)

Six sampling sites were established in Angolares (Figure 2.3), two in the Água de São Pedro creek (A1 and A6) in the southern part of the mangrove system, and four in the Rio de São João (A2, A3, A4 and A5) in the northern part of the mangrove system:

- A1 being more downstream surrounded by ferns in a shallow sandy area.
- A6 is more upstream in a deeper canal surrounded by large mangrove trees.
- A2 was established in the coastal lagoon of the Rio de São João.
- A3 and A4, are in the rivers canal surrounded mainly by mangrove trees.

- A5 is further upstream and flanked mostly by ferns.

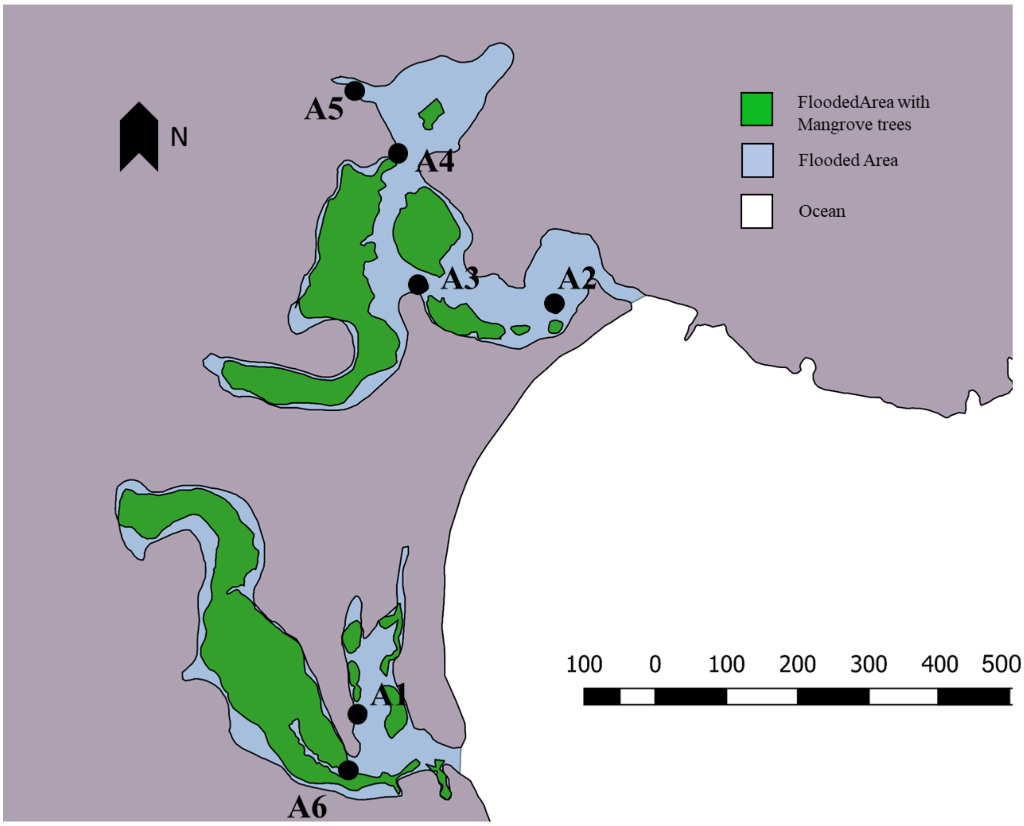

Figure 2.3 - Map of the location of the sampling sites in Angolares (black dots)

Four sampling sites were established in Diogo Nunes (Figure 2.4):

- DN1 - in the river mouth, with high water depth during the high tide.
- DN2 - in an arm of the mangrove near the Diogo Nunes village, fed mainly by sea water intrusion.
- DN3 - in the intermediate zone of the main tributary, where seawater influence was felt during high tide but not during low tide.
- DN4 - at the upstream limit of the mangrove.

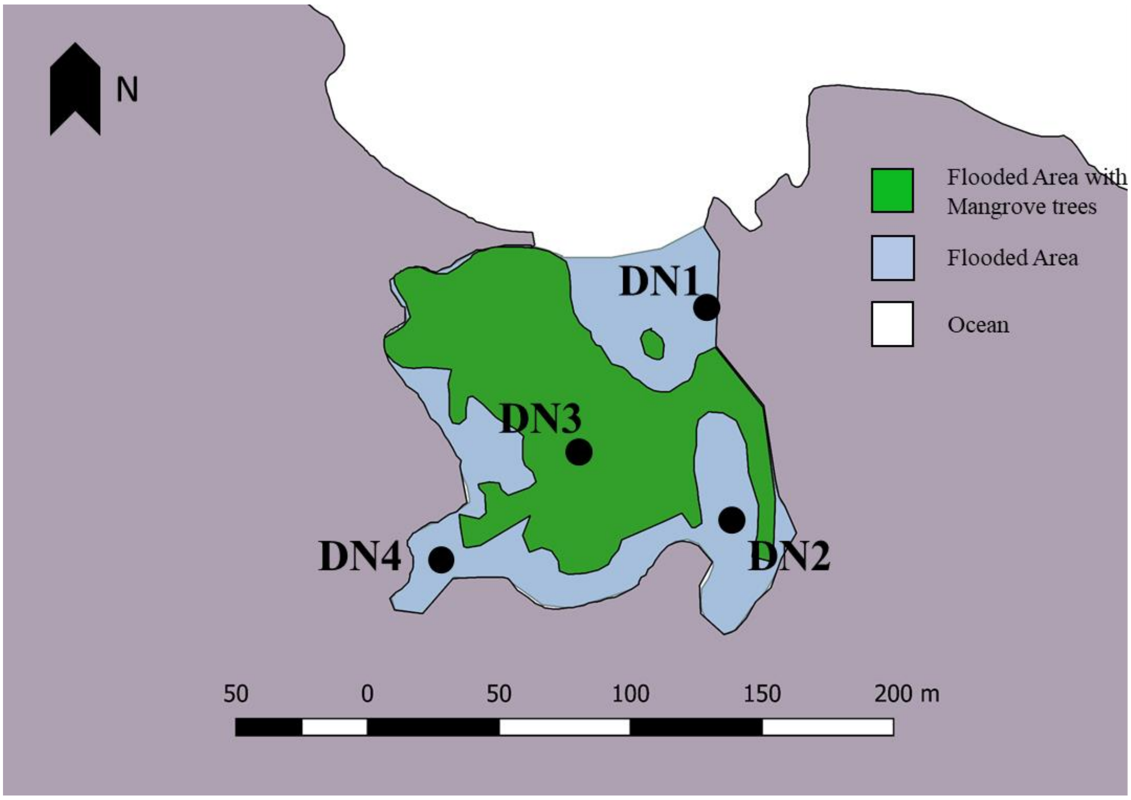

Figure 2.4 - Map of the location of the sampling sites in Diogo Nunes (black dots)

2.2. Sampling design

To maximize sampling effort and to capture the highest variety of fish possible, mangroves were sampled according to a multi-habitat sampling strategy, using all fishing gear available that could be used at each sampling site (Table 2.1). To ensure correct usage, the fishing gear were handled by professional fishermen. This sampling strategy was adopted because of the variability of sampling sites that precluded the standardization of the sampling procedure. Thus, this sampling strategy implied that the fish communities were evaluated at the mangrove level and not the sampling site level, therefore, catches were considered as a whole for the mangrove comparison and only the sum of its samplings sites deemed representative of the system.

Table 2.1 *- Fishing gear used at each sampling site, including a brief description of its characteristics.*

Gear type	Fishing gear	Characteristics	Mangroves	Sampling sites
Passive Gear	**Fish trap**	0.61 m X 0.29 m, mesh size: 15 mm	Diogo Nunes, Malanza	DN1, M2, M3, M4
	Gill net	42 m X 2 m, mesh size: 45 mm	Angolares, Malanza	A3, A4, A6, M3, M4
	Longline	200 m, 38 hooks	Angolares, Malanza	A1, M3
Active	**Angling**	Nylon line	Malanza	M2, M3

Gear	**Cast net**	diameter: 5.6 m, mesh size: 15 mm	Angolares, Diogo Nunes, Malanza	A4, A6, DN1, M1, M2, M3
	Hand net	diameter: 40 cm, mesh size: 10 mm	Angolares, Diogo Nunes, Malanza	A1, DN1, DN4, M2, M5
	Seine net	4 m X 2 m, mesh size: 10 mm	Diogo Nunes, Praia das Conchas	DN1, DN4, PC3

All fish specimens were measured (Total length ±1 mm), weighted (Total weight ± 0.1 g) and photographed. Specimen of species that could not be identified in the field were fixed in a 4% formalin-buffered solution and later transferred to increasing concentrations of ethanol up to 70%, with an increase in 20% at each step every three days and stored for later identification in the laboratory.

During each sampling event environmental parameters were recorded with a multiparametric sonde, namely temperature (°C ±0.01), salinity and dissolved oxygen (% ±0.1). Water column vertical profiles were performed, with measurements taken at depth intervals of 50 cm. When water depths were shallower than 50 cm, a surface and a bottom measure was taken, when waters were shallower than 20 cm only one measure was taken, at the surface. Sediment samples were collected at each sampling site and frozen for subsequent analyses of granulometry and total organic matter (TOM) in the laboratory. Water samples were collected in triplicates and frozen (-20 °C) for quantification of nutrients (ammonium, nitrite and nitrate, phosphate and silicate). The samples collected for ammonium followed indophenol blue method proposed by Koroleff (1969). To preserve the ammonium, 1.5 mL of a solution of phenol and sodium nitroprusside (reagent 1) and 1.5 mL of another solution containing bisodium citrate, sodium hydroxide dehydrated and sodium hypochlorite (reagent 2) were added to those samples. From each sampling site, approximately 0.3 L were also collected and immediately filtered using a 47 mm GF/F filter, with a 0.7 µm pore size (GE Whatman) to quantify chlorophyll *a* concentrations. All filters were frozen (-20 °C) to preserve the samples for laboratory analysis.

2.3. Laboratory analyses

All stored fish specimens were identified to the species level using identification guides, based on morphological features, for the Gulf of Guinea (Schneider, 1990), African brackish waters (Stiassny et al., 2007a, 2007b), West Africa (Edwards et al., 2001), central Atlantic (Carpenter and De Angelis, 2016a, 2016b; Fischer et al., 1981a), North East Atlantic (Whitehead et al., 1989a, 1989b, 1989c) and other relevant publications (Afonso et al., 1999; Dawson, 1984; Lévêque et al., 1992, 1990; Smith and Heemstra, 1986; Wirtz et al., 2007). The list of species was ordered taxonomically (Nelson, 2006), each individual was classified as adult or juvenile according to the length of first maturity (Fishbase), and threat status was checked (IUCN, 2019). All specimens were tagged and stored in 70% ethanol and deposited in the zoological collection ‘MB-Museu Bocage’ of the Museu Nacional de História Natural e da Ciência (MUHNAC, Lisbon, Portugal).

To determine grain size (granulometry), sediment samples were dried and divided with calibrated sieves into size classes, silt (< 0.063 µm), fine sand (0.063 µm ≤ x ≤ 0.250 µm), medium sand (0.250 µm ≤ x ≤ 0.500 µm), coarse sand (0.500 µm ≤ x ≤ 2 mm) and gravel (> 2 mm) and weighted to determine the percentage of each size class (Félix et al., 2017).

Ammonia concentration (µmol.L^{-1}) was determined from water samples through spectrophotometry with a Shimadzu UV-1603 UV-visible spectrophotometer at the wavelength of 630 nm (Koroleff, 1969). Phosphorus concentrations (µmol.L^{-1}) were obtained from the water samples with the aid of the FossTecator FIASTAR 5000 ANALYSER (Murphy and Riley, 1962).

Concentrations of chlorophyll *a* (µg/L) were obtained from water samples through HPLC analysis (High Performance Liquid Chromatography) (Brito et al., 2017). For extraction of pigments, filters were placed in a screw-cap centrifuge tube with 6 mL of 95% cold-buffered methanol (2% ammonium acetate) containing 0.05 mg.L^{-1} trans-β-apo-8'-carotenal (Fluka) as internal standard. The samples were sonicated in an ice-water bath for 5 minutes, placed at -20°C for 30 minutes, and then centrifuged at 4000 rpm for 15 min at 4°C. The supernatants were filtered through Fluoropore PTFE membrane filters (0.2 µM pore size), to clear the extract from remains of filter and cell debris and immediately injected. For separation of pigments, a C18 column was used for reverse phase chromatography (Supelcosil, 0.46 25 cm, 5 mm particles) and an injection volume of 100 µL. The solvent gradient had a flow rate of 0.6 ml.min^{-1} and a run time of 35 min and followed Kraay et al. (1992) adapted by Brotas and Plante-Cuny (1996). The detection limit and quantification procedure of this method followed Mendes et al. (2007). Pigment identification was made from both absorbance spectra and signal retention times in the photodiode array detector (SPD-M20A) or fluorescence detector (RF-10AXL; Ex. 430 nm/Em. 670 nm). The LC-Solution software was used to integrate peaks. For calibration, pigment standards from DHI (Institute for Water and Environment, Denmark) were used. The concentration of the pigments was normalized to the internal standard for correction losses and volume changes (Brito et al., 2017).

Chapter I

Fish diversity in the mangroves of São Tomé Island: influence of mangrove characteristics

3. Fish diversity in the mangroves of São Tomé Island: influence of mangrove characteristics

3.1. Introduction

Measuring community diversity is an important facet of ecology, but there is a large variety of diversity metrics (Boyle et al., 1990), showing the complexity of the topic and that there is no consensus on how to measure diversity. The most commonly used characteristics in the study of species assemblages are species richness, abundance and evenness (MacDonald et al., 2017). The two most frequently used indices that combine these aspects of diversity are the Shannon-Wiener Index and the Simpson Index of Diversity, each with their own restrictions and biases (Kim et al., 2017). Despite the challenges associated with measuring biodiversity, it is broadly accepted that diversity significantly affects ecosystem productivity and resilience (Duffy, 2009; Duffy et al., 2017), incrementing biomass production and the ability to recover from external stressors. Therefore, more diverse communities tend to have higher productivity (Stachowicz et al., 2008) and to be more resilient (Sakschewski et al., 2016).

Estuaries possess favourable conditions for a multitude of marine, freshwater and estuarine fish species (Elliott et al., 2007), providing food and shelter (Sheaves et al., 2014). Most knowledge on estuarine fish assemblages focusses on temperate estuaries, while tropical estuaries remain less studied (Pasquaud et al., 2015). The contrasting characteristics of temperate and tropical estuaries, regarding their environmental conditions and vegetation, stress the need of a better understanding of tropical systems to recognise global diversity patterns. Mangrove trees are characteristic of tropical and subtropical estuaries, creating complex ecosystems that represent vital habitats for many fish species through their complex root systems not found in other estuaries (Nanjo et al., 2014). The importance of mangroves is widely recognized, notably as nursery for fish species (e.g. 2014; Mumby et al., 2004; Nagelkerken et al., 2000; Vidy, 2000). Moreover, mangroves are also important as feeding grounds for fish species from adjacent habitats (Dorenbosch et al., 2005; Lugendo et al., 2007). While the importance of mangroves as food source for fish varies greatly between fish species and life stages (Nagelkerken and Van Der Velde, 2004; Zagars et al., 2013), mangroves are an important food source often increasing fish biomass in comparison with areas without mangroves (Mumby et al., 2004).

Mangroves are important habitats, generally with high fish diversity, but global fish diversity of mangroves is not uniformly distributed, varying at different scales (Blaber, 2007). At the regional level, mangroves in the Indo-West Pacific (IWP) have the highest fish diversity, especially near the Equator (Blaber, 2007), the reason for which is still unclear (Matias and Riginos, 2018). Mangroves of eastern Pacific and Atlantic have lower species richness, the latter having the lowest (Mouillot et al., 2014). At a smaller scale, habitat heterogeneity, hydrological conditions, structure of mangroves, as well as the age of the mangrove system were identified as important factors influencing fish diversity (Castellanos-Galindo et al., 2013; Ikejima et al., 2003; Nanjo et al., 2014; Yeager et al., 2011). Older and larger mangrove forests that offer a broad variety of habitats with stable hydrological conditions seem to promote fish diversity.

Mangrove fish communities are strongly shaped by seasonality. Generally, the onset of the rainy season increases fish abundance, especially of juveniles, and changes species composition in mangroves, showing that seasonal climate cycles have a strong effect on fish communities (Whitfield, 2017). Most of the studies about fish assemblages in mangroves are focused on American (de Azevedo et al., 2016; González-Acosta et al., 2015; MacDonald and Weis, 2013) and Asian mangroves (Ikejima et al., 2003; Mumby et al., 2004; Nanjo et al., 2014), with meagre information on African mangrove fish assemblages, especially on insular mangroves, representing a gap in the knowledge about global mangrove fish diversity (Félix et al., 2017).

Most publications on the ichthyofauna of São Tomé focus on marine species and refer to: i) species lists (Afonso et al., 1999; Vasco-Rodrigues et al., 2016; Wirtz et al., 2007); ii) new species or new records (Fricke, 2007; Kovačić and Schliewen, 2008; Schliewen and Kovacic, 2008); and iii) distribution patterns (Maia, 2018). In fact, mangrove fish communities and habitat usage remain little studied (Cravo, 2021; Félix et al., 2017). As a result, the ecological role of mangroves for fish assemblages remains poorly understood. The volcanic origin of São Tomé, its location close to the equator and the fact that it was never connected to the mainland creates a potential for uniqueness regarding the fish assemblages of its brackish systems (Quimbayo et al., 2019), thus emphasizing the relevance of on-site studies on ecology and system functioning. Besides its ecological importance, the smaller size and consequent greater ease of studying these systems comparing to continental mangroves make Santomean mangroves valuable study sites.

3.2. Objectives

The main objective of this work is to evaluate how environmental conditions affect fish community composition and structure in four Santomean mangroves: Malanza, Angolares, Diogo Nunes and Praia das Conchas (see detailed description in section 1.3). Specific objectives seek to:

- identify major differences in the environmental conditions between mangroves.
- determine taxonomic richness, diversity and composition of the fish communities in STP mangroves.
- Relate fish communities to mangrove environmental conditions.

3.3. Data analysis

Fish communities and environmental conditions were analysed at mangrove level, with sampling events considered as replicates for each mangrove (see details in section 2.2). This approach aimed to maximize detection to improve species richness estimates for each system, as fish sampling in mangroves tends to underestimate richness, due to the of lack of suitable sampling methodologies that are suitable for all micro-habitats, such as root systems of mangrove trees that provide shelter for numerous fish species (Thayer et al., 1987). Environmental data analysis was performed solely for the mangroves of Malanza, Angolares and Diogo Nunes since Praia das Conchas was only sampled once.

To assess the viability of the occupation of the water column by fishes, a binary stratification variable was created based on salinity, temperature, and dissolved oxygen profiles at each sampling point. Stratification was positive when a high variation in temperature, salinity and dissolved oxygen readings was observed, and null otherwise. For the data analysis, a total of 11 environmental parameters were considered (Table 3.1).

Table 3.1 *- Environmental parameters used for data analysis, their unit of measurement and range of values.*

Environmental parameter	Measurement (unit)	Range of measured values
Site depth	Meter (m)	0.05-2.2
Temperature	Degree Celsius (°C)	23.27-30.24
Salinity	Practical Salinity Unit - PSU	0.08-32.94
Stratification	Binary	0 or 1
Percentage of silt	Percentage (%)	0.23-42.97
Percentage of sand	Percentage (%)	20.41-99.13
Percentage of gravel	Percentage (%)	0-78.01
Concentration of Chl *a*	Microgram per litre (µg/L)	0.08-70.58
Concentration of phosphate (PO_4^{3-})	Micromole per litre ($\mu molL^{-1}$)	0.362-5.242
Concentration of ammonia (NH_4)	Micromole per litre ($\mu molL^{-1}$	0-21.112
Mangrove area	Square kilometres (km^2)	0.01-1.52

The abundance of each fish species was classified for each mangrove according to catches and expert opinion, the latter based on the species life-history and knowledge of its ecology (Table 3.2), since there was no standardized capture per unit of effort (cpue). The study of diversity based on this classification allows the distinction between rare and abundant species. A total of five abundance classes were established to reflect the occurrence of each species in the studied mangroves, the abundance classes were numbered in order to reflect the abundance of the species as well as the statistical distance between them *i.e.* abundance classes were not numbered sequentially from 1 to 5 but rather non-sequentially from 1 to 10 so that the statistical distance between abundance classes is larger.

Table 3.2 *– Species abundance classes and criteria for classification, based on sampling data and expert opinion.*

Abundance Class	Abundance Category	Criteria
0	NA	No occurrences in the sampling area.
1	Rare	Captured in a single sampling event.
4	Frequent	Captured more than once but only one or two individuals each time.
7	Abundant	Frequent and abundant but restricted to a particular area of the mangrove.
10	Very abundant	High occurrence and abundance throughout the mangrove.

The abundance classes of the fish species were used for all statistical analysis. Differences in environmental parameters and fish communities between mangroves were tested with a one-way Permutational Analysis of Variance (PERMANOVA) (Anderson, 2001), using sampling locations as units and considering mangrove as a fixed factor with three levels: Malanza, Angolares and Diogo Nunes and making pairwise tests for the factor Mangrove a significance level of 0.05 was considered. The environmental parameters were normalized, and a resemblance matrix was done based on Euclidean distances (Clarke and Gorley, 2006). The fish community data was log (X+1) transformed and the Bray-Curtis similarity coefficient was used to create a resemblance matrix (Clarke et al., 2006). A Similarity Percentages routine (SIMPER) was carried out to identify the environmental variables responsible for the dissimilarity between the mangroves, as well as between sampling sites inside each mangrove. A cut-off value of 90% was established for the SIMPER analysis. A Nonmetric Multi-dimensional Scaling (NMDS) was applied on the environmental data, as well as the community data, to help visualise the similarities and dissimilarities between mangroves. PERMANOVA, NMDS and SIMPER were calculated using PRIMER v6 software (Clarke and Gorley, 2006).

Multiple alpha and beta diversity indices were used to assess different aspects of diversity. Species relative abundance was used to assess the diversity of each mangrove (α-diversity), while the inter-system comparison was based on composition similarity (β-diversity) (Whittaker, 1960). The alpha diversity indices used were the Shannon-Wiener Index (H'), the Simpson Index of Diversity (1-D) and the Taxonomic Distinctness Index (TDI). The beta diversity indices were Pielou's J and the Jaccard similarity.

The H' and 1-D are amongst the most widely used indices in ecology because they provide a synthetic summary of the community's composition and diversity (Oldeland et al., 2010). While H' is strongly influenced by rare species therefore being more sensitive to small changes, 1-D favours more abundant species, thus rare species do not have a great impact on the value of the index (Nagendra, 2002).

Contrary to H' and 1-D, the TDI is independent of sampling effort and is, therefore, a useful tool to compare studies with different sampling efforts (Clarke and Warwick, 1998). The TDI (Delta+) measures taxonomic relatedness through the mean path length of the taxonomic tree of the sample connecting any two individuals given that they belong to different species (Clarke and Warwick, 1998). Delta+ was used to increase comparability between studies, since this index is not dependent on abundances but instead uses species presence/absence data. Additionally the variation in taxonomic distinctness (Lambda) was calculated as the variance among the path lengths connecting all pairs of species (Clarke and Warwick, 2001).

Evenness of species abundance at each site was estimated using Pielou's evenness (J). Pielou's evenness is the observed H' divided by the theoretical maximum H' where every species would be equally abundant, therefore it suffers from the disadvantages of the Shannon-Wiener Index.

The Jaccard similarity (Jaccard, 1912) returns the similarity of two datasets by dividing the number of shared species by the total number of species of the two sets (Jaccard, 1912). Unweighted Pair Group Method with Arithmetic Mean (UPGMA) is a hierarchical clustering method that was applied to the Jaccard Similarity. The UPGMA returns a dendrogram that is built based on the pairwise similarities given by a similarity matrix, in this case the similarity matrix of the species composition of the mangroves. The dendrogram given by the UPGMA helps visualise the overall similarity of the mangroves and see the relationship between them.

3.4. Results

3.4.1. Environmental data

Environmental conditions varied between and within the mangroves, evidencing the variability of these coastal systems (Table 3.3). Sand was the dominant sediment size class in all mangroves, but other sediment size classes were also important in Malanza, Angolares and Praia das Conchas (Figure A.4, Figure A.5, Figure A.6). In all sites except A5 and PC2, sand made up over 50 percent of the sediment. The highest proportions of sand were mostly found at the more downstream areas of the mangroves. Gravel and silt were more common in the upstream area of Malanza, while silt concentration was higher at the sites A3, A4, and A5 of Angolares, being dominant in the latter. In

Diogo Nunes, substrate composition remained relatively similar between sampling sites, sand being the dominant grain size followed by silt, and gravel always having less than 1 %. At Praia das Conchas sand was the dominant size class both at PC1 and PC3 while at PC2 gravel was the dominant size class, at site PC3 silt also had a high contribution to the granulometry.

Sites within each mangrove had a similar range of water temperatures, especially the larger systems. These also presented lower temperatures (23-26 °C), while Diogo Nunes and Praia das Conchas had higher temperatures (25-27 °C) (Figure A.1). The overall salinity of Malanza was higher, over 20 PSU in almost all sites, than that of the other mangroves, below 10 PSU at most sites (Figure A.2). Stratification was observed in Malanza and in Angolares but not in Diogo Nunes and Praia das Conchas. While site depth varied greatly within mangroves, largest depths were registered in Malanza, followed by Angolares. Diogo Nunes and Praia das Conchas were by far the shallowest mangroves. Generally, temperature was lower in the upstream areas (Figure A.1). In Malanza temperatures varied little between sampling rounds showing the greatest stability among all mangroves. In Angolares, temperature was much higher in the northern part of the mangrove system during Round 1, showing differences of up to 5 °C, while values were much more homogeneous during Round 3, having maximum differences of 2 °C between sites. In Diogo Nunes, temperature was highly variable due to the intertidal nature of the mangrove. Highest temperatures, of approximately 30°C, were registered at site DN2. The highest salinity values were observed in the most downstream area of the Malanza mangrove system, reaching 32, where tidal influence was highest. At Jalé, site M1, there were also high values of salinity of up to 28 PSU, attributable to oceanic intrusion by percolation. In Angolares, salinity increased from Round 1 to the two subsequent rounds, due to a rupture of the sand-barrier that isolated the mangrove from the sea (Figure A.2). Salinity was rather variable at Diogo Nunes, reaching the highest value (24 PSU) at site DN2 during the first round.

Primary production was very variable, being highest in Malanza and lowest in Diogo Nunes (Figure A.3). Due to technical constraints during the field operations the Chl *a* samples could not be processed for site M5, during the first sampling round, and from sites A1 and A6, during the second sampling round. The highest Chl *a* concentration, up to 70 µg/L, was observed at Jalé, site M1, in Malanza, during the first round, but it is an outlier that might be due to contamination from the sediment, since this is a shallow area. Chl *a* decreased towards downstream areas. At Angolares, Chl *a* reached the highest concentrations during Round 1 in the north arm and was highest in the downstream area. In Diogo Nunes, Chl *a* concentration was consistent throughout all three rounds except for sampling site DN2 during the third round where Chl *a* reached concentrations of 7.24 µg/L.

***Table 3.3**- Mean values (± Standard deviation) of each environmental parameter, for each sampling station of the mangroves Angolares, Diogo Nunes, Malanza and Praia das Conchas (only one sampling occasion). Percentage of Silt (%), Sand (%) and Gravel (%) was obtained from a single sampling occasion.*

Site	*Site*	*Site Depth (m)*	*Mangrove area (Km^2)*	*Silt (%)*	*Sand (%)*	*Gravel (%)*	*Temperature (°C)*	*Salinity (PSU)*	*Ammonia (µmol N /L)*	*Phosphate (µmol P /L)*	*Chl a (µg/L)*
Praia das Conchas	PC1	0.2	0.01	0.23	98.17	1.60	27.49	0.20	4.04±1.94	3.74±0.29	1.22
	PC2	0.2		1.44	47.96	50.60	27.44	0.18	2.51±0.64	4.07±0.64	1.55
	PC3	0.2		19.17	79.71	0.58	27.10	0.18	1.85±1.10	5.24±0.68	0.93
Diogo Nunes	DN1	0.18±0.16	0.01	7.62	91.85	0.53	25.98±1.05	5.44±5.75	0.50±0.67	1.80±0.90	0.36±0.20
	DN2	0.20±0.21		10.43	89.54	0.03	27.57±2.00	9.09±7.20	1.11±1.53	1.57±0.81	3.29±2.83
	DN3	0.47±0.11		10.46	89.47	0.07	26.33±1. 62	6.01±7.26	1.19±1.65	1.56±0.27	0.60±0.38
	DN4	0.16±0.16		6.02	93.83	0.15	25.94±1.47	1.50±3.04	0.50±0.67	1.65±0.36	0.27±0.07
Angolares	A1	0.40±0.17	0.13	0.87	99.13	0.00	25.23±0.76	23.51±5.76	7.05±9.94	0.56±0.38	1.74±0.67
	A2	0.86±0.40		1.20	98.80	0.00	24.50±0.54	7.44±7.33	0.01±0.01	1.37±0.23	3.47±3.80
	A3	1.32±0.43		37.10	53.78	9.12	24.24±0.45	3.67±3.97	0.01±0.01	1.64±0.19	2.24±2.28
	A4	0.94±0.48		28.99	66.78	4.23	23.98±0.46	1.47±0.14	0.01±0.01	1.80±0.26	1.75±1.49
	A5	0.61±0.25		1.58	20.41	78.01	23.64±0.29	0.67±0.29	0.01±0.01	1.82±0.51	0.95±0.35
	A6	1.02±0.43		4.15	95.76	0.09	24.67±0.76	20.21±6.95	3.43±4.82	1.59±0.36	1.30±0.09
Malanza	M1	0.10±0.6	1.52	42.70	55.42	1.88	26.81±1.15	21.69±6.58	4.23±3.34	1.60±0.39	53.44±12.12
	M2	0.5±0.0		1.04	98.96	0.00	26.28±0.95	29.30±1.34	0.43±0.60	1.68±1.32	0.78±0
	M3	1.06±0.43		12.00	85.17	2.83	25.67±0.65	27.48±2.68	0.48±0.73	0.64±0.14	1.07±0.28
	M4	1.37±0.20		7.56	85.45	6.98	25.46±0.60	25.70±1.92	1.05±0.97	0.86±0.10	1.26±0.22
	M5	1.02±0.29		21.22	61.11	17.67	25.40±1.55	22.01±3.50	0.38±0.52	0.72±0.25	3.39±0.69
	M6	0.24±0.22		18.23	56.28	25.49	24.53±0.21	9.99±3.18	0.17±0.22	1.42±0.58	3.20±0.84
	M7	0.11±0.09		19.74	64.98	15.28	24.02±0.27	0.40±0.12	2.78±1.98	0.63±0.19	5.07±5.04

The NMDS based on the environmental data matrix (stress of 0.17) groups Diogo Nunes samples close together in a single closely related group (Figure 3.1). The sites from Malanza are distributed in three groups, one formed by M1, a shallow area with saltwater intrusion, another by M6 and M7, shallow areas at the border of the mangrove, and the other by M2, M3, M4 and M5, sites in the deeper central part of the mangrove. This latter group shows features similar to Angolares (A1, A2, A3, A4 and A6), except for the uppermost sampling station (A5) which is isolated form other sampling locations. Although, in general, the environmental traits of Angolares are closely related to those of Malanza, the former depicts a high temporal variability, and a higher spatial heterogeneity, when compared to Malanza and Diogo Nunes. Samples from the same site tend to group closely together, especially for Malanza and Diogo Nunes, indicating temporal stability of the environmental conditions over sampling rounds, in Angolares this pattern is not observed, except for site A5.

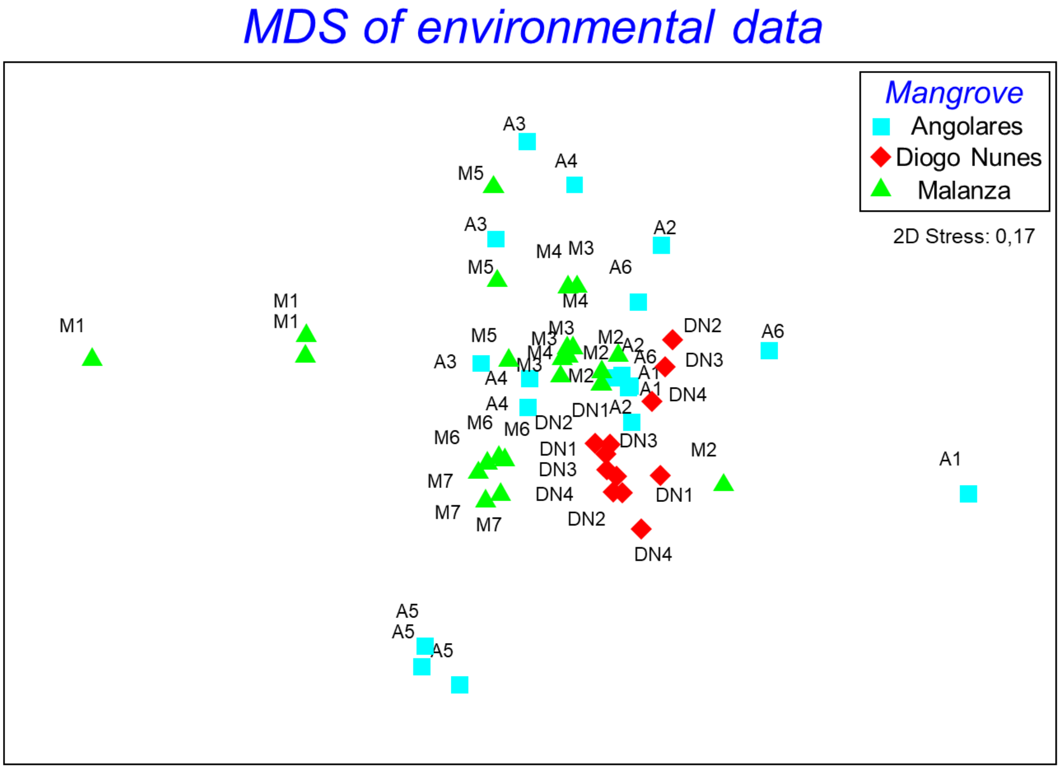

Figure 3.1 - NMDS of the replicated sampling sites according to environmental parameters. Colour and shape distinguish the mangroves. Each point represents a sample, in which the letter represents the mangrove in which the measurement was done, the number represents the sampling point at which the environmental parameter were taken.

The overall and pairwise PERMANOVA tests both indicated significant differences between the environmental parameters of the three mangroves (Table 3.4, Table 3.5).

Table 3.4 - Result of the PERMANOVA test of the environmental parameters for the Malanza, Angolares and Diogo Nunes mangroves.

Source	df	SS	MS	p-value	Unique perms
Mangrove	2	82.948	41.474	0.0001	9918
Residuals	23	192.05	8.3501		
Total	25	275			

Table 3.5 *- Results of the Pairwise PERMANOVA of the environmental parameters for the Malanza, the Angolares and the Diogo Nunes mangroves.*

Groups	t	p-value	Unique perms
Malanza, Angolares	1.9793	0.0016	9695
Malanza, Diogo Nunes	2.5553	0.0003	5940
Angolares, Diogo Nunes	2.1938	0.0012	1285

SIMPER showed that area, stratification and ammonia concentration were the most important variables to distinguish Malanza and Angolares: The first and third having higher values in Malanza, while the second had the highest values in Angolares (Table 3.6).

Salinity, area and phosphate concentration contributed the most for the dissimilarities between Malanza and Diogo Nunes (Table 3.7). The average salinity and area in Malanza were higher than those in Diogo Nunes whilst the phosphate concentration was higher in Diogo Nunes.

The variables that explained most dissimilarities between Angolares and Diogo Nunes were salinity, depth, percentage of gravel, stratification and temperature (Table 3.8). Salinity, depth, percentage of gravel and stratification were higher or more common in Angolares while the temperatures recorded for Diogo Nunes were higher.

Table 3.6 *- Average squared distance of the variables between the sites of the Malanza and the Angolares mangroves and the percentual contribution of the variables to the overall distance between systems resulting of the SIMPER analysis (cut-off 90 %). The average squared distance between Malanza and Angolares was 23.62*

Malanza X Angolares

Variable	Av. Value Malanza	Av. Value Angolares	Contribution %	Cumulative %
Area	0.979	-0.916	15.2	15.2
Stratification	-0.179	0.627	11.47	26.67
NH4	9.82E-02	6.33E-03	10.73	37.4
Sand	9.28E-03	-0.445	9.6	47
Gravel	6.30E-02	0.398	9.45	56.45
Silt	-1.75E-02	0.406	9.36	65.82
PO4	-0.635	0.583	9.13	74.95
Chl *a*	0.346	-0.325	9.04	83.98
Site Depth	-2.06E-02	0.641	8.15	92.14

Table 3.7 *- Average squared distance of the variables between the sites of the Malanza and the Diogo Nunes mangroves and the percentual contribution of the variables to the overall distance between systems resulting of the SIMPER analysis (cut-off 90 %). The average squared distance between Malanza and Diogo Nunes was 26.00*

Malanza X Diogo Nunes				
Variable	**Av. Value Malanza**	**Av. Value Diogo Nunes**	**Contribution %**	**Cumulative %**
Salinity	0.393	-1.75	21.46	21.46
Area	0.979	-1.08	16.3	37.77
PO4	-0.635	0.718	14.02	51.78
Temperature	9.14E-02	-0.166	8.83	60.61
Chl *a*	0.346	-0.38	8.5	69.11
Site Depth	-2.06E-02	-0.971	7.39	76.49
Silt	-1.75E-02	-0.604	5.63	82.12
Gravel	6.30E-02	-0.801	5.57	87.69
Sand	9.28E-03	0.687	5.28	92.97

Table 3.8 *- Average squared distance of the variables between the sites of the Angolares and the Diogo Nunes mangroves and the percentage contribution of the variables to the overall distance between systems resulting of the SIMPER analysis (cut-off 90 %). The average squared distance between Angolares and Diogo Nunes as 25.63*

Angolares X Diogo Nunes				
Variable	**Av. Value Angolares**	**Av. Value Diogo Nunes**	**Contribution %**	**Cumulative %**
Salinity	0.454	-1.75	22.83	22.83
Site Depth	0.641	-0.971	13.67	36.5
Gravel	0.398	-0.801	11.3	47.8
Stratification	0.627	-0.537	10.68	58.48
Temperature	-4.45E-02	-0.166	10.45	68.93
Sand	-0.445	0.687	9.61	78.54
Silt	0.406	-0.604	7.64	86.18
NH4	6.33E-03	-0.265	7.44	93.63

SIMPER analysis showed that the two most similar mangroves were Malanza and Angolares (average squared distance of 23.62), complementing the results of the PERMANOVA, while the least similar were Malanza and Diogo Nunes (average squared distance of 26.00).

The highest homogeneity in water parameters at the mangrove level was obtained for the Diogo Nunes mangrove (average squared distance of 5.15), while the highest heterogeneity was observed in Angolares (average squared distance of 9.79) (Table 3.9, Table 3.11). According to the SIMPER, the granulometric features were the parameters common to both larger mangroves (Malanza and Angolares) with a high percentage of contribution to the dissimilarity between sampling sites inside each mangrove, a feature not relevant in the much smaller Diogo Nunes mangrove. At Malanza, variations in Chl *a* concentration and site depth, along with the granulometric features, were also responsible for largest part of the dissimilarity between sampling sites (>10%) (Table 3.9). Chl *a* concentration had the highest contribution in Malanza, probably due to the extremely high value obtained for the M1 sampling point. At Angolares, water characteristics such as ammonia concentration, stratification and temperature along with the granulometric features, were the most important. In Diogo Nunes, differences in sampling sites were promoted by its water characteristics, temperature, phosphate concentration and salinity (Table 3.11).

Table 3.9 *- Average value and squared distance of the variables between sites of the Malanza mangrove and their percentage contribution to the overall distance between sites resulting of the SIMPER analysis (cut-off 90 %). The average squared distance between the sampling sites of the Malanza mangrove was 8.58*

Malanza				
Variable	**Av. Value**	**Av. Sq. Distance**	**Contribution %**	**Cumulative%**
Chl *a*	0.346	1.82	21.22	21.22
Silt	-1.75E-02	1.21	14.1	35.32
Sand	9.28E-03	0.985	11.49	46.81
Site Depth (cm)	-2.06E-02	0.887	10.34	57.15
NH4	9.82E-02	0.853	9.95	67.1
Stratification	-0.179	0.764	8.91	76.01
Gravel	6.30E-02	0.755	8.81	84.82
Temperature	9.14E-02	0.7	8.16	92.98

Table 3.10 *- Average value and squared distance of the variables between sites of the Angolares mangrove and their percentage contribution to the overall distance between sites resulting of the SIMPER analysis (cut-off 90 %). The average squared distance between the sites of the Angolares mangrove was 9.79*

Angolares				
Variable	**Av. Value**	**Av. Sq. Distance**	**Contribution%**	**Cumulative %**
NH4	6.33E-03	1.99	20.3	20.3
Gravel	0.398	1.63	16.62	36.92
Stratification	0.627	1.55	15.81	52.73
Sand	-0.445	1.32	13.44	66.17
Temperature	-4.45E-02	1.2	12.3	78.47
Silt	0.406	1.05	10.69	89.16
Site Depth (cm)	0.641	0.766	7.82	96.98

Table 3.11 *- Average value and squared distance of the variables between sites of the Diogo Nunes mangrove and their percentage contribution to the overall distance between sites resulting of the SIMPER analysis (cut-off 90 %). The average squared distance between the sampling sites of the Diogo Nunes mangrove was 5.15*

Diogo Nunes				
Variable	**Av. Value**	**Av. Sq. Distance**	**Contribution %**	**Cumulative %**
Temperature	-0.166	1.98	38.42	38.42
PO4	0.718	1.69	32.82	71.24
Salinity	-1.75	1.13	21.92	93.16

3.4.2. Community data

A total of 22 species were recorded in the four mangroves and during all sampling rounds (Table 3.12). These belonged to 19 genera and 14 families. The highest mangrove species richness was 18 in Malanza, followed by 11 in Diogo Nunes, and 10 in Angolares. The lowest species richness was observed in Praia das Conchas, where only *Oreochromis mossambicus* was recorded. *Parachelon grandisquamis, Periophthalmus barbarus* and *O. mossambicus* were the species with the highest overall abundance.

Table 3.12 *– List of species captured in São Tomé mangroves, with the indication of their abundance class and life stage at capture. Four abundance classes were established, abundance class 10 is for very abundant species, class 7 is for abundant species, class 4 is for frequent, abundance class 1 is for rare species and 0 is given when the species was not caught in the mangrove. The life stage refers to the species reproductive stage at capture, based on size at first maturity: (J) as juvenile or (A) adult. For some species this trait was not possible to determine (NA) due to inexistent maturity data on the species.*

Species	**Abundance Class**				**Life stage**
	Praia das Conchas	**Diogo Nunes**	**Angolares**	**Malanza**	
Abudefduf saxatilis (Linnaeus, 1758)	0	0	0	4	NA
Abudefduf taurus (Müller & Troschel, 1848)	0	0	0	4	NA
Bathygobius casamancus (Rochebrune, 1880)	0	4	0	1	A
Bathygobius soporator (Valenciennes, 1837)	0	7	0	4	A
Caranx latus Agassiz, 1831	0	1	0	4	J
Cephalopholis nigri (Günther, 1859)	0	0	0	1	NA
Eleotris annobonensis Blanc, Cadenat & Stauch, 1968	0	10	0	4	A
Eleotris vittata Duméril, 1861	0	7	4	0	A
Epinephelus aeneus (Geoffroy Saint-Hilaire, 1817)	0	0	0	4	J
Ethmalosa fimbriata (Bowdich, 1825)	0	0	7	0	A
Eucinostomus melanopterus (Bleeker, 1863)	0	0	4	7	J, A
Gymnothorax mareei Poll, 1953	0	1	0	0	J
Lutjanus goreensis (Valenciennes, 1830)	0	7	4	7	J, A
Megalops atlanticus Valenciennes, 1847	0	0	0	1	J
Monodactylus sebae (Cuvier, 1829)	0	0	10	10	J, A
Mugil bananensis (Pellegrin, 1927)	0	10	10	10	J
Oreochromis mossambicus (Peters, 1852)	7	0	10	10	J, A
Parachelon grandisquamis (Valenciennes, 1836)	0	7	10	10	J, A
Periophthalmus barbarus (Linnaeus, 1766)	0	10	10	10	J, A
Plectorhinchus macrolepis (Boulenger, 1899)	0	0	7	0	A
Pomadasys jubelini (Cuvier, 1830)	0	0	7	4	J, A
Stegastes imbricatus Jenyns, 1840	0	0	0	4	NA

One third of the species caught in Malanza included both adult and juvenile individuals. In Angolares, about half of the species were represented only by adult individuals, while at Diogo Nunes, almost half of the species were represented only by juvenile individuals. At Praia das Conchas, the life stage of the only observed species could not be determined (Figure 3.2).

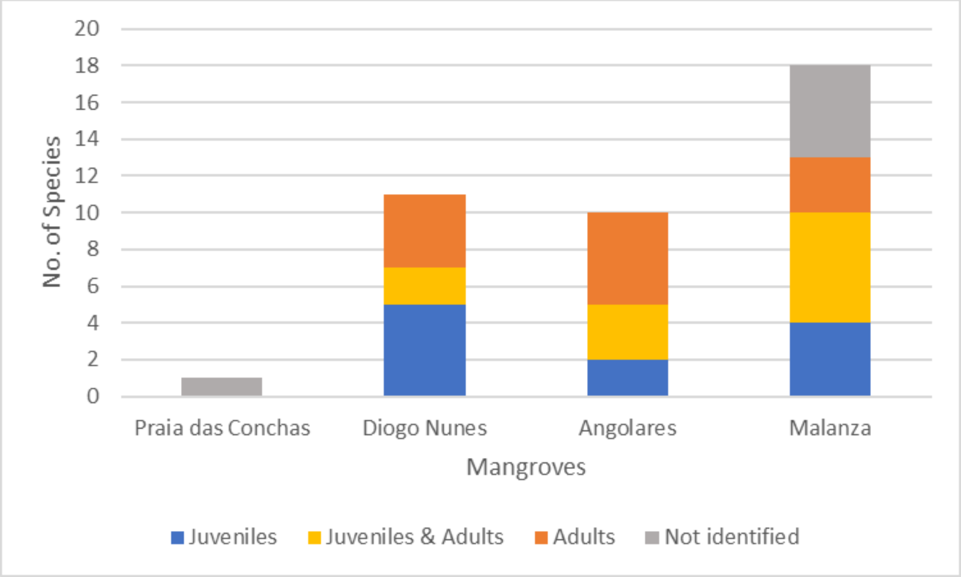

Figure 3.2 *- Number of fish species caught in each mangrove, classified by life stage, with species only captured as juveniles, species captured only as adults, species captured in both stages and species for which the life stage couldn't be determined*

3.4.3. Diversity indices

The highest diversity was obtained for Malanza, using both H' (2.71) and 1-D (0.93). Both diversity indices returned only slightly lower values for Angolares (2.24 and 0.89, respectively) and Diogo Nunes (2.25 and 0.89, respectively). The highest evenness value was obtained for Angolares (0.97), closely followed by Diogo Nunes (0.94) and Malanza (0.94) (Table 3.13).

The highest average taxonomic distinctness (Delta+) was obtained for Angolares and the lowest value was calculated for the Malanza system. The highest variation in taxonomic distinctness (Lambda), was observed in the Diogo Nunes mangrove while the lowest value was obtained for the Malanza mangrove (Table 3.13).

Table 3.13 - Result of the various diversity indices of the fish assemblages in the studied mangroves. As Praia das Conchas only had one species various indices could not be calculated.

	H'	**1-D**	**Pielou's evenness**	**Delta+**	**Lambda**
Praia das Conchas	0.00	0.00	NaN	NaN	NaN
Diogo Nunes	2.25	0.89	0.94	70.36	600.43
Angolares	2.24	0.89	0.97	74.11	438.44
Malanza	2.71	0.93	0.94	62.04	268.26

3.4.4. Comparison of assemblage structure

The pairwise PERMANOVA test (Table 3.15) indicates that the Malanza fish community was significantly different from that of Angolares and Diogo Nunes. However, no significant differences were found between the latter.

Table 3.14 - Result of the PERMANOVA for the fish community abundance data of the studied mangroves.

Source	df	SS	MS	p-value	Unique perms
Mangrove	2	12217	6108.4	0.0019	9908
Residues	23	51928	2257.7		
Total	25	64145			

Table 3.15 *- Results of the Pairwise PERMANOVA for the fish community abundance data, comparing Malanza, Angolares and Diogo Nunes mangroves in 2017*

Groups	pseudo-t	p-value	Unique perms
Malanza, Angolares	2.0598	0.0028	627
Malanza, Diogo Nunes	1.7811	0.0126	7989
Angolares, Diogo Nunes	1.2008	0.1932	5033

According to the Jaccard Similarity (Table 3.16 & Figure 3.3), Malanza and Diogo Nunes had the most similar fish communities, followed by Malanza and Angolares, while Praia das Conchas and Angolares were completely dissimilar.

Table 3.16 *- Similarity matrix of the fish communities between each pair of mangroves according to the Jaccard similarity index.*

	Praia das Cocnhas	Diogo Nunes	Angolares
Praia das Conchas			
Diogo Nunes	0.09		
Angolares	0.00	0.31	
Malanza	0.06	0.45	0.33

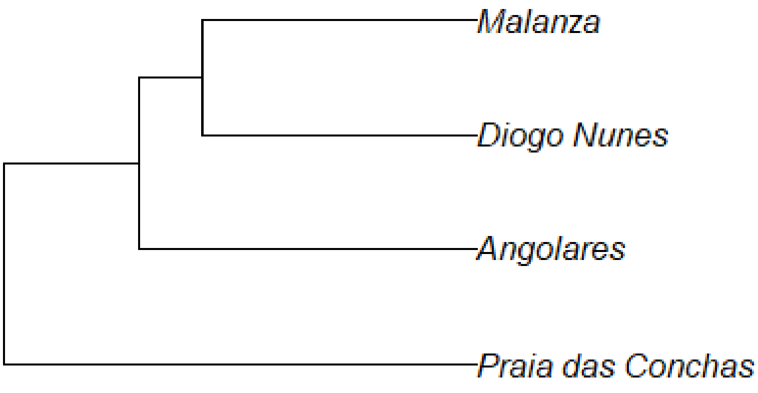

Figure 3.3 *- UPGMA dendrogram of the pairwise similarities returned by the Jaccard similarity matrix.*

3.4.5. Discussion

Mangrove environmental conditions played a central role in determining community composition and structure, which is in line with findings on multiple mangrove fish assemblages in the tropical Eastern Pacific (Castellanos-Galindo et al., 2013). The studied mangroves had differing environmental conditions. Malanza had three areas with different sets of environmental conditions that were consistent over sampling rounds, differentiating it from the other mangroves. The environmental conditions of Angolares were not consistent over time and varied greatly, especially due to the sudden opening of the sand barrier to the sea, a dynamic feature that creates a highly variable environment, typical of enclosed lagoons (Félix et al., 2013), which is natural and periodic in Angolares. In Diogo Nunes environmental conditions showed low spatial and temporal variations but, due to technical constrains, sampling was only possible during low tides. Thus, the results must be interpreted considering this constraint, which show that this mangrove has a narrow but stable environment during low tide. These results are in line with the findings for other mangroves in the country (Cravo, 2021) and in other regions (e.g. McGregor and Strydom, 2018), that reported environmental heterogeneity between areas of a mangrove while there was a overlap between areas of different mangroves. Species richness differed considerably between the studied mangroves. Malanza had the highest richness and Praia das Conchas the lowest; Angolares and Diogo Nunes presented similar richness and diversity, despite their contrasting size and dynamics. Mangrove size, spatial heterogeneity of environmental conditions and its temporal stability seem to favour species richness and diversity in the studied mangroves. These results match those of other authors that reported an increase in fish richness and diversity in more heterogeneous habitats (Yeager et al., 2011).

The species richness observed in the mangroves of São Tomé Island, especially in Malanza, is similar to that found in other insular mangroves of similar size in the Caribbean (Jaxion-Harm and Speight, 2012; Nagelkerken et al., 2010, 2000; Nagelkerken and Faunce, 2008; Vaslet et al., 2012), Taiwan (Lin and Shao, 1999), Japan (Nanjo et al., 2014) and east African islands (Dorenbosch et al., 2005) as well as to continental mangroves with a similar size (El-regal and Ibrahim, 2014; Koranteng et al., 2000; McGregor and Strydom, 2018; Zagars et al., 2013). The richness found between Angolares and Diogo Nunes was very similar, despite their size differences, and it was also similar to the richness found in other small mangroves on the nearby Príncipe Island (Cravo, 2021). However, the richness in Diogo Nunes is potentially underestimated, as the average number of species using this system might be higher during high tide. On the other hand, despite the relative larger size of Angolares, the high variability of its environmental conditions limits the number of species' occurrences, while in Diogo Nunes the reduced size was compensated by a more stable set of environmental conditions. In general, the richness found in the mangroves of São Tomé is lower than that of much larger mangrove systems in the nearby African mainland (Baran, 2000; Ekpo et al., 2014; Simier et al., 2006; Vidy, 2000). This can be explained by the smaller size (Pasquaud et al., 2015; Vasconcelos et al., 2015) and lower number of freshwater fish species in insular mangroves (Blaber, 2000; Lévêque et al., 2008), since many freshwater species migrate into brackish systems during a part of their life cycle and some of the mangroves have freshwater.

Malanza was the most diverse mangrove, according to both diversity indices (Shannon-Wiener and Simpson Diversity). However, these differences in diversity between mangroves were minimal. The higher diversity of Malanza in comparison to the other studied mangroves is assured by its heterogeneity. The high environmental stress in Angolares, induced by its periodic isolation from the sea, plays a significant role in lowering its species richness and diversity. Enclosed brackish systems show a typical dominance of a reduced number of tolerant species from different *taxa* (Pedro

M. Félix et al., 2013) The higher evenness of species abundances in Angolares when compared to Diogo Nunes is the reason for higher diversity values in Angolares despite having a lower species richness. The presence of some rare marine species is increasing the richness and diversity of fish assemblage in Diogo Nunes, but it is reducing its evenness, this might be a consequence of the sampling that did not occur during the high tide, when the presence of marine species would be more likely to occur, which would increase the richness and evenness of the mangroves fish community.

Taxonomic distinctness is seldom used to deal with fish assemblages in transitional waters (*e.g.* Collie et al., 2008; Miranda et al., 2005; Mouillot et al., 2005). The few existing studies were conducted in large continental lagoons (Miranda et al., 2005; Mouillot et al., 2005) and in a continental estuary (Collie et al., 2008), both of which had slightly higher taxonomic distinctness than the mangroves of São Tomé. The value of Angolares is the closest to the values observed in those studies. Despite the differences in sampling techniques that hamper comparisons, it still helps contextualizing the state of Santomean mangroves in a more global context. The variability of environmental conditions in Angolares and Diogo Nunes, creating different niches due to temporal changes (i.e. sand barrier overflow and tidal cycle, respectively), might increase the taxonomic distinctness, due to the occasional presence of species from different taxonomic groups. However, the dominance of tolerant species that belong to different families in Angolares, 10 species from 8 families, and the absence of rare species, *i.e.* with abundance class 1, explains why this system had the highest taxonomic distinctness. In Malanza, the higher diversity of environmental conditions provided the conditions for a community to establish where different taxa are evenly represented, at the mangrove level, resulting in an even taxonomic tree and a lower variation in taxonomic distinctness because the different families were similarly abundant.

The occurrence of juveniles of marine migrant species, such as *Caranx latus* (Whitehead et al., 1989b) and *Epiphenelus aeneus* (Heemstra and Randall, 1993) suggests that these systems are used as nursery grounds. The mangroves are also used as opportunistic feeding grounds as shown by the presence of marine stragglers, such as *Megalops atlanticus*. The species that use the system throughout the whole year are species that mature in the mangroves, *e.g. Monodactylus sebae* (Whitfield, 2005) or species that inhabit mangroves, although not exclusively, throughout their whole life, *e.g. Periophthalmus barbarus* (Etim et al., 2002).

Our findings support the idea that larger mangroves with a variety of niches and more stable conditions support more diverse fish assemblages. The almost total absence of freshwater species in the mangroves confirms the pattern of a low richness of freshwater fish species on islands (Lévêque et al., 2008). The presence of juveniles of marine species highlights the usage of mangroves as nursery and feeding grounds for a variety of fishes. This is one of the first studies on mangrove fish diversity on São Tomé and islands in the east Atlantic and should serve as basis for future research and management decisions of insular mangroves. It highlights the importance of these systems for different ecological guilds of marine and estuarine fish species, supporting a complex biological network, even in the small Santomean mangroves. Management measures that favour habitat complexity and spatial heterogeneity are beneficial for the fish communities.

Chapter II

Functional diversity and redundancy of the fish assemblages

4. Functional diversity and redundancy of the fish assemblages

4.1. Introduction

Identifying the ecological functions of species within communities is a main concern for ecologists, since they are crucial to understand how ecosystems work. In the last decades, the idea of classifying or grouping species according to their function within communities has gained importance, and it was made possible by the development of tools to assess functional diversity (Petchey et al., 2009). In the early stages, species were grouped into ecological guilds, according to how they exploit the available resources (Root, 1967). While no clear definition of functional diversity has been developed, it is often described as the “range and value of those species and organismal traits that influence ecosystem functioning” (Petchey and Gaston, 2006; Tilman, 2001). Functional diversity has some advantages over taxonomic diversity indices, namely by providing a link to assess ecosystem functioning (Tilman, 2001; Van Der Linden et al., 2016). It also provides valuable information on species-environment relationships, such as productivity, resilience to perturbation and the regulation of matter flux (Villéger et al., 2008).

While a sort of agreement has been reached on the definition of functional diversity, its measurement remains controversial, and various indices have been developed in recent years (Teichert et al., 2018; Van Der Linden et al., 2016). This variety of indices to measure the same facet of diversity is a drawback, as it reflects the uncertainty of how functional diversity should be measured. Another difficulty in measuring functional diversity is related to the identification of which species traits are important for ecosystem functioning (Petchey et al., 2009). The definition of categories within traits is also complicated, especially when working with continuous traits, since the decision of when a species stops belonging to one category and belongs to another is, in most cases, subjective and arbitrary (Petchey et al., 2009)

In this context, the concept of functional redundancy appeared as an important complement to functional diversity. Rather than measuring the number of functions of a system, functional redundancy refers to the extent to which different species perform similar functions (Loreau, 2004; Micheli and Halpern, 2005; Rosenfeld, 2002). Higher degrees of functional redundancy are believed to assure ecosystem function, increasing resilience in the case of species loss (Camilo et al., 2018). As functional redundancy is calculated from the data established for the functional diversity, it is also affected by some of the same drawbacks, namely by the difficulty in defining which and how many traits are relevant to the ecosystem functioning. A challenge in the interpretation of functional redundancy is the identification of its origin. Functional redundancy might be high in a pristine system because it is species-rich, but also in a disturbed system because some functional groups of species were eliminated and groups with similar functions dominate (Van Der Linden et al., 2016). Nevertheless, functional redundancy can be a useful tool in identifying how susceptible a system is to disturbance, since low redundancy translates into higher vulnerability. Thus, it is especially useful in combination with functional diversity, as it is possible to identify what are the functions at risk and what preventive actions can be taken.

The identification of ecosystem vulnerability to disturbance is key for management, especially when working with systems at high risk of species loss, such as islands (Kier et al., 2009). The mangroves of São Tomé Island are in general heavily impacted by a variety of anthropogenic pressures such as logging, fishing and clearance for construction and agriculture, among many others (Afonso, 2019). These disturbances threaten mangrove fish populations, and therefore ecosystem functioning. The characterization of the functional diversity and redundancy of these fish communities will allow a better understanding of mangrove vulnerability.

Despite the insight that functional diversity gives on community functioning, its use in animal ecology is poorly developed in comparison to plant ecology (Blaum et al., 2011). While some work has been done on fish functional diversity (e.g. Halpern and Floeter, 2008; Pool et al., 2010; Stuart-Smith et al., 2013; Villéger et al., 2010; Wiedmann et al., 2014; Teichert et al., 2017a) few studies have applied it to mangrove fish communities when compared to other tropical estuaries and coastal lagoons (Dolbeth et al., 2016; Miranda et al., 2005; Mouillot et al., 2007; Silva-Júnior et al., 2016).

4.2. Objectives

The objective of this study was to explore the usage of multiple functional diversity indices to compare the functional diversity and redundancy of fish communities in different mangroves in São Tomé Island, to evaluate their potential vulnerability. Additionally, functional indices are compared to taxonomic indices calculated in the previous chapter, to assess management implications.

4.3. Methods

The data needed to estimate functional diversity and redundancy, as well as the environmental characteristics of the mangroves are presented in section 3.

4.3.1. Trait Selection and Assessment

Trait selection is an important step when evaluating the functional diversity of a community. A trait is a characteristic of the organism that influences the ecosystem processes (Petchey and Gaston, 2006). For the present study, five traits were identified and assessed for each species based on the literature: Ecological Guild, Vertical Distribution Guild, Substratum Preference Guild, Feeding Guild and Reproductive Guild (Table 4.1).

***Table 4.1** – Mangrove fish species traits. Categories are listed and described for each trait type. Trait relevance is also explained for each trait type.*

Trait	Category	Description	Relevance
Ecological Guild	Marine Stragglers (MS)	Marine species that appear occasionally in the mangrove	The ecological guild relates to the transport of nutrients and biomass between ecosystems and their productivity (Elliott and Dewailly, 1995; Koutsidi et al., 2016; Törnroos and Bonsdorff, 2012; Whitfield, 2005)
	Marine Migrant (MM)	Marine species that enter the mangrove at a specific point of their life cycle	
	Estuarine Residents (ES)	Complete their life cycle in the mangrove	
	Freshwater (FW)	Freshwater species that are occasionally found in the mangrove	
Vertical Distribution Guild	Benthic (B)	Lives directly over the substrate	The position in the water column is critical to determine the ecological niche and the vertical transference of nutrients and reflects if fish use the whole water column (Elliott and Dewailly, 1995; Koutsidi et al., 2016; Mouillot et al., 2014)
	Demersal (D)	Lives in the water column but has some level of dependency on the substrate	
	Pelagic (P)	Lives solely in the water column	
Substrate Preference	Sandy (S)	Lives predominantly on sandy substrates	Substrate Preference reflects habitat availability and usage as well as feeding habits (Elliott and Dewailly, 1995; Koutsidi et al., 2016; Stuart-Smith et al., 2013)
	Soft (F)	Lives on mobile substrates (sand, silt and/or fine gravel)	
	Rough (R)	Lives on hard substrates (rocks, stones and/or pebbles)	
	Mixed (M)	It has no clear preference for substrate type	
	Vegetation (V)	Lives mostly on vegetation	
Feeding Guild	Strict planktivorous (PS)	Filters plankton from the water column	The Feeding Guild reflects the position of the species in the trophic web and how the species use the habitat regarding the resource

	Feeding strictly on invertebrates (IS)	Preys exclusively on macroinvertebrates	availability (Elliott and Dewailly, 1995; Halpern and Floeter, 2008; Henriques et al., 2017; Mouillot et al., 2014; Poff and Allan, 2016; Stuart-Smith et al., 2013; Teichert et al., 2017a)
	Strict piscivorous (FS)	Preys exclusively on other fish	
	Feeding on invertebrates and fish (IF)	Feeds on other fish and macroinvertebrates	
	Other Carnivorous (CS)	Feeds on other animals, but does not match categories above, *e.g.* species feeding on invertebrates and plankton but not other fish	
	Partly carnivorous, partly herbivorous but not omnivorous (HC)	Species specialized on certain food items of animal and vegetable origin, but not being omnivorous	
	Omnivorous (OV)	Generalist feeders	
	Strictly herbivorous (VS)	Feeds on macroalgae and/or plants	
Reproductive Guild	Ovoviviparous (W)	Free-living progeny, first enclosed in eggs	The Reproductive Guild is related to competition for habitat, the parent's mobility and to the initial stages of the life cycle(Elliott and Dewailly, 1995; Teichert et al., 2017a)
	Pelagic (OP)	It has pelagic eggs	
	Guarded (OG)	Eggs are not protected by a structure but are guarded by one or both parents	
	Protected (OS)	Eggs are protected in a nest, case or pouch	

4.3.2. Data analysis

Functional diversity was calculated as Functional Richness (FRic - Mason et al., 2005) and Functional Evenness (FEve - Villéger et al., 2008) using the FD package developed by (Laliberté et al., 2015) in R (R Core Team, 2014). Functional Divergence (FDiv) could not be calculated, since only categorical traits were available (Mason et al., 2005). Since the FD package tolerates missing values, no alterations were done on the matrix of functional traits where 7 traits could not be determined.

To calculate the indices, a species by trait matrix and a species abundance matrix is required. From these matrices a species-species Euclidean distance matrix was constructed, using the "Cailliez" (Cailliez, 1983) correction to deal with negative eigenvalues. Using the corrected species-species distance matrix, a Principal coordinates analysis (PCoA) was done, and the resulting axes were then used as traits to estimate the functional diversity indices:

- FRic measures the volume of the functional space occupied by a community (Villéger et al., 2008), *i.e.* the amount of niche space occupied by the community, reflecting the number of functions performed. Therefore, a community with a higher FRic performs a higher quantity of functions.
- FEve is the evenness of the distribution of function abundance in niche space and reflects the evenness with which the resources are used. Thus, a high FEve indicates that all functions are similarly performed while a low value indicates that some functions are more represented than others.
- Functional Dispersion (FDis) calculates how cluttered species are in the functional space (Laliberté and Legendre, 2010). It does so by calculating the mean distance of each species to the centroid of all species. A low FDis indicates that species have similar functional traits and are close to each other in the functional trait space.
- Functional Group Richness (FGR) was calculated *a posteriori* based on functional classification (Petchey and Gaston, 2006) of a dendrogram, created from the corrected species-species distance matrix. This groups the species based on the similarity of their traits. The number of functional groups is defined upon visual assessment of the dendrogram by the user. The user defines a value at which the dendrogram is cut and defines the groups. A community with a higher FGR would have a higher functional diversity since there is a higher number of species with different combinations of functions/traits.
- Based on the groups established in FGR the abundance of functional groups is computed. The abundance of a functional group is calculated by adding the abundance of each species belonging to that functional group in that mangrove. This allows to understand what functional group is more abundant in each mangrove system.
- The Community-level Weighted Mean (CWM) calculates the dominant category for each trait (Lavorel et al., 2008) , *i.e.,* function, for each trait, indicating what is the most performed function by a community in an assemblage.
- Functional Redundancy (FRed) was calculated as the relationship between functional diversity and species diversity (De Bello et al., 2007). Functional diversity being calculated as Rao's quadratic entropy (RaoQ) and species diversity as the Simpson Index of Diversity (1-D). RaoQ is a functional diversity index that measures the dissimilarity between pairs of species (Botta-Dukát, 2005). If functional diversity is equal to species diversity, redundancy will be zero, because all species are

> functionally different. On the other hand, if functional diversity is zero, redundancy will be maximized and equal to the species diversity since all species are functionally the same.

Pearson correlation (significant at $p<0.05$) was used to check the relationship between functional diversity indices and taxonomical diversity indices. The correlation between species richness and FRic and functional group richness was checked, FRic was compared to the Simpson Diversity Index, the Shannon-Wiener Index and the Average Taxonomic Distinctness, and FEve was compared to Pielou's evenness and to the variation in taxonomic distinctness. These analyses were performed at the mangrove level, considering sampling events as replicates to maximize mangrove sampling representativity.

4.4. Results

4.4.1. Functional traits

A total of 20 functional traits belonging to the 5 functional guilds were identified (Table 4.2), *i.e.*, 4 ecological traits, 3 vertical distribution traits, 3 substrate preference traits, 7 feeding traits and 3 reproductive traits. For some species it was not possible to determine all of their traits due to lack of information on the life cycle. With information lacking for the Substratum Preference Guild for two species, and the Feeding Guild for five species.

Table 4.2 *- List of functional traits per functional guild of each species identified in the sampled mangroves. In the Ecological Guild, MS stands for Marine Stragglers, MM for Marine Migrants, ES for Estuarine species and FW for Freshwater species. In the Vertical Distribution Guild, B is for Benthic species, D for demersal species and P for pelagic species. In the Substratum (preference) Guild, F for species that prefer soft substrate, R is for species that prefer hard substrate and M is for species without a substratum preference. In the Feeding Guild, PS is for strict planktivores, IS is for strict insectivores, FS is for strict piscivores, IF is for insectivorous and piscivorous species, CS is for species that are carnivorous but other than the previous, e.g., species feeding on invertebrates and plankton but not other fish (CS), HC is for species that are partly carnivorous, partly herbivorous but not omnivorous (HC), OV is for omnivores and VS is for strict herbivores. In the Reproductive Guild, OP is species with pelagic eggs, OG is for species where the eggs are guarded by one or both parents but are not protected in a structure like a nest and OS is for species where the eggs are shed into/protected in a nest, case or pouch.*

Species	***Ecological Guild***	***Vertical Distribution Guild***	***Substratum (preference) Guild***	***Feeding Guild***	***Reproductive Guild***
***Abudefduf saxatilis* (Linnaeus, 1758)**	MS	D	M	OV	OG
***Abudefduf taurus* (Müller & Troschel, 1848)**	MS	D	R	HC	OG
***Bathygobius casamancus* (Rochebrune, 1880)**	ES	B	M	-	OG
***Bathygobius soporator* (Valenciennes, 1837)**	ES	B	M	OV	OG
***Caranx latus* Agassiz, 1831**	MS	P	P	IF	OP
***Cephalopholis nigri* (Günther, 1859)**	MS	D	M	FS	OP
***Eleotris annobonensis* Blanc, Cadenat & Stauch, 1968**	ES	B	R	-	OG
***Eleotris vittata* Duméril, 1861**	ES	B	R	OV	OG
***Epinephelus aeneus* (Geoffroy Saint-Hilaire, 1817)**	MM	D	M	IF	OP
***Ethmalosa fimbriata* (Bowdich, 1825)**	ES	P	P	PS	OP
***Eucinostomus melanopterus* (Bleeker, 1863)**	MM	D	F	OV	OP
***Gymnothorax mareei* Poll, 1953**	MS	B	M	IS	OP
***Lutjanus goreensis* (Valenciennes, 1830)**	MM	D	R	IF	OP
Megalops atlanticus	MS	P	P	IF	OP

Valenciennes, 1847					
***Monodactylus sebae* (Cuvier, 1829)**	MM	D	M	IS	OP
***Mugil bananensis* (Pellegrin, 1927)**	MM	D	F	OV	OP
***Oreochromis mossambicus* (Peters, 1852)**	FW	D	M	OV	OS
***Parachelon grandisquamis* (Valenciennes, 1836)**	MM	P	P	OV	OP
***Periophthalmus barbarus* (Linnaeus, 1766)**	ES	B	F	HC	OG
***Plectorhinchus macrolepis* (Boulenger, 1899)**	MM	D	-	IF	OP
***Pomadasys jubelini* (Cuvier, 1830)**	MM	D	F	IF	OP
***Stegastes imbricatus* Jenyns, 1840**	MS	D	R	VS	OG

Five species clusters were identified based on functional traits (Figure 4.1). The first group (FG1) is composed of five benthic estuarine species that guard their eggs (trait category OG). The second group (FG2) is made up of four pelagic species that have pelagic eggs. The third group (FG3) is composed of six demersal marine migrant species that lay pelagic eggs. The fourth group (FG4) includes two demersal marine stragglers that prefer rocky substrates. The fifth group (FG5) is composed of five demersal species with no clear substrate preference.

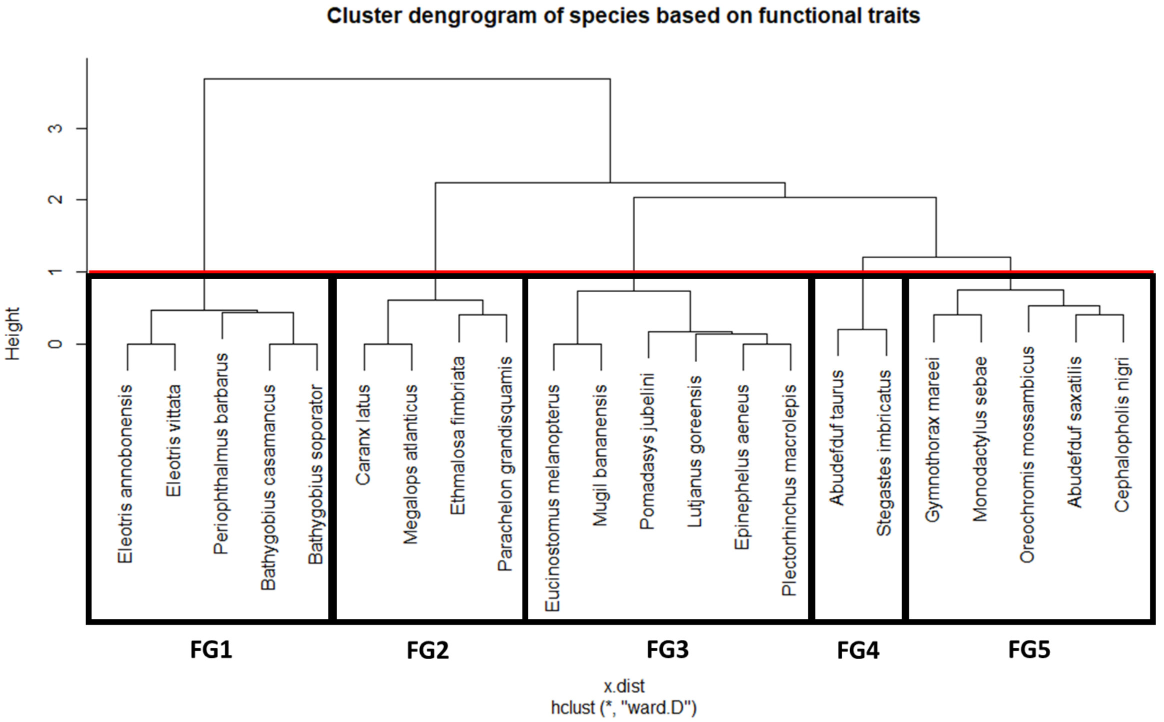

Figure 4.1 - Cluster dendrogram of species based on functional traits. In red is the line showing the cut-off that divided species into functional groups. Species of the same functional group are in the same box with the number of the functional group written below the box.

In Angolares and Malanza, the functional group (FG) that has the most abundant species is FG3, while in Diogo Nunes is FG1. In fact, it is also in Diogo Nunes that this functional group is more abundant overall. FG4 only occurs in Malanza. FG5 has similar abundance in all mangroves except in Malanza, where its abundance more than doubles comparing to the other systems, it is also the only FG that occurs in Praia das Conchas. FG2 has similar abundance in Malanza and Angolares but only half in Diogo Nunes (Table 4.3).

Table 4.3 *– Total abundance of functional groups in each mangrove. Abundance of functional groups is the sum of the abundance class of the species composing the functional group in each mangrove.*

	Functional Group 1	**Functional Group 2**	**Functional Group 3**	**Functional Group 4**	**Functional Group 5**
Praia das Conchas	0	0	0	0	7
Diogo Nunes	38	8	17	0	11
Angolares	14	17	32	0	10
Malanza	19	15	32	8	25

4.4.2. Functional diversity

The highest FRic was observed in Malanza, meaning that this mangrove has the highest number of unique trait combinations (Figure 4.2). The next highest FRic was observed in Diogo Nunes, followed by Angolares, and Praia das Conchas.

Malanza was the system with the highest FGR with all functional groups found, followed by Angolares and Diogo Nunes, where both had four functional groups missing the group of demersal marine stragglers. The lowest FGR was found in Praia das Conchas with only one functional group present, the group of demersal species without a specific substratum preference (Figure 4.2).

Angolares was the system with the highest FEve (Functional Evenness), followed by Malanza (Figure 4.3). Diogo Nunes had the lowest FEve, while it could not even be calculated for the Praia das Conchas, since it only had one species.

The highest value for FDis (Functional Dispersion) was obtained for Diogo Nunes, meaning that species had more dissimilar traits than in other mangroves. It was followed by Malanza, Angolares, and Praia das Conchas system with a value of zero due to the occurrence of a single species (Figure 4.3).

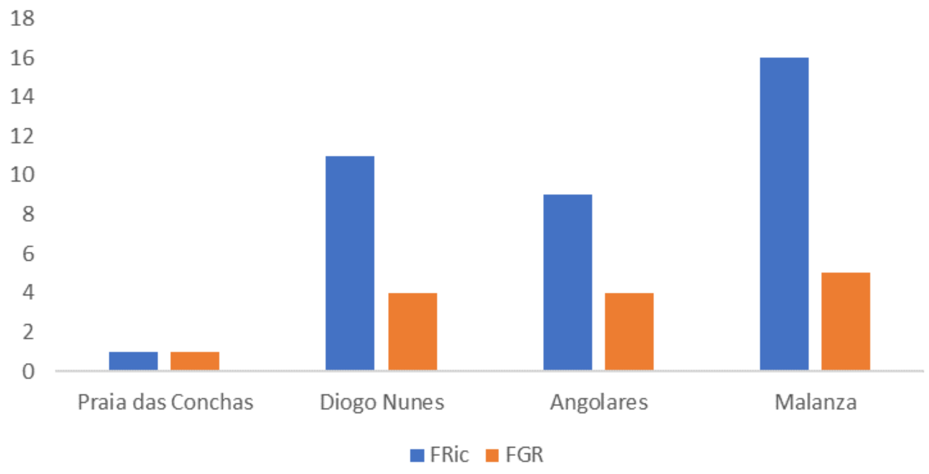

***Figure 4.2** - Values of Functional Richness (FRic) and functional group richness (FGR) for each mangrove.*

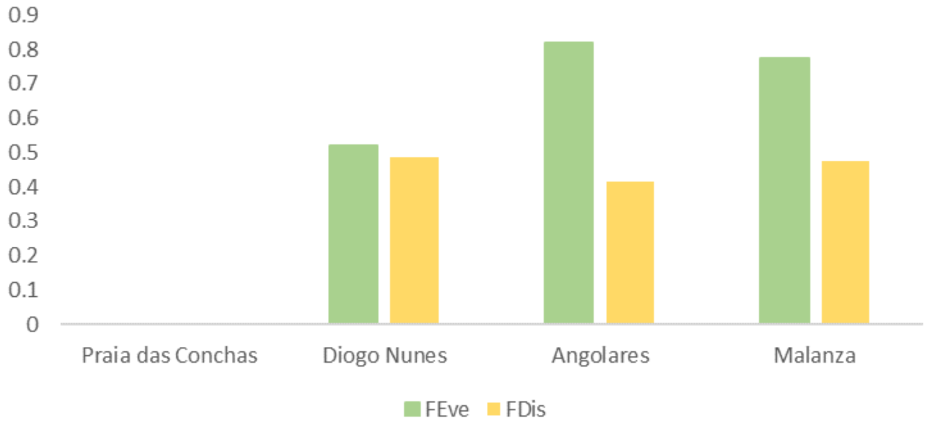

***Figure 4.3** - Values of functional evenness (FEve) and functional dispersion (FDis) for each mangrove.*

Since all traits were categorical, CWM (Community-level Weighted Mean) shows the dominant trait category for each trait (Table 4.4). In Angolares and Malanza, marine migrant species were the dominant ecological guild, while estuarine residents dominated in Diogo Nunes and freshwater species in Praia das Conchas.

As for the vertical distribution guild, demersal species dominated all systems, except for Diogo Nunes, which was dominated by benthic species (Table 4.4).

Regarding substratum preference guilds, Diogo Nunes was dominated by hard substrate, while Angolares was dominated by soft substrate, and Malanza and Praia das Conchas were dominated by mixed substrate preferences (Table 4.4).

Omnivorous species dominated the feeding guild in all mangroves (Table 4.4).

Laying pelagic eggs (OP) was the dominant trait for Malanza and Angolares, eggs that are guarded by one or both parents (OG) was the dominant trait in Diogo Nunes and eggs that are protected in a netst, case or pouch (OS) was the dominant trait in Praia das Conchas for the reproductive Guild (Table 4.4).

***Table 4.4** - Community-level Weighted Mean of each functional guild in every mangrove system. MM stands for Marine Migrant species, FW for Freshwater species, ES for Estuarine species, D for Demersal species, B for Benthic species, F for*

species with a preference for soft substrate, R for species with a preference for hard substrate, M for species without a substrate preference, OV for omnivorous species, OP for species that lay pelagic eggs, OG for species where one or both parents guard the eggs and OS for species where the eggs are protected in a nest, case or pouch.

Community-level Weighted Mean					
	Ecological Guild	Vertical Distribution Guild	Substratum preference Guild	Feeding Guild	Reproductive Guild
Praia das Conchas	FW	D	M	OV	OS
Diogo Nunes	ES	B	R	OV	OG
Angolares	MM	D	F	OV	OP
Malanza	MM	D	M	OV	OP

4.4.3. Functional redundancy

The FRed values calculated were all similar, being highest (0.690) in Angolares, followed by Malanza (0.686), and Diogo Nunes (0.643). It was not possible to calculate FRed for the Praia das Conchas system

4.4.4. Linking functional and taxonomic indices

A strong correlation between species richness and FRic was observed as well as between species richness and functional group richness (Figure 4.4).

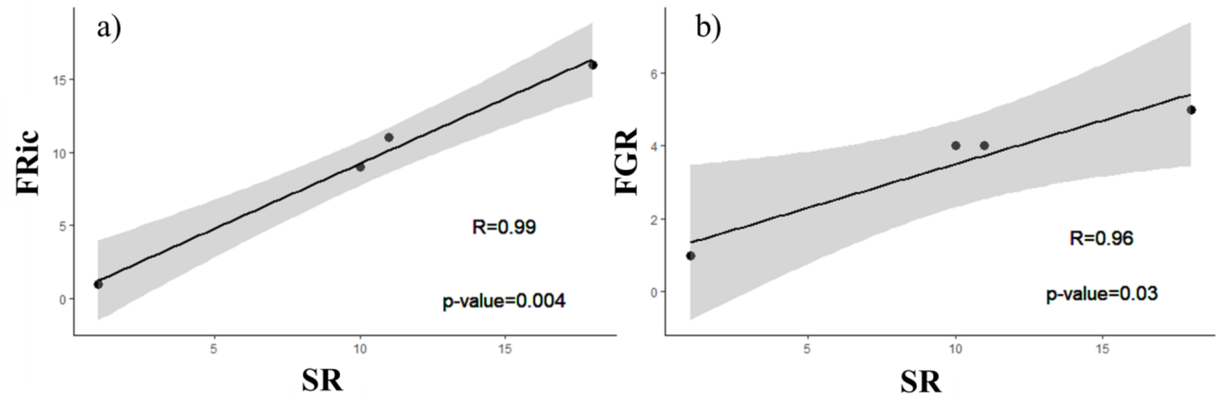

Figure 4.4 *- Correlation of species richness with the richness components of functional diversity. In a) is shown the correlation between Functional Richness (FRic) and Species Richness (SR). In b) is shown the correlation between Functional Group Richness (FGR) and Species Richness (SR). In both graphs is shown the Pearson correlation (R) and the associated p-value (p). The grey area corresponds to the 95% confidence interval.*

The FRic yielded significant positive correlation with the Shannon-Wiener Index (Figure 4.5-B, p-value =0.05) and significant negative correlation with the Average Taxonomic Distinctness (Figure 4.5-C, p-value <0.05). The correlation between FRic and the Simpson Diversity Index was positive, but not significant (Figure 4.5-A, p-value >0.05).

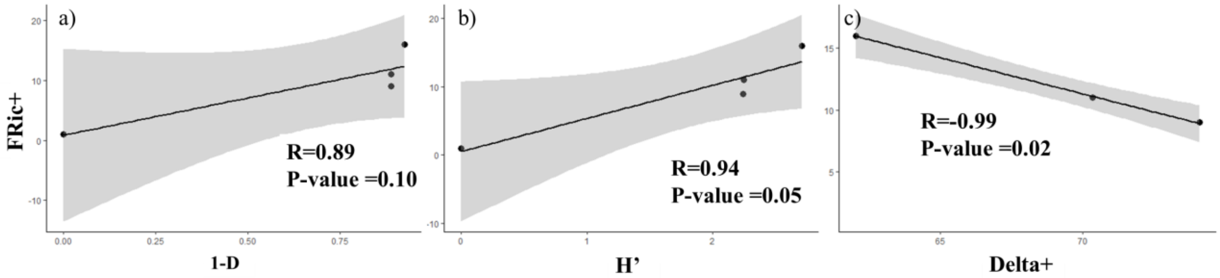

__Figure 4.5__ – Pearson correlation analyses between Functional Richness (FRic) and the Traditional Diversity Indices: a) FRic and the Simpson Diversity Index (1-D); b) FRic and the Shannon-Wiener Index (H'); c) FRic and the Average Taxonomic Distinctness (Delta +). The grey area corresponds to the 95% confidence interval.

The correlation between the FEve and the traditional evenness indices was weak and not significative (Figure 4.6), indicating that they are not related.

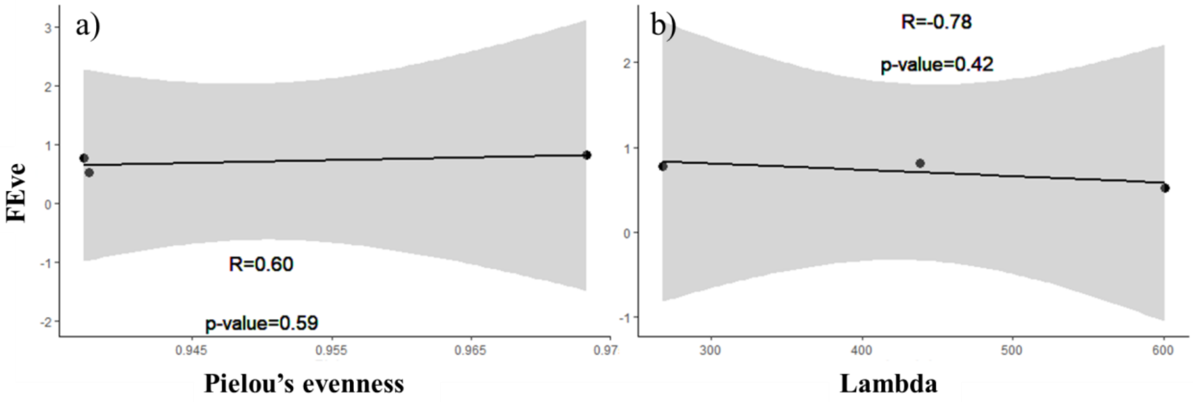

__Figure 4.6__ - Pearson correlation analyses between Functional Evenness (FEve) and the traditional evenness indices; a) FEve and Pielou's evenness: b) FEve and the variation in taxonomic distinctness (Lambda). The grey area corresponds to the 95% confidence interval.

4.5. Discussion

This study was one of the first to describe functional fish diversity and redundancy on island mangrove systems. The Santomean mangrove fish assemblages had high variation of functional diversity between mangroves, with large mangroves, like Malanza, having a high number of functions dominated by pelagic marine species, while smaller mangroves, like Diogo Nunes, have fewer functions and are dominated by estuarine demersal and benthic species. The values obtained for FEve are similar to values obtained in other studies (Pool et al., 2010; Silva-Júnior et al., 2016), indicating that the distribution in the functional space is similar in brackish systems. Meanwhile FDis values were within the average of another study, from a subtropical bay (Koochaknejad et al., 2020), indicating that the average occupied functional space in Santomean mangroves is similar. There was a correlation between the FRic and species richness and diversity suggesting that assemblages with a larger number of species will perform a higher number of functions (Teichert et al., 2017a). Meanwhile species evenness was not correlated with FEve.

In the present study, FRic only indicates the number of trait combinations and is not related to the volume occupied by the community in the multidimensional trait space since only categorical traits were used. It showed that the variability and total number of functions was higher in Malanza, the largest and most diverse system, since new species are likely to introduce additional ecological functions in the system, increasing its FRic (Pool et al., 2010; Schleuter et al., 2010).

FEve weighs the abundance of the different trait categories against each other and is able to indicate if some traits are under or over performed. The lowest FEve, observed in Diogo Nunes, is the result of a higher number of estuarine and benthic species (that permanently inhabit the mangrove) comparing to marine and demersal species (that occasionally enter the mangrove), which is probably related to the fact that Diogo Nunes is a small intertidal mangrove, as well as to an eventual sample bias induced by the low sampling effort during high tide. Nevertheless, these species that potentially enter the mangrove during high tide are visitors and will probably have a lower impact than species that are present during both high and low tide since they spend less time in the mangrove. The highest FEve observed in the Angolares mangrove indicates a similar abundance of estuarine and marine species, benthic and demersal species. This is probably because of its high natural variability that led to the community being reduced to a core group of tolerant species, typical of enclosed systems (Félix et al., 2013). In Malanza FEve was high indicating that, like in Angolares, functions were similarly performed, but unlike Angolares, this is because of the high diversity of the fish assemblage and the environment that allowed for a higher niche diversity.

In some studies, FDis is used as a measure of functional diversity (Koec.k et al., 2014) probably because of its high correlation with RaoQ (Laliberté and Legendre, 2010). RaoQ is a popular measure of functional diversity due to its relation to the Simpson’s diversity index (Botta-Dukát, 2005). Although FDis and RaoQ are highly correlated, they measure different aspects of functional diversity in the multidimensional trait space, therefore the usage of FDis as a measure of functional diversity should be done with caution. The highest FDis value was observed in Diogo Nunes indicating that species with extreme traits are present and there is a low overlap between the species. This low overlap of the species is probably due to the intertidal nature of the mangrove, as marine species enter the mangrove during the high tide and during the low tide mainly estuarine species remain, these two groups of species have contrasting sets of traits resulting in contrasting functions, and are therefore more dispersed in the functional space than the species in Malanza and Angolares. In Angolares the instability of environmental conditions (see Section 3), reduces the available niches, therefore functionally similar species remain, resulting in a community with a higher overlap of ecological functions (Warwick and Clarke, 1998). Probably because of a higher overlap of species in the functional space in Malanza FDis was a little lower than in Diogo Nunes. This higher overlap is due to the presence of species with intermediate trait combinations, between estuarine and marine species, owing to the gradient of environmental conditions in the Malanza mangrove.

In plant ecology FGR is a rather commonly used measure of functional diversity. On the contrary, in animal ecology it is not widely accepted (Blaum et al., 2011), likely due to the critics it has received regarding the lack of an objective measure of what a functional group is (Petchey et al., 2009). Despite that, it can provide a relevant insight on the functional composition of a community, such as the higher FGR in Malanza due to the presence of a Functional Group not present in the other systems. The absence of Functional Group 4 in Angolares, Diogo Nunes and Praia das Conchas indicates that these systems are not as suitable as Malanza for marine stragglers, which might be explained by the absence of adequate feeding resources. The high abundance of FG2 and the higher abundance of FG3 in the larger mangroves (Angolares and Malanza) hints the importance of these larger and deeper systems to marine migrant and pelagic species. Diogo Nunes appears to have a rather large resident community occupying benthic habitats, as indicated by the high abundance of FG1, which makes up half of the community. The reduced number of marine species in this mangrove is most likely linked to the sampling being done during low tide when depth and salinity were reduced preventing the entrance of these species.

The CWM allows for a quick analysis of the functional composition of a community since it highlights the predominant functions in each system, identifying key functions of the communities, such as the marine dominance in Malanza and Angolares. The results of the CWM confirm the tendencies described by the FGR in larger mangroves dominated by marine species with a lower affinity to the bottom, facilitated by the larger depths in these mangroves, and the smaller mangroves by benthic species. The preference for the substrate varies with mangroves, with a higher preference for soft substrate in the Angolares system, and a preference for hard substrate in Diogo Nunes. The latter contrasts with the conditions found in the mangrove, where sand was the dominant grain size class (Figure A.6), but might be explained by the existence of solid structures of the nearby village. The omnivorous feeding group was the dominant category in all mangroves, which indicates that generalist species occur more often. The dichotomy observed for reproductive traits is probably related to the characteristics of the mangroves, in the larger and deeper mangroves pelagic eggs have a higher chance of survival than in the shallower systems where the existence of parental care increases the chance of survival (Teichert et al., 2017b). The smaller mangroves have a more specific trait combinations showing that communities are adapted to the available niches. As in the Praia das Conchas system only one species was caught, the dominant traits of this species are adapted to the major attributes of this mangrove.

Literature on functional fish diversity is scarce, especially for tropical estuaries, making it difficult to place our results in a wider context. Furthermore, most work done on fish functional diversity uses continuous traits, again making it difficult to compare to our results, especially FRic and CWM. Additionally, other reasons further hamper comparisons to other studies, some of which are arbitrary: the choice of the traits to be used in the calculation of the indices vary between studies, the categories to be included in a certain trait are user dependent, as well as the classification of functional groups in the dendrograms. Moreover, from the three studies found in the literature, two were conducted in temperate estuaries (Pool et al., 2010; Van Der Linden et al., 2016) and the remaining in tropical estuaries on the American mainland (Silva-Júnior et al., 2016). In all studies, data were collected continuously over an extended period, integrating data from different seasons and years. This additional difference also hinders the direct comparison of results.

The FRed, depicting the trait-similarity of species within a community, was higher in the larger mangroves, showing that, in these communities, the same functions were performed by more than one species. This also portrays the two scenarios in which FRed is high, the first in a system with a reduced human pressure (Malanza) where there is a high overlap regarding functions due to the high species diversity. The second scenario of high FRed is in a system, with a high human pressure as well as natural pressure (Angolares) in which the community is reduced to a core group of tolerant species with low species diversity and repeating functions (Van Der Linden et al., 2016). The low FRed in the smaller systems shows how vulnerable these systems are to disturbance, given that this low FRed value is a result of low species diversity and high functional diversity. This shows that the larger mangroves should be able to maintain system functioning after disturbance while the smaller systems are more susceptible to the loss of functions after degradation. Thus, extinction phenomena have a higher impact where there are ecological functions ensured by few or one species, the extreme example of this is Praia das Conchas where the only present species is a non-native species that is extremely tolerant to stress (King and Sardella, 2017), being the only species able to survive evidencing the ecological vulnerability of this mangrove.

The correlation analyses showed that increased species richness, assured by a higher diversity of habitats found in the larger mangroves, and species diversity were positively related with FRic, *i.e.*, number of functions performed. Taxonomic distinctness had a negative relationship with FRic, most likely because assemblages with a higher taxonomic distinctness (*e.g.*, Angolares) were less species rich. This shows that species from different taxa may perform similar functions and that taxonomic distinctness does not ensure functional diversity. FEve was neither correlated with species evenness nor taxonomic evenness, evidencing that an evenly represented community may perform similar functions leading to the over representation of some functions. This indicates that the functional diversity indices have the advantage of showing underlying patterns overlooked by the traditional diversity indices, mainly regarding how evenly functions are performed by the species, nevertheless these results have to be considered carefully due to the low sample size.

The usage of traditional diversity indices based on species richness (SRDI) in association with functional diversity indices (FDI) helped contextualizing and interpreting our findings. The usage of a multitude of functional diversity indices that evaluate different facets of functional diversity also helped drawing a more extensive image of the fish communities from these insular mangroves. The FDI, just like the SRDI, identified the largest mangrove (Malanza) as the most diverse system. The low FDis and high FEve of Angolares also confirms the findings of the SRDI, that this coastal lagoon system with significant fluctuations in the environmental conditions, hosts a small community of tolerant species which are functionally similar. The Diogo Nunes mangrove, while similar to Angolares regarding the species richness and diversity, was more functionally diverse, and this functional diversity was at a higher risk than in the other mangroves.

This type of knowledge may help in the development of management plans, since the information given by the FDI rarely is contradictory to the SRDI, but it rather complements it. This makes it easier to take directed action since the indices together indicate which communities are the most vulnerable allowing to take action in the systems that are at risk, but also which system is more important for a specific group of species that share similar traits allowing to set priorities. Therefore, the usage of complementary taxonomic and functional diversity metrics allows for a better-informed decision-making process as it allows to identify the mangroves that are more vulnerable as well as the mangroves that host a higher diversity being able to recognize which mangrove to prioritize according to the objectives of the management plan.

5. Conclusions

I concluded that the complementary use of traditional taxonomic diversity metrics and functional diversity metrics allows to identify different aspects of mangrove fish diversity. While both metrics had concurring results, the use of functional diversity indices adds value, as these are able to identify the ecological functions within a community and, consequently, the vulnerability of an estuarine system, based on its fish assemblage. Diversity *per se* does not represent resilience, and more traditional taxonomic methods lack the representation of functional groups which are key for ecosystem functioning. Functional diversity metrics also enable to pinpoint specific ecological functions in a given system, that are lacking or poorly represented and which can be targeted within management actions to decrease the system's vulnerability by avoiding function loss. Therefore, functional diversity metrics are a highly relevant complement to taxonomic diversity metrics.

I noticed that the larger and deeper mangroves, *i.e.*, Malanza and Angolares, play a central role for pelagic marine fish species, serving as feeding and nursery grounds. Smaller mangroves, like Diogo Nunes, are important for estuarine resident species as well as for juveniles of some species, acting as nursery grounds.

Results also pointed to the fact that larger mangrove size is not an assurance for higher diversity and that other factors such as stability of environmental conditions also influence the diversity of fish assemblages. This becomes clear since the diversity found in Angolares, one of the largest mangroves of the island, is similar to that found in the much smaller Diogo Nunes mangrove. However, size appears to be of importance when considering how species use and interact with the system, as the two larger mangroves, Malanza and Angolares were of a major importance for marine species. The two smaller mangroves, Diogo Nunes and Praia das Conchas, were more important for estuarine species and a freshwater species, respectively. Thus, these results also highlight the importance of the functional diversity indices in the identification of the roles the mangroves play for the fish communities. The communities from these smaller systems tend to be less resilient to disturbances and are more vulnerable to extinction events due to a higher susceptibility of the communities to function loss, as they have a much lower functional redundancy. This shows that these smaller systems need close attention regarding the impacts that may eliminate ecological functions performed by one or a small number of species. Changes that preclude the continuity of these species (or functions they represent) are those that the system is more susceptible to.

Both indices, taxonomic and functional, were not able to differentiate between systems with different degrees of human impact, but with successive sampling over time, changes in the indices and a more robust data set, mainly in the functional diversity indices, these should be able to identify negative impacts on the fish communities such as loss of functions or decrease in their redundancy.

Overall, I conclude that large and more heterogeneous mangroves with stable conditions host more diverse fish assemblages. This higher diversity is observed both in taxonomic and functional diversity metrics. In the future, mangroves should be sampled periodically to understand how diversity changes along the year and what triggers these changes. Smaller mangroves tended to be important for resident fish species, especially in mangroves with high tidal influence. There was a high agreement between the results of the traditional diversity indices and the functional diversity indices, except for the evenness. The advantage of the functional diversity indices was the addition of information about ecosystem functioning comparing to taxonomic diversity indices, and the potential input these can provide to conservation measures. Thus, the findings of this work can support future decisions concerning the prioritization of conservation measures based on these assessment tools, as they show

how different metrics help identifying the functional structure of fish communities and their most susceptible elements.

6. References

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7. Appendix

Table A.7.1 *- Environmental data of each sampling site used for the nMDS (Fig. 5.7) in Chapter I. Data from Praia das Conchas were not included due to the absence of replicates. Whenever possible to avoid missing values those were replaced with average values for that point of the variable, this was done when the values between rounds were conservative, showing negligible changes.*

	Site Depth (cm)	*Temperature (°C)*	*Salinity (PSU)*	*Stratification*	*Silt (%)*	*Sand (%)*	*Gravel (%)*	*Chla (µg/L)*	*PO4(µmolL^{-1})*	*NH4 (µmolL^{-1})*	*Mangrove area (Km^2)*
M1_1	10	24.88	28.74	0	42.70	55.42	1.88	70.58	2.14	8.18	1.52
M2_1	50	25.31	29.64	0	1.04	98.96	0.00	0.79	0.95	1.28	1.52
M3_1	50	25.60	29.81	0	12.00	85.70	2.83	1.42	0.52	0.00	1.52
M4_1	120	26.06	28.99	0	7.56	85.45	6.98	0.95	0.74	2.35	1.52
A4_1	160	29.14	23.92	1	28.99	66.78	4.23	3.85	1.75	0.00	0.13
A6_1	50	24.50	28.50	1	4.15	95.76	0.09	1.21	2.09	10.25	0.13
DN1_1	10	26.07	0.21	0	7.62	91.85	0.53	0.24	1.10	1.45	0.01
DN4_1	50	28.46	15.39	0	6.02	93.83	0.15	0.34	1.40	1.45	0.01
M1_2	20	27.55	26.07	0	42.70	55.42	1.88	44.59	1.23	4.48	1.52
M3_2	100	25.53	28.43	1	12.00	85.70	2.83	0.74	0.56	1.51	1.52
M5_2	120	24.48	24.81	1	7.56	85.45	6.98	1.41	0.98	0.78	1.52
M4L	100	25.48	29.13	0	37.10	53.78	9.12	0.78	1.62	0.02	0.13
A1_2	87	25.57	28.12	0	28.99	66.78	4.23	0.63	1.52	0.02	0.13
A6_2	100	25.63	29.66	1	4.15	95.76	0.09	1.30	1.41	0.02	0.13
DN1_2	10	25.40	11.80	0	7.62	91.85	0.53	0.21	1.24	0.02	0.01
M1_3	10	27.79	20.40	0	42.70	55.42	1.88	45.14	1.42	0.02	1.52
M2_3	50	25.54	28.58	0	1.04	98.96	0.00	0.78	0.56	0.02	1.52
M3_3	100	25.65	28.76	0	12.00	85.70	2.83	1.03	0.83	0.02	1.52
M4_3	120	25.86	27.71	0	7.56	85.45	6.98	1.40	0.87	0.02	1.52
A3_3	133	25.43	29.28	1	37.10	53.78	9.12	0.47	1.87	0.00	0.13
A4_3	44	25.96	29.21	0	28.99	66.78	4.23	0.77	2.14	0.00	0.13
A6_3	103	25.34	29.25	0	4.15	95.76	0.09	1.38	1.27	0.00	0.13
DN1_3	50	25.09	20.28	0	7.62	91.85	0.53	0.64	3.07	0.02	0.01
DN4_3	10	23.62	0.15	0	6.02	93.83	0.15	0.20	2.17	0.02	0.01
M2_4	50	27.26	29.94	0	1.04	98.96	0.00	0.78	0.76	0.65	1.52
M3_4	83	27.17	30.37	0	12.00	85.70	2.83	1.07	0.64	0.51	1.52

Table A.7.2 - Table containing the references for the functional straits of each species, each table cell corresponds to a specie's trait. Cells in blank correspond to specie's traits with no available information.

Species	***Ecological Guild***	***Vertical Distribution Guild***	***Substratum (preference) Guild***	***Feeding Guild***	***Reproductive Guild***
Abudefduf saxatilis	Carpenter, 2002		Carpenter, 2002	Carpenter, 2002	Carpenter, 2002
Abudefduf taurus	Carpenter, 2002	Aguilar-Medrano, 2018	Carpenter, 2002	Carpenter, 2002	Carpenter, 2002
Bathygobius casamancus	Patzner et al., 2012	http://www.fishbase.org, accessed 1st of January 2019	Miller and Smith, 1989		http://www.fishbase.org, accessed 1st of January 2019
Bathygobius. soporator	Whitfield, 2005	Emmanuel and Ajibola, 2010	Miller and Smith, 1989	Emmanuel and Ajibola, 2010	Emmanuel and Ajibola, 2010; Miller and Smith, 1989
Caranx latus	Carpenter and De Angelis, 2016b; Whitehead et al., 1989b	Gasparini and Floeter, 2001		Silvano, 2001	Whitehead et al., 1989b
Cephalopholis nigri	Heemstra and Randall, 1993	http://www.fishbase.org, accessed 1st of January 2019	Heemstra and Randall, 1993	Roméo et al., 1999	Whitehead et al., 1989b
Eleotris annobonensis	http://www.fishbase.org, accessed 1st of January 2019				http://www.fishbase.org, accessed 1st of January 2019
Eleotris vittata	Whitfield, 2005	http://www.fishbase.org, accessed 1st of January 2019		Ekpo et al., 2015	http://www.fishbase.org, accessed 1st of January 2019
Epinephelus aeneus	Heemstra and Randall, 1993	http://www.fishbase.org, accessed 1st of January 2019	Edwards et al., 2001	Heemstra and Randall, 1993	Whitehead et al., 1989b
Ethmalosa fimbriata	Whitfield, 2005	Charles-Dominique and Albaret, 2003		Whitehead, 1985	Fagade and Olaniyan, 1972
Eucinosotmus melanopterus	Whitfield, 2005	http://www.fishbase.org, accessed 1st of January 2019	Lévêque et al., 1990	Gning et al., 2010	Chaves and Robert, 2001
Gymnothorax mareei	Carpenter and De Angelis, 2016a	https://www.iucnredlist.org/, accessed 1st of	https://www.iucnredlist.org/, accessed 1st of	Fischer et al., 1981b	

		January 2019	January 2019		
Lutjanus goreensis	Whitfield, 2005	Nelson, 2006; Nelson et al., 2016	Allen, 1985	Allen, 1985	Allen, 1985
Megalops atlanticus	Whitfield, 2005	Cervingón et al., 1992		Fischer et al., 1981b	Taylor et al., 2011
Monodactylus sebae	Whitfield, 2005	Faye et al., 2011		Gning et al., 2008	Akatsu et al., 1977
Mugil bananensis	Whitfield, 2005	http://www.fishbase.org, accessed 1st of January 2019		Carpenter and De Angelis, 2016a	Crosetti and Blaber, 2016
Oreochromis mossambicus	Whitfield, 2005	Piet and Guruge, 1997		De Moor et al., 1986	Amorim et al., 2003
Parachelon grandisquamis	Whitfield, 2005	Njoku and Ezeibekwe, 1996			Crosetti and Blaber, 2016
Periophthalmus barbarus	Etim et al., 2002	Udo, 2002	Etim et al., 2002	Udo, 2002	Etim et al., 2002
Plectorhynchus macrolepis	Whitfield, 2005	http://www.fishbase.org, accessed 1st of January 2019		Stiassny et al., 2007a	http://www.fishbase.org, accessed 1st of January 2019
Pomadasys jubelini	Whitfield, 2005	Cervingón et al., 1992		Diouf, 1996	http://www.fishbase.org, accessed 1st of January 2019
Stegastes imbricatus	Carpenter and De Angelis, 2016b	Aguilar-Medrano, 2018		Canterle, 2017	Nelson, 2006; Nelson et al., 2016

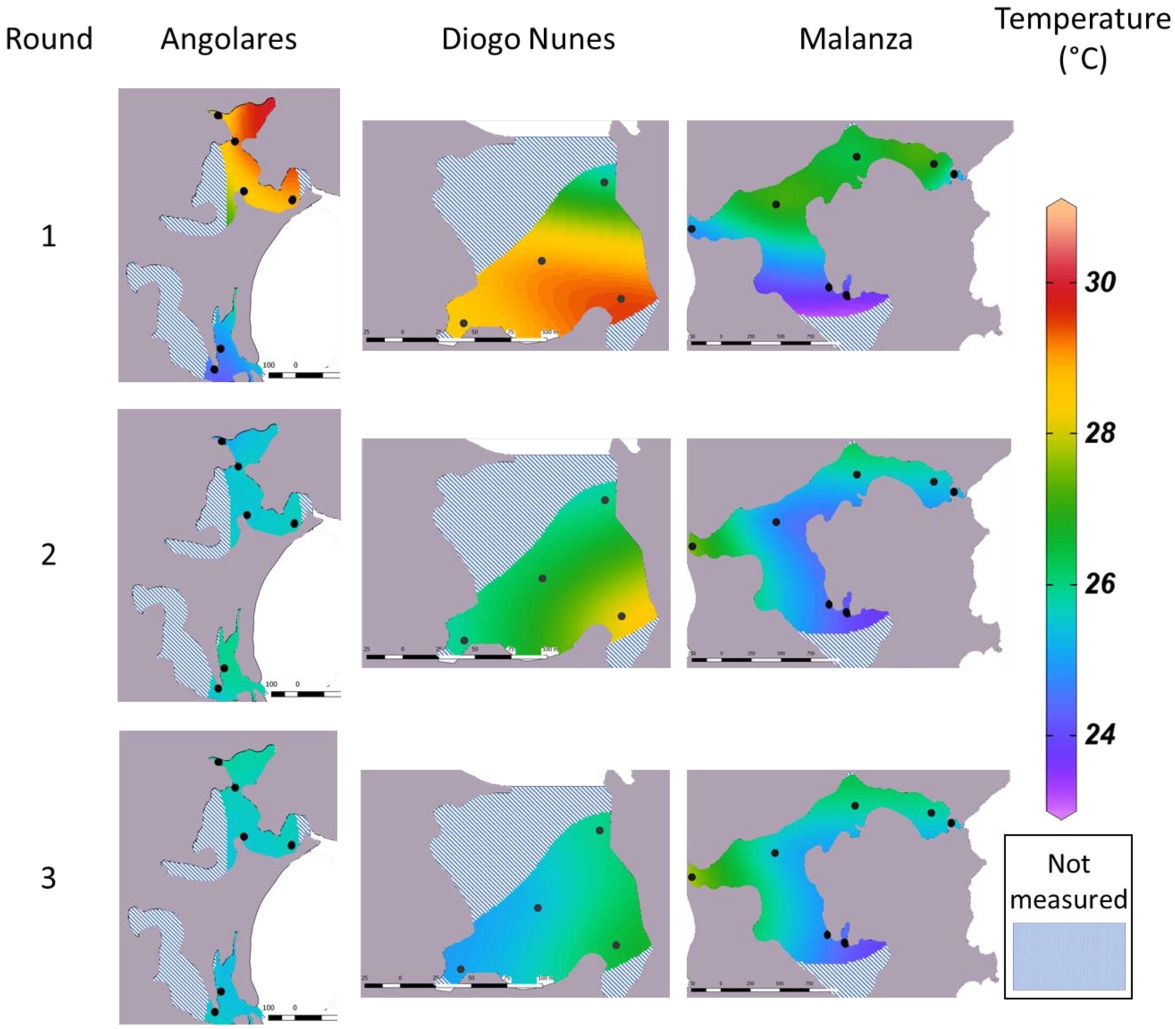

Figure A.1 - *Temperature values (ºC) for Angolares, Diogo Nunes and Malanza mangroves during three sequential rounds throughout August 2017.*

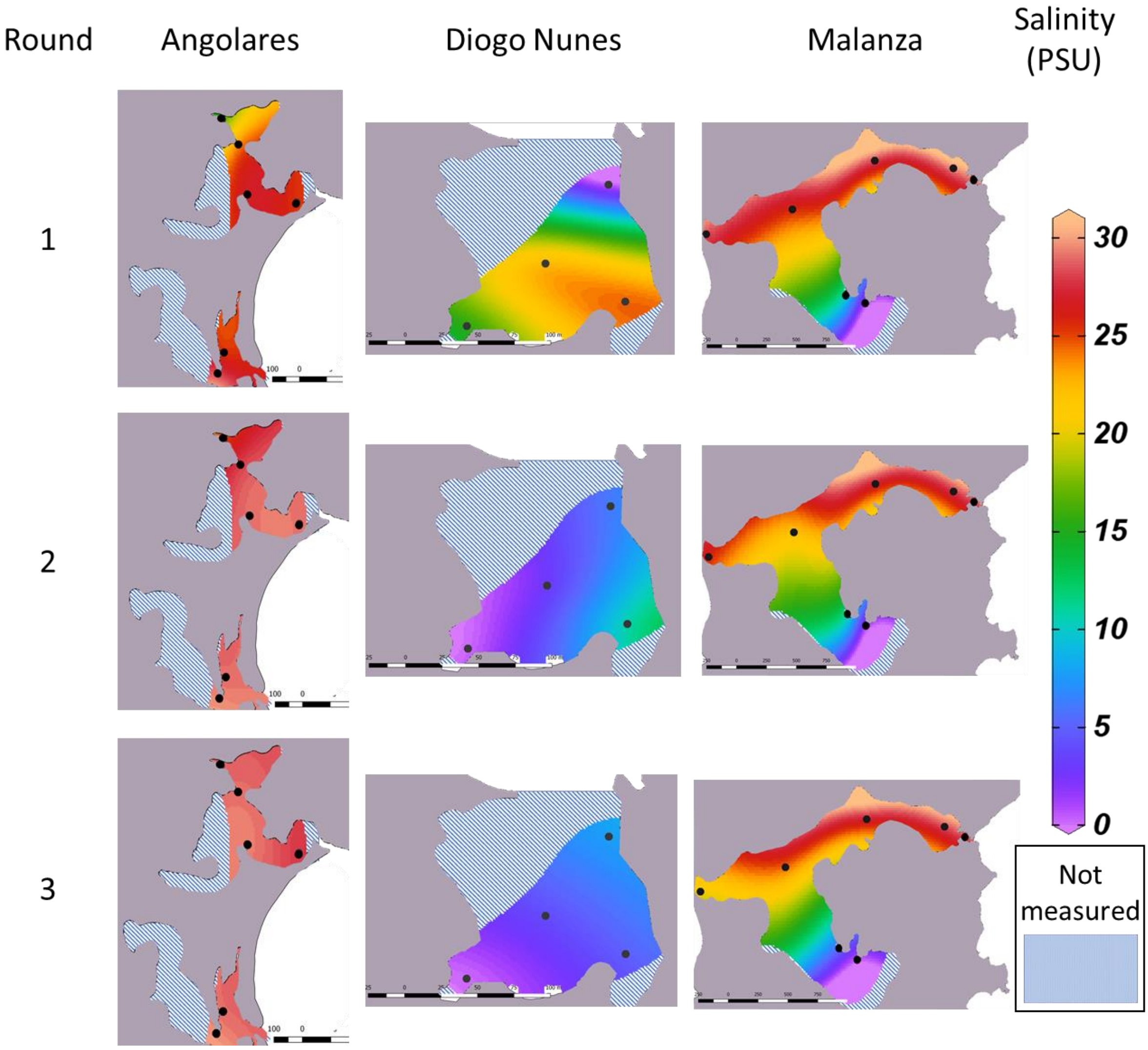

Figure A.2 *- Salinity in the Angolares, Diogo Nunes and Malanza mangroves during three sequential rounds throughout August 2017.*

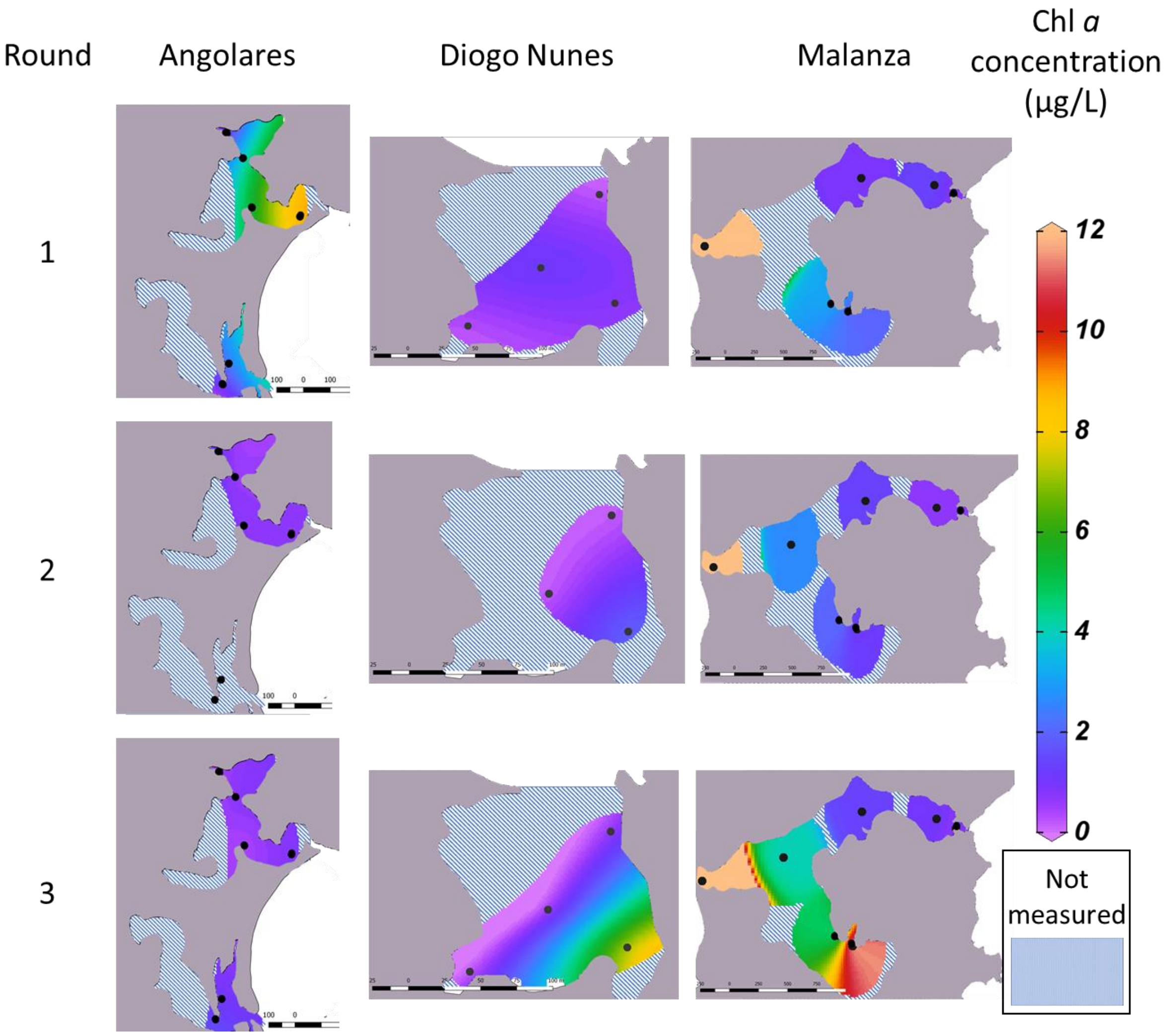

Figure A.3 *- Chlorophyll a concentrations (ug/L) in the Angolares, Diogo Nunes and Malanza mangroves during three sequential rounds throughout August 2017.*

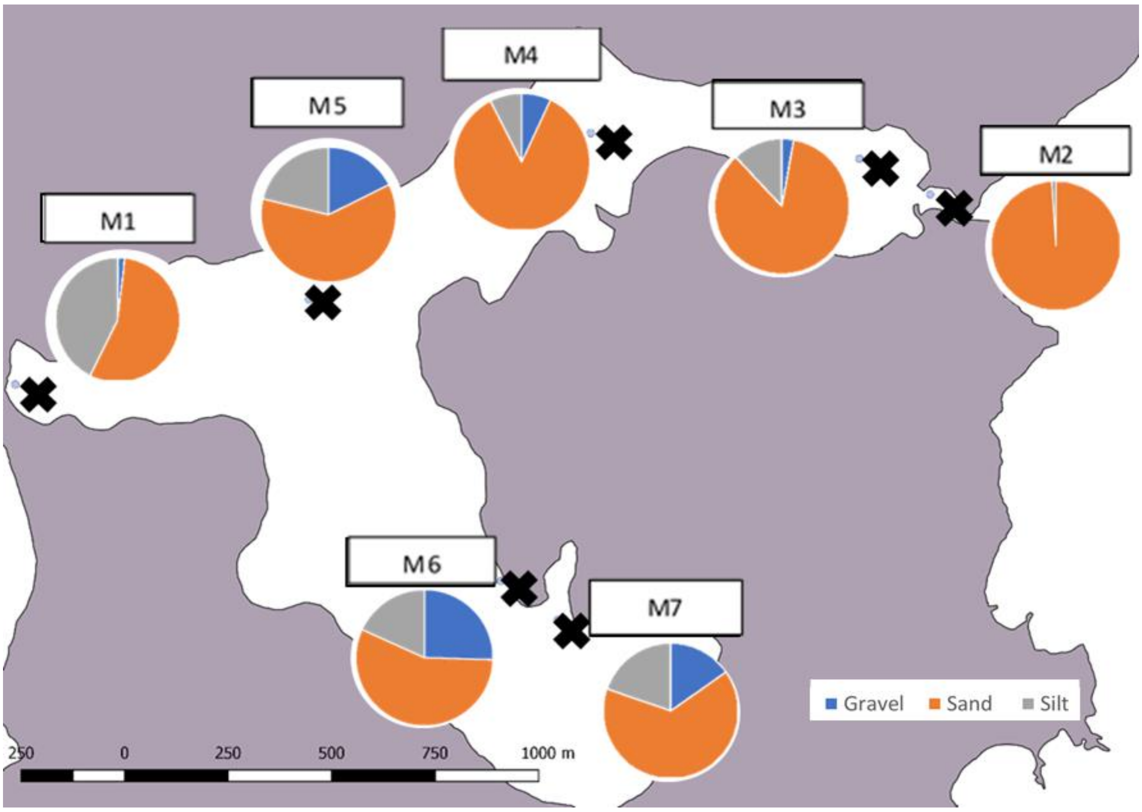

Figure A.4 - *Granulometry at the sampling sites in Malanza during the 2017 sampling. Percentage of each grain size class is shown in pie charts for each sampling point.*

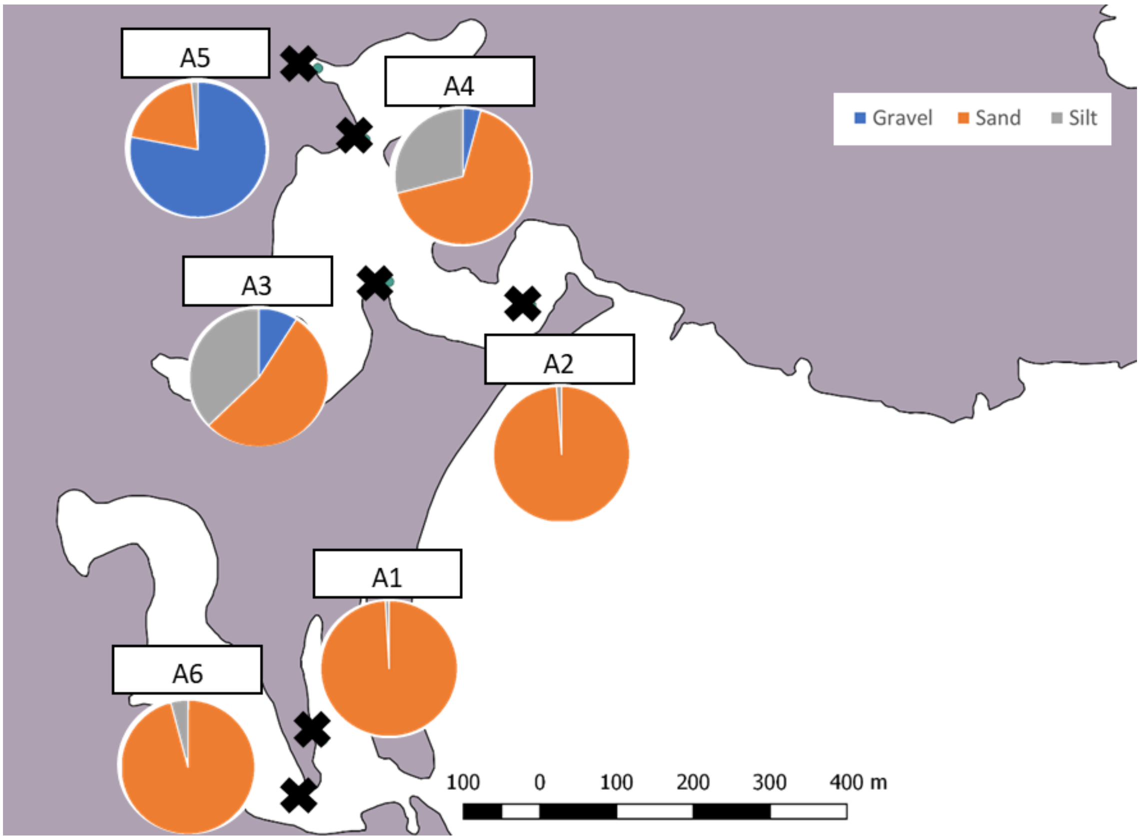

Figure A.5 - *Granulometry at the sampling sites in Angolares during the 2017 sampling. Percentage of each grain size class is shown in pie charts for each sampling point.*

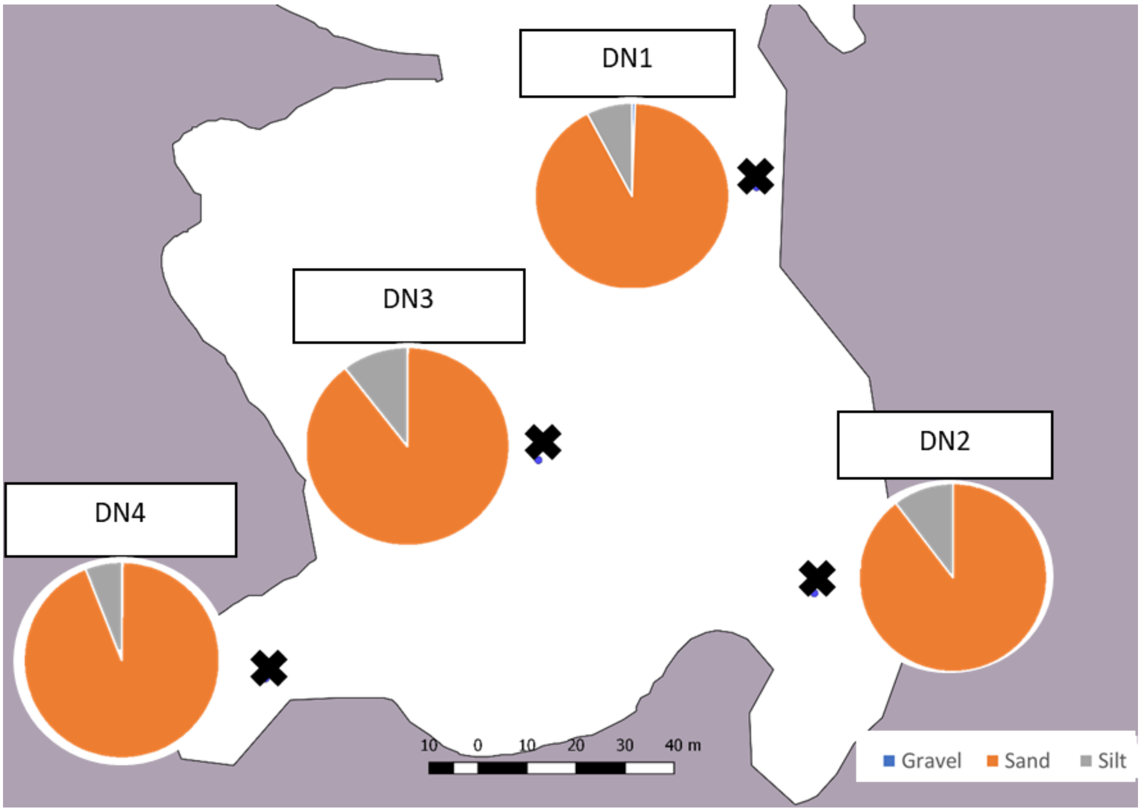

Figure A.6 *- Granulometry at the sampling sites in Diogo Nunes during the 2017 sampling. Percentage of each grain size class is shown in pie charts for each sampling point.*

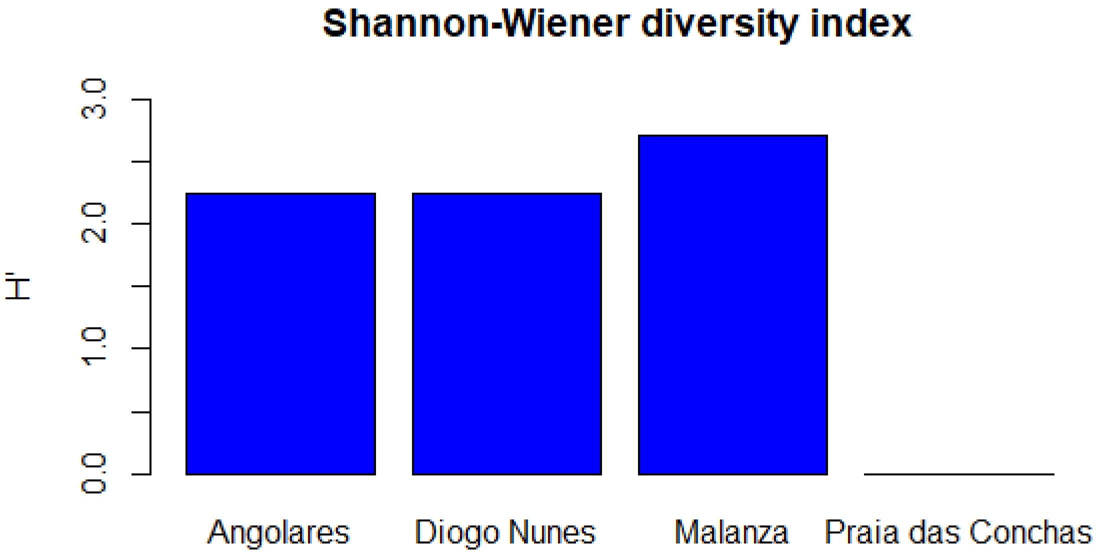

Figure A.7 *- Values obtained for the Shannon-Wiener diversity index (H') for each mangrove.*

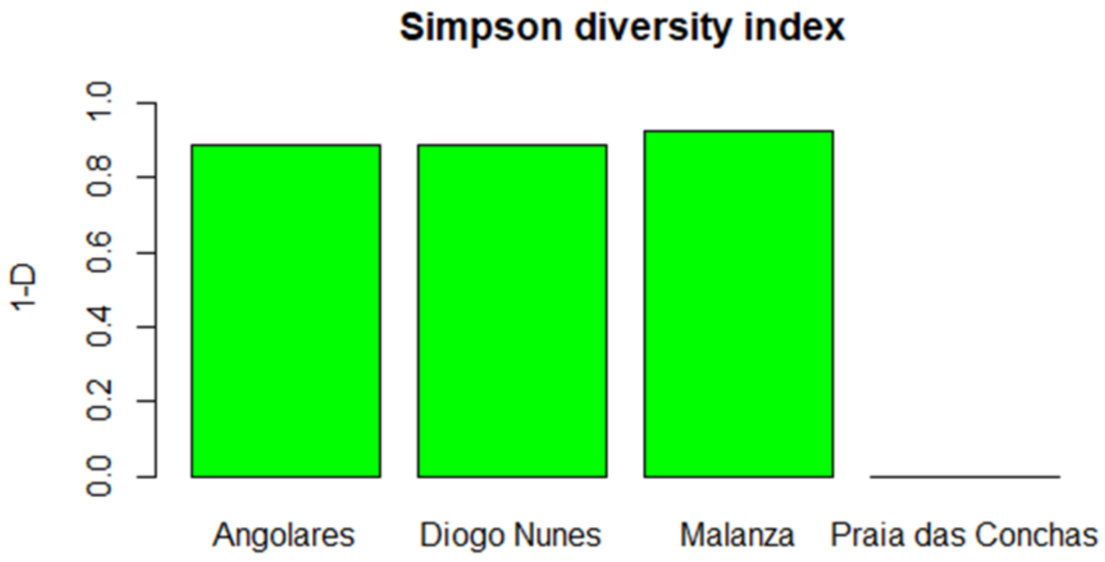

Figure A.8 *- Values obtained for the Simpson diversity index (1-D) for each mangrove.*

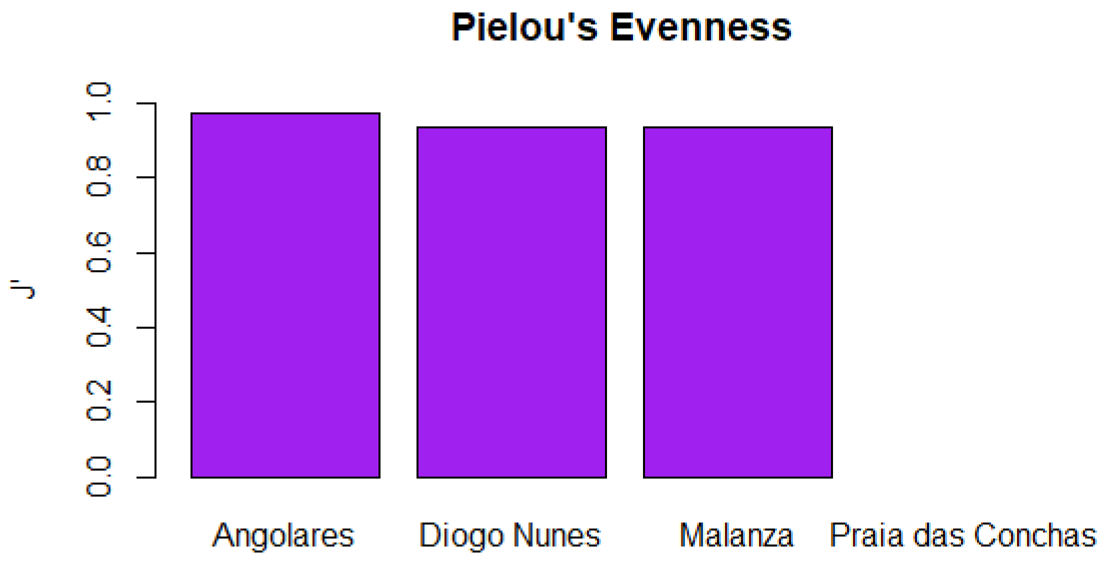

Figure A.9*- Values obtained for the Pielou's evenness (J') for each mangrove. In Praia das Conchas only one species was caught, therefore an evenness value could not be calculated.*

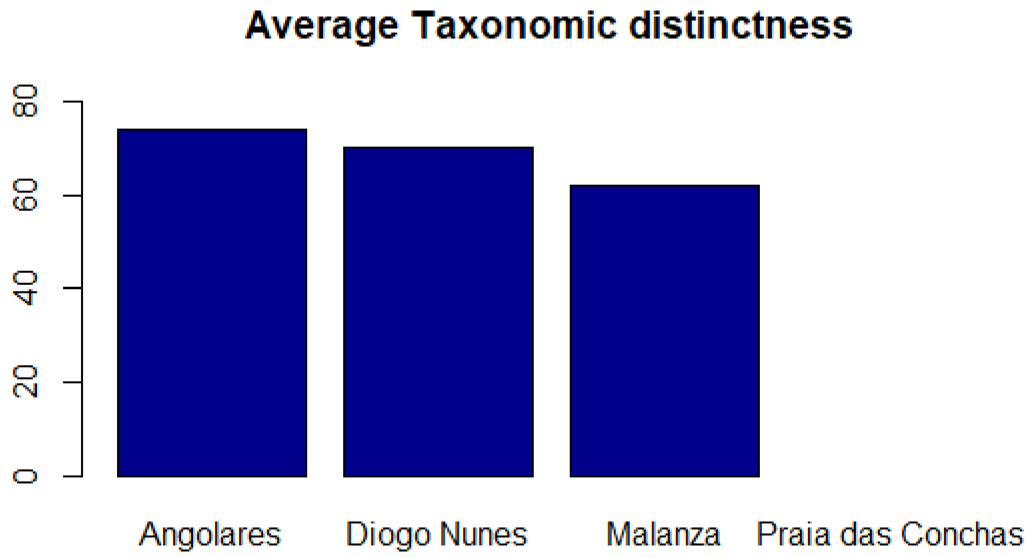

Figure A.10 *- Values obtained for the Average Taxonomic Distinctness (Delta+) for each mangrove. In Praia das Conchas only one species was caught and therefore the index could not be calculated).*

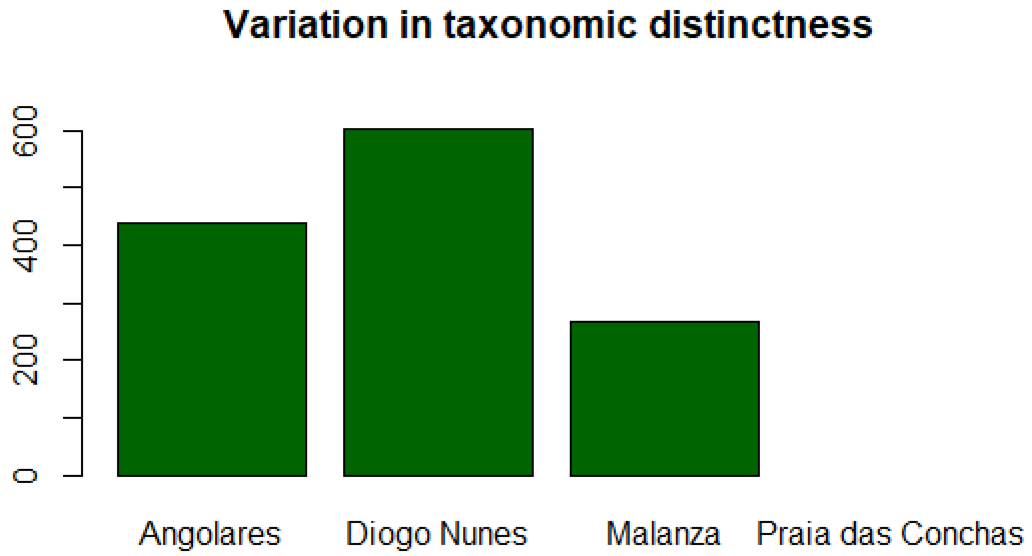

Figure A.11 *- Values obtained for the Variation in Taxonomic Distinctness (Lambda) for each mangrove. In Praia das Conchas only one species was caught and therefore the index could not be calculated.*