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**CAROLLINNY VILAS BOAS DOS PASSOS**

**DIVERSIDADE FUNCIONAL DE ASSEMBLEIAS DE PEIXES EM ECOSSISTEMAS  
TROPICAIS COSTEIROS**

Maceió – AL  
Fevereiro / 2014

**CAROLLINNY VILAS BOAS DOS PASSOS**

**DIVERSIDADE FUNCIONAL DE ASSEMBLEIAS DE PEIXES EM ECOSISTEMAS  
TROPICAIS COSTEIROS**

Dissertação apresentada ao Programa de Pós-Graduação em Diversidade Biológica e Conservação nos Trópicos, Instituto de Ciências Biológicas e da Saúde da Universidade Federal de Alagoas, como requisito para obtenção do título de Mestre em CIÊNCIAS BIOLÓGICAS, área de concentração em Conservação da Biodiversidade Tropical.

Orientadora: Nídia Noemi Fabr 

Coorientadora: Dra. Ana Cl udia Mendes Malhado

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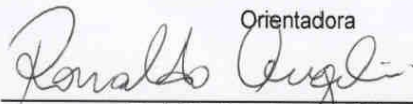
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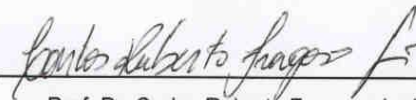
Orientadora



Prof. Dr. Ronaldo Angelini – UFRN  
(membro titular)



Prof. Dr. Fabrício Barreto Teresa – UEG  
(membro titular)



Prof. Dr. Carlos Ruberto Fragoso Junior – UFAL  
(membro titular)

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## RESUMO

Os ecossistemas costeiros tropicais estão entre os ambientes mais importantes do planeta, pois atuam como áreas de transição podendo afetar características estruturais do ambiente e padrões de distribuição de espécies de peixes. Estes locais podem também ser afetados por um processo conhecido como estuarização da plataforma que ocorre em regiões tropicais de plataformas continentais estreitas, devido a extensão das condições estuarinas e assim, espécies estuarinas podem ser responsáveis pela alteração na diversidade e abundância destes locais. Entre as diferentes medidas de biodiversidade, a Diversidade Funcional é uma chave para compreensão dos processos ecossistêmicos em áreas costeiras. Considerando regiões de estudo (influência de recifes, influência de lagoas e influência de estuário) três estratos de profundidade (10, 10 e 30 metros) e dois períodos sazonais (seco e chuvoso), o objetivo deste estudo foi avaliar de forma comparativa a diversidade funcional e os processos mais dominantes (filtragem de nicho e similaridade limitante) em um trecho de plataforma continental tropical da região costeira do Atlântico Sudoeste. A amostragem dos peixes foi realizada em três regiões costeiras durante estação chuvosa e seca, em três diferentes isóbatas. Foram utilizadas características relacionadas a morfologia, dieta e uso de hábitat das espécies. O índice de diversidade funcional utilizado foi  $SES_{MPD}$ . Este estudo evidenciou que os processos de regras de montagem de assembleias como a similaridade limitante são aplicáveis nos três ecossistemas costeiros estudados e ambos os locais possuem diversidade funcional alta em profundidades menores desta forma são encontradas mais espécies complementares e de baixa redundância funcional, sofrendo efeitos da estuarização. As regiões próximas ao Rio São Francisco em particular, também mantém uma baixa redundância funcional em profundidades maiores, porém não foi possível observar efeito de estuarização nestas isóbatas, devido ao efeito aos impactos sofridos ao longo do rio que alteram sua vazão natural. Isto demonstra que este ambiente em particular deve ser avaliado cuidadosamente, pois a retirada de determinadas espécies podem gerar efeitos drásticos para o ecossistema.

**Palavras-chave:** Ecossistemas costeiros. Plataforma continental. Estuarização. Regras de Montagem. Índice de Diversidade Funcional.



## ABSTRACT

Tropical coastal ecosystems are one of the most important environments on the planet because they act as transition areas that may affect the structural characteristics of the environment and distribution patterns of fish species. These sites may also be affected by a process known as estuarization of the shelf that occurs in tropical regions of narrow continental shelves, because the extent of estuarine conditions and thus estuarine species may be responsible for changes in diversity and abundance of these sites. Among the different measures of biodiversity, functional diversity is a key to understanding ecosystem processes in coastal areas. Whereas regions of study (influence of reefs, lagoons and influence of estuarine influence) three different depths (10, 20 and 30 meters) and two (dry and wet), seasons. The aim of this study was to evaluate comparatively the functional diversity and the most dominant processes (niche filtering and limiting similarity) in a stretch of tropical continental shelf of the coastal region of the southwest Atlantic. Fish sampling was conducted in three coastal regions during the rainy and dry season in three different isobaths. Related to morphology, diet and habitat use of species traits were used. The functional diversity index used was SESMPD. This study showed that the processes of assemblage rules as limiting similarity are applicable in the three coastal ecosystems and both places have high functional diversity at shallower depths thus more species are found additional functional and low redundancy conceding estuarization effects. The next to the São Francisco River in particular regions also maintains a low functional redundancy at greater depths but it was not possible to observe the effect of these estuarization isobaths due to the effect the impacts suffered along the river altering its natural flow. This demonstrates that this particular environment should be carefully evaluated, since the removal of certain species can cause drastic effects on the ecosystem.

**Key-words:** Coastal Ecosystem. Continental Shelf. Estuarization. Assemblage Rules. Functional Diversity Index.

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## 1. APRESENTAÇÃO

Esta dissertação apresenta uma avaliação da diversidade funcional, similaridade limitante e filtros ambientais em um trecho de plataforma continental com influência diferenciada de formações recifais costeiras e estuarinas (sistema de lagoas costeiras e desembocadura do principal rio da região nordeste do Atlântico Sul ocidental, Rio São Francisco). Para esta finalidade, iniciamos a dissertação com uma revisão da literatura, onde apresentamos bases conceituais sobre ecossistemas costeiros, diversidade funcional, características e grupos funcionais, relação entre a diversidade funcional e específica e variação das variáveis ambientais sobre a diversidade funcional, contextualizando o presente trabalho e fornecendo informações sobre a tema abordado.

A segunda parte da dissertação refere-se ao manuscrito intitulado: “Estuarization increases functional diversity of fish assemblages in tropical coastal ecosystems”, cujo objetivo foi avaliar de forma comparativa a diversidade funcional e os processos mais dominantes (filtragem de nicho e similaridade limitante) em um trecho de plataforma continental tropical da região costeira do Atlântico Sudoeste, com influência diferenciada de formações recifais costeiras, de sistema de lagoas costeiras e da desembocadura do Rio São Francisco (principal rio da região nordeste do Atlântico Sul ocidental).

A conclusão do trabalho encontra-se na penúltima sessão do manuscrito, no qual apresentamos conclusões e sugestões gerais relacionadas ao principal objetivo do trabalho. Desta maneira, esta dissertação gera informações de extrema relevância para o ecossistema costeiro situado no Nordeste do Atlântico sul, e oferece subsídios para projetos futuros de conservação nestes ambientes.

## 2. REVISÃO DA LITERATURA

### 2.1. Ecossistemas costeiros tropicais

Os ambientes costeiros tropicais – estuários, lagoas e formações recifais - estão entre os ecossistemas mais importantes e produtivos do planeta (Roberts et al., 2002; Babier et al., 2011; Pérez-Ruzafa & Marcos, 2012) além de fornecerem maior número de bens e serviços, atingindo 43% do total mundial (Constanza et al., 1997; Harley et al., 2006). Devido à variedade e complexidade destes ecossistemas, muitas espécies utilizam estes locais como área de reprodução, desenvolvimento e alimentação pela grande oferta de alimento disponível (Gaelzer & Zalmon, 2003). Desta maneira, estes locais oferecem às espécies de peixes associadas uma grande diversidade de nichos, sendo, por isto, indicadores relevantes das condições ambientais em diferentes escalas espaciais e temporais (Whitfield & Elliott, 2002; Babier et al., 2011).

Por outro lado, os ecossistemas costeiros são áreas de transição ecológica, expostos a processos marinhos e terrestres, fato que influencia as características estruturais e padrões de distribuição de assembleias de peixes (Nero & Sealey, 2006). Estudos demonstram que em regiões tropicais, grande parte das plataformas continentais é estreita, permitindo que algumas espécies de peixes, principalmente os juvenis utilizem o interior destas plataformas continentais assim como utilizam os estuários (Blaber & Blaber, 1980; Blaber, 1981; Longhurst & Pauly, 1987). Assim, não se pode limitar a classificar espécies estuarinas como aquelas que possuem um ciclo de vida associado a estuários (Baran, 2000). Outros fatores como biogeografia, extensão da zona estuarina, diversidade de habitat e abertura adjacente à ecossistemas, podem também determinar a diversidade de espécies destes locais (Albaret, 1999).

A impossibilidade de distinguir a fauna de peixes de estuários e do mar encontradas nos trópicos é resultado da entrada de espécies estuarinas no mar durante a estação de monções, fenômeno conhecido como “estuarização” da plataforma (Longhurst & Pauly, 1987). A estuarização da plataforma se dá pela expansão de algumas condições estuarinas como baixa salinidade e depósitos de lama (Lowe-McConnell, 1962; Rainer, Blaber et al., 1989). A redução de água doce nestes locais, seja por efeitos sazonais ou ao longo do tempo, poderia permitir que espécies tipicamente de plataforma continental ocorram em regiões subjacentes aos

estuários (Able, 2005), portanto, fatores físicos como entrada de água doce, turbidez (Blaber e Blaber, 1980), diminuição na ação das ondas de algumas áreas (Able, 2005) tornam estes locais como habitats alternativos.

De acordo com Hughes et al., (2003) as alterações na composição da diversidade e estruturação das assembleias, provocadas por algum tipo de alteração no ambiente seja ele natural ou antrópico, podem atrapalhar as funções ecológicas desempenhadas por conjuntos de espécies. Saber o quanto estas assembleias são resistentes ou não a estes distúrbios dependerá o grau de redundância ecológica no sistema, ou seja, quais espécies são distintas taxonomicamente, porém exibem as mesmas funções ecológicas (Walker 1992, 1995; Lawton & Brown 1993; Naim 1998; Micheli & Halpern, 2005).

Para explicar as possíveis consequências ecológicas na perda de espécies foi proposta a estimativa da relação entre a Diversidade Funcional (DF) e a Diversidade de Espécies (DE) (Petchey & Gaston, 2002; 2006); assim o padrão de composição dos grupos funcionais pode ser utilizado para avaliar as causas ou consequências na perda de espécies. Hughes (1994, 2003), por exemplo, observou uma redução de peixes herbívoros pela pesca, seguido por mortalidade em massa de ouriços-do-mar no início de 1980, provavelmente causado pelo aumento de algas que dominaram os recifes de corais. Micheli e Halpern, (2005), também comprovaram que baixos níveis de redundância nas características funcionais, tendem a remover grupos funcionais inteiros em ecossistemas marinhos costeiros. Desta forma, determinar as relações entre a Diversidade Funcional e a Diversidade de Espécies para diferentes assembleias, é uma questão de fundamental, principalmente para ecossistemas que passam por perturbações humanas, alterando então seus padrões de diversidade (Micheli & Halpern, 2005).

## **2.2. A Diversidade Funcional e características funcionais**

A diversidade funcional (DF) é uma medida que incorpora as semelhanças ecológicas das espécies, assim como, o valor das diferenças funcionais entre as espécies em uma comunidade (Tilman et al., 1997 e Mayfield et al., 2005). Tem se tornado uma ferramenta utilizada com sucesso em ecossistemas terrestres principalmente para plantas (Tilman et al., 2001; Diaz e Cabido, 2001) e, nos últimos anos, vem sendo estimada também para aves (Petchey et al., 2007; Hidas-

Neto, 2012), insetos (Woodcock et al., 2014) e microrganismos (Rondon et al., 2000; Kumar et al., 2014). No caso de ambientes aquáticos para ecossistemas lagunares (Mouillot et al., 2007, Villéger et al., 2010), estuarinos (Nicholas et al., 2011), rios e riachos (Noble & Cowx, 2007; Teresa & Casatti, 2010). Uma atenção maior tem sido dada aos recifes, pois são ambientes complexos responsáveis por disponibilizar diversos microhabitats e abrigarem uma alta diversidade de peixes (Bellwood, 2004; Halpern & Floeter, 2008; Cole et al., 2008; Hastings & Galland, 2010; Plaisance et al., 2011; Stuart-Smith, 2013).

Diversas definições têm sido propostas para definir diversidade funcional: “O número do tipo de funções realizadas por organismos dentro de um ecossistema” (Diaz & Cabido, 2001), “Um conjunto de atributos funcionais dentro de uma comunidade” (Tesfaye et al.; 2003), “A variedade de características ecológicas e a história de vida das espécies em uma assembleia local” (Petchey & Gaston, 2006) . As definições que permeiam este conceito levantam outras questões sobre como medir a diversidade de características funcionais, as quais são componentes de características fenotípicas de um organismo, podendo influenciar os processos ecossistêmicos (Petchey & Gaston, 2006). Por estas razões, alguns índices de Diversidade Funcional têm sido propostos, estes índices diferem na forma de como quantificar a diversidade (Petchey & Gaston, 2006), pois incorporam as semelhanças ecológicas e quantificam o valor das diferenças funcionais entre as espécies de uma comunidade (Tilman et al., 1997; Mayfield et al., 2005).

A escolha das características funcionais deve ser feita a priori, pois é necessário que se conheça sobre estas características e que se entenda sobre as teorias ecológicas e os processos de regras de montagem que estruturam as comunidades a serem estudadas (Petchey et al., 2004; Petchey e Gaston, 2006; Petchey et al., 2007). Desta maneira, estas características devem então explicar e prever as variações nos processos a nível ecossistêmico (Lavorel et al., 1997; Walker et al., 1999; Petchey & Gaston, 2002; Ricotta, 2005; Naeem, 2002).

Uma característica funcional é qualquer característica morfológica, fisiológica ou fenológica mensurável em um indivíduo (Violle et al., 2007). O que se sabe é que todas as características são importantes para as espécies, porém em nível ecossistêmico, algumas características não são funcionalmente informativas, isto depende de estudos baseados em observações, estudos experimentais e uma literatura rica e relevante (Petchey & Gaston 2007). A respeito da quantidade de



características funcionais a serem utilizadas, não se deve ter como alvo o número de características e sim o número de características funcionalmente importantes (Petchey & Gaston, 2006). Segundo Mouillot et al., (2007) em peixes as características funcionais devem ser mais estudadas, pois estas podem ser futuramente os parâmetros-chave para se entender a estrutura da comunidade deste grupo.

### **2.3. Relação entre a DF e DE**

Medidas tradicionais da diversidade de espécies nas comunidades são baseadas nos índices e modelos de diversidade que relacionam o número e abundância das espécies (Pielou, 1969; Begon, et al. 2007). Porém estes índices são baseados apenas nas características taxonômicas, desta maneira, a importância do papel funcional e como as espécies podem responder às condições ambientais não é considerado (Petchey, 2004; Petchey et al., 2004; Villéger et al., 2010). Frente a estas questões, Petchey & Gaston (2002), Nummelin & Kaitala (2004), Ernst et al., (2006), Hidasi-Neto et al., (2012), sugerem estimativas alternativas baseadas na função das espécies no ecossistemas e que expliquem como as comunidades estão estruturadas, os índices de diversidade funcional.

A perda da biodiversidade marinha gera consequências inesperadas para o funcionamento ecossistêmico, por este motivo, é importante a compreensão de como estão as propriedades estruturais estão organizadas assim como o número e a composição de espécies, abundância relativa e como estas estão relacionadas com as funções ecológicas desempenhadas pelas espécies (Micheli & Halpern, 2005). O grande desafio é que o quanto a Diversidade de espécies e a Diversidade Funcional estão relacionadas é desconhecida para a maioria dos ecossistemas (Naeem, 2002) e esta relação dependerá principalmente da extensão da redundância ecológica dentro da assembleia (Lawton & Brown, 1993; Naeem, 1998; Walker, 1999; Micheli & Halpern, 2005).

A redundância funcional implica no número de espécies distintas que apresentam funções ecológicas semelhantes (Lawton & Brown, 1993; Naeem, 1998). Baixa redundância funcional indica que a medida que a diversidade de espécies de um sistema diminui, o número de características funcionais também são perdidas, por outro lado, alta redundância funcional indicam que mesmo que a diversidade de espécies de um sistema diminua, o número de características

funcionais continua robusto, isto está relacionado à capacidade de recuperação das assembleias frente a estas perdas (Micheli & Halpern, 2005).

#### **2.4. As variáveis ambientais e a Diversidade Funcional**

Os ecossistemas costeiros possuem características particulares, são áreas de transição ecológica, expostos a processos marinhos e terrestres, fato que influencia as características estruturais e padrões de distribuição de assembleias de peixes (Nero & Sealey, 2006). Isto porque estes locais passam por influências de lagoas e estuários, tendo assim um grande aporte de nutrientes provenientes de fontes externas, sendo dispersos no mar até profundidades de aproximadamente 15-20 metros, as chamadas zonas de transição (Longhurst e Pauly, 1987; Blaber, 2002). Os processos sazonais também podem acarretar no aumento ou diminuição de alguns fatores abióticos, desta forma, a composição de peixes de zonas costeiras pode ser influenciada (Blaber, 1995, 2002).

Neste contexto, alguns os fatores como oxigênio dissolvido, temperatura, turbidez, produtividade primária e profundidade estão relacionados com a variação sazonal influenciando a distribuição, abundância e hidrodinâmica das espécies (Lowe-McConnell, 1987; Paperno et al.,2001). Desta maneira, os fatores abióticos e os gradientes ambientais são capazes de gerar mudanças graduais da composição de peixes, desde águas doces e rasas para águas marinhas e profundas, sendo assim, além destas mudanças caracterizarem as assembleias de peixes da plataforma costeira (Jaureguizar, et al. 2004), é necessário saber se estes fatores podem explicar também a variação da diversidade funcional.

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### 3. Estuarization increases functional diversity of fish assemblages in tropical coastal ecosystems

VILAS-BOAS, C.P.<sup>1\*</sup>; FABRÉ, N.N.<sup>1</sup>; MALHADO, A.C.M.<sup>1</sup>; LADLE, R.J.<sup>1</sup>

1. Federal University of Alagoas, Institute of Biological Sciences and Health, Fish Ecology and Fisheries Lab, Rua Aristeu de Andrade 452, Farol, Maceió, Alagoas, 57051-090, Brasil

\* Corresponding author: e-mail: [caroll\\_vilas@hotmail.com](mailto:caroll_vilas@hotmail.com)

#### 3.1 Abstract

Two contrasting processes are thought to control functional diversity within ecological communities: abiotic filters increase functional similarity by selecting species with similar traits while biotic interactions, mainly competition, limit the functional similarity of co-occurring species. Here, we investigate this hypothesis by assessing the effect of seasonal fluctuations in abiotic conditions on the functional diversity (FD) of tropical coastal fish assemblages. Specifically, we predict that FD will increase in the rainy season (relative to the dry season) in shallow coastal areas as estuarine adapted species enter coastal waters. Fish sampling was carried out in three regions in northeast Brazil, predominantly influenced by reefs, lagoons and estuaries, respectively. Sampling was conducted over both seasons (rainy and dry) and in three different depth strata (10, 20 and 30 meters). FD was estimated through a functional diversity index ( $SES_{MPD}$ ) based on key phenotypic and behavioural characteristics (morphology, diet and habitat use). All three sites had higher functional diversity in the rainy season at shallower depths, indicating a greater number of complementary species with low functional redundancy in areas impacted by seasonal inundations. Deeper sites had lower FD than shallow sites, although this difference was less pronounced for Region 3, which was strongly affected by the São Francisco River. The higher FD in these sites may be due to the increased impact of such a large water source. Our results support the hypothesis that abiotic filters constrain FD in the dry season and that the alterations in abiotic conditions caused by estuarization in the rainy season allow estuarine-adapted fish with different functional traits to invade shallow coastal regions.



**Keywords:** Coastal zone; continental shelves; environmental factors; species diversity; assembly rules; estuarization.

### 3.2 Introduction

A functional approach to community ecology has considerable potential for providing insights into ecological processes such as ecosystem invasibility and community assembly (Byun et al., 2013; McGill et al., 2006; Messier et al., 2010; Violle et al., 2007). Indeed, by concentrating on the analysis of functional traits - “components of an organism’s phenotype that influence ecosystem level processes” (Petchey and Gaston, 2006, p. 742) – it may be possible to untangle the complex interactions that determine which species enter assemblages when biophysical conditions alter. Measures of FD can thus be used to better understand how local communities are assembled from regional species pools (Pavoine et al., 2009; Petchey et al., 2004; Weiher and Keddy, 1999).

Two contrasting processes have been identified as crucial for structuring local assemblages: environmental filtering and limiting similarity (Chase et al., 2005; Pavoine et al., 2011). Environmental filtering assumes that abiotic factors (e.g. salinity, temperature, etc.) act to constrain certain traits within limits and, by extension, limits membership of assemblages to species that possess these traits. In contrast, limiting similarity operates through interspecific interactions (e.g. competition) that prevent the coexistence of species that are too similar in their resource requirements (Pavoine et al., 2011). Thus, whereas the presence of environmental filters generates functional similarity by selecting, for example, a suite of species due to their shared tolerance to prevailing abiotic conditions (Mouchet et al., 2010), limiting similarity generates functional dissimilarity by excluding species that are too functionally similar to one or more species in the assemblage (Hidasi-Neto et al., 2012).

Transitional habitats, where abiotic conditions vary over time and space, have considerable potential for assessing the relative roles of limiting similarity and environmental filtering in assemblage formation. For example, the abiotic conditions in coastal shelf ecosystems may be strongly influenced by input from the land (e.g. rivers, run-off, etc.), the degree of influence being a product of the magnitude of the input and the geophysical characteristics of the shelf (e.g. depth, presence of reefs, etc.) (Nero and Sealey, 2006). In turn, alterations in the abiotic characteristics of the

coastal shelf environment have the potential to influence the patterns of distribution, migration and abundance of fish (Longhurst and Pauly, 1987; McConnell and Lowe-McConnell, 1987; Paperno et al., 2001).

The extension of estuarine conditions (e.g. low salinity and high sediment loads) onto the coastal shelf is known as "estuarization" and is particularly prevalent in the tropics where the shelf is often short and shallow with abundant freshwater inputs (Able, 2005; Longhurst and Pauly, 1987). Estuarization will typically increase in the rainy season during which estuarine species may enter marine regions altering the diversity and abundance of fish assemblages (Able, 2005; Blaber, 2002). Here, we use a functional diversity (FD) approach to investigate the influence of estuarization on fish assembly structure in a region of the tropical Atlantic coast in northeast Brazil. This region has a narrow continental shelf (50 km) and is therefore strongly influenced by reef and estuarine ecosystems. Specifically, we test two interlinked hypotheses related to the concept of environmental filtering (i) FD will decrease in the dry season when estuarine-adapted species are abiotically restricted to rivers and lagoons; (ii) changes in FD induced by seasonal changes in abiotic conditions will be more apparent in shallow coastal areas than deep coastal areas.

### 3.3 Materials and Methods

#### 3.3.1 Study area

The study area is located in the Southwest Atlantic Tropical coastal region of northeast Brazil, between 09°47'80.4"S, 35°49'56"O and 10°21'26.8"S, 36°05'32.9"O (Figure 1), extending approximately 300 km. The entire region is characterized by a narrow continental shelf and which contains abundant reef formations, lagoons and estuarine areas (Medeiros et al., 2007). This section of coastline falls into three geomorphologically distinct areas which were used to stratify our samples:

Region 1: Northern section characterized by a continental shelf of ~20 km of up to 40 m depth. This region contains a high frequency of barrier reefs (formed from beach-rock) making up 23% of the total area.

Region 2: Mid-section characterized by a continental shelf of ~30 km of up to 50 m depth. Biophysical conditions in this region are influenced by one of the largest lagoons of Brazil, the Mundaú-Manguaba complex: in Portuguese, the *Complexo Estuarino-Lagunar Mundaú-Manguaba* (CELMM). The CELMM has an area of 23,122 km<sup>2</sup> (Melo-Magalhães et al., 1998) and influences the surrounding coastal

area through a recurrent plume of sediment that may extend as far as 6 km from the beach line with a total length of up to 12 km.

Region 3: Southern section with a continental shelf of up to 50 km and 80 m depth. This region is strongly influenced by the São Francisco River, the third largest river in Brazil with a drainage area of 639,219 km<sup>2</sup> (Santos, 1996). The depth of the estuary is variable, reaching about 14 meters near the mouth. The pro-delta of the São Francisco River is located between 0.5 and 2.5 km from the mouth, and is characterized by high waves and submerged sand banks (Medeiros et al., 2007). Sediment plumes from the river may extend for 10 km from the beach line and have a length of up to 20 km.

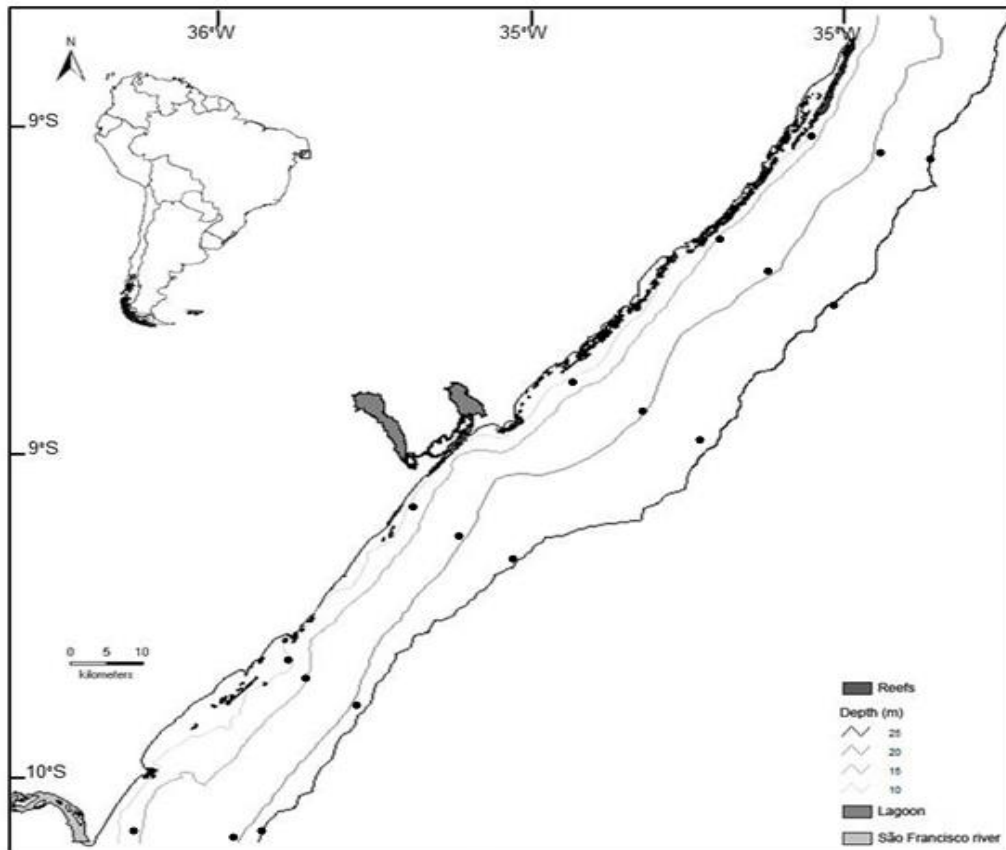
### 3.3.2. *Experimental design and data collection*

The study area was divided into three latitudinal strata of 1.5' (corresponding to regions 1, 2 and 3 – see above). Each stratum contained six sampling sites, making a total of 18 sampling points (Figure 1).

Data were collected in the dry season (January-April 2013) and the rainy season (May-July 2013). At each sampling point the following physicochemical and environmental parameters were recorded: temperature, turbidity, salinity, dissolved oxygen, primary productivity (Chlorophyll a) and depth. Variables were recorded with a Multiparameter Sonde (YSI 6600 V2) except for depth, which was measured with an Echo Sounder (SDE-28S).

Fish were caught with a set of ten nylon gillnets. Each net was approximately 100 m long, 2.90 m high and had a mesh sizes ranging from 20 to 80 mm between opposite knots. The net was set at the bottom for catching demersal species. Fish were identified to species level using Figueredo and Manezes (1978) and Lessa and Nobréga (2000). The following measurements were taken from each individual: total length (TL), maximum body height (MBH), eye height (EH), caudal peduncle length (CPdL), head length (HdL) and head height (HdH).

Figure 1. Sampling sites on the Alagoas Coast (Region 1: influenced by reef formations; Region 2: influenced by lagoons; Region 3: influenced by the estuary of São Francisco River) at depths of 10, 20 and 30 meters, in Northeastern Brazil, Atlantic Ocean.



Fonte: Autora da dissertação, 2014.

Data were collected in the dry season (January-April 2013) and the rainy season (May-July 2013). At each sampling point the following physicochemical and environmental parameters were recorded: temperature, turbidity, salinity, dissolved oxygen, primary productivity (Chlorophyll a) and depth. Variables were recorded with a Multiparameter Sonde (YSI 6600 V2) except for depth, which was measured with an Echo Sounder (SDE-28S).

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### 3.3.3 Functional traits

Functional traits were based on diet and habitat use of the species (Table 1) and also with mobility (territorial, migratory and highly mobile species). Functional characteristics relating to ecosystem processes such as trophic dynamics, matter and energy cycling, population control and prey relationships were based on the trophic guild of each species (herbivores, carnivores, omnivores and piscivores). These data were obtained from the Fishbase ([www.fishbase.org](http://www.fishbase.org)) open access database. Standard length (SL) and weight (mass) were estimated following Teixeira and Bennemann (2007) and Mouillot et al., (2007).

**Table 1: Functional traits (after Micheli and Halpern, 2005; Mouillot et al., 2007; Teixeira and Bennemann, 2007).**

<b>Morphological relationships</b>	<b>Formulas</b>	<b>Description</b>
Relative head length	HdL/SL	Directly related to the consumed food size (Gatz Jr, 1979).
Eye position	EH/HdH	High values show eyes dorsally positioned, characteristic of benthic fish (Watson and Balon, 1984).
Relative body eight	MBH/SL	Directly related to the ability move vertically and inversely related to high hydrodynamics environments (Pouilly et al., 2003).
Relative length of the caudal peduncle	CPdL/SL	Longer peduncles indicate good-swimmers that inhabit high hydrodynamic environments (Watson and Balon, 1984).
Mobility	TE, HM, M	Characteristics associated with the habitat use of species (Micheli and Halpern, 2005).
Trophic guild	CA,OM, HE	Characteristics associated with diet type of the species (Mouillot et al., 2007).

**Fonte: Autora da dissertação, 2014**

### 3.3.4 Functional diversity indices

Based on each species collected (rows) and its respective functional traits (columns) (annex 1), a matrix was constructed for obtaining a functional dendrogram. An adaptation of the Gower distance (Pavoine et al., 2009) was used to calculate similarity, because the data was continuous and discrete. The Unweighted Pair Group Method with Arithmetic mean (UPGMA) algorithm was used for dendrogram construction and clustering.

The FD index was calculated using the mean pairwise distance (MPD), a measure influenced by basal variations of the functional dendrogram (because it calculates the average pairwise distance between each species in the assemblage).

To test whether the species coexisting in the observed assemblages are more or less similar than the expected by chance, a null model was used to compare the MPD values with a mean value obtained from 1000 randomly generated assemblages. To achieve this purpose, the independent swap algorithm (Gotelli and Entsminger, 2001) was adopted. The regional pool of species represented all the species collected in the area, including dry and rainy seasons. Standardized effect size ( $SES_{MPD}$ ) was calculated as the difference between the observed value (MPD value) and random value (mean value of randomized communities) divided by the standard deviation values obtained from the 1000 randomizations.

The MPD standardized effect size values indicate whether there was a functional overdispersion (values greater than 0) or functional clustering (values lower than 0) (Gomez et al., 2010). These analyses were carried out in R (RDevelopment, 2010), using the 'ses.mpd' functions from the picante package (Hidasi-Neto et al., 2012; Kembel et al., 2010).

### *3.3.5 Environmental filtering*

Principal components analysis (PCA) was performed to assess environmental filtering and variations in functional diversity, clustering samples according to environmental similarity and testing differences in FD among groups. The analyses were based on a correlation matrix composed of variables that may act as filters: temperature, depth, dissolved oxygen, salinity, turbidity and primary productivity. Statistical computations were performed with STATISTIC program (version 7.1). PCA scores were orthogonally spatially designed to identify which depth strata has the highest functional diversity.

## **3.4 Results**

### *3.4.1 Functional clustering*

Seven combinations of functional traits were used for the formation of functional clustering (Carnivorous: High Mobility, Carnivorous: Migratory, Carnivorous: Territorial, Herbivorous: Territorial, Omnivorous: High Mobility, Omnivorous: Migratory

and Omnivorous: Territorial) (Table 2). Functional traits such as trophic guilds and mobility, when used alone, are not able to explain the variations of functional diversity indices, although migratory groups tend to exhibit higher variation in functional diversity values.

**Table 2: Functional clustering in the three study regions (region 1 - influenced by reef formations, region 2 - influenced by lagoons and region 3 - influenced by estuary) in dry and rainy seasons. S: Season; D: Dry; R: Rainy.**

Region	S	Carnivorous: High mobility	Carnivorous: migratory	Carnivorous: territorial	Herbivorous: territorial	Omnivorous: high mobility	Omnivorous: migratory	Omnivorous: territorial	Total
1	D	4	4	4	-	3	1	1	17
2	D	6	2	5	-	5	1	2	21
3	D	6	1	6	-	4	3	2	22
1	R	6	2	5	-	3	3	3	22
2	R	6	2	4	1	2	2	3	20
3	R	6	5	6	-	5	-	2	24

**Fonte: Autora da dissertação, 2014.**

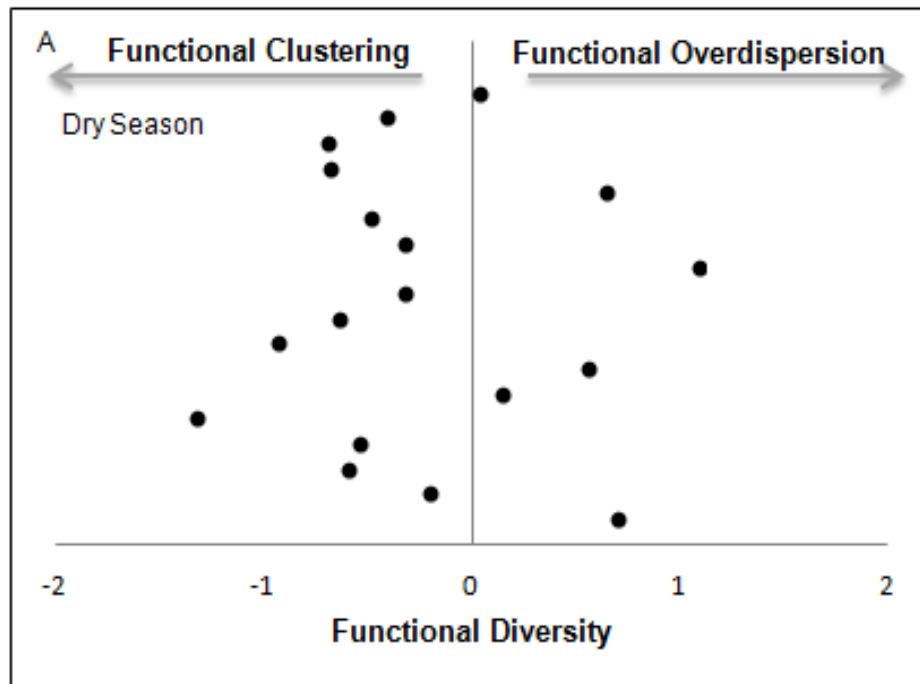
### 3.4.2 Seasonal variation in FD

A total of 1,039 individuals were collected: 333 from region 1 (reef influenced), 372 from region 2 (lagoon influenced) and 334 from region 3 (influenced by the São Francisco estuary). The functional dendrogram associated the 85 species collected into two main groups for shared functional traits (guild, mobility and morphological characteristics). The first group is represented by Lutjanidae, Carangidae, Polynemidae, Ariidae, Haemulidae, Mullidae, Triglidae and Acanthuridae. The second group is represented by Sciaenidae, Clupeidae, Scombridae, Scaridae, Sphyraenidae and another three families from Chondrichthyes (Rhinobatidae, Sphyrnidae and Carcharhinidae). Several species were unique to each geomorphologically distinct region (eg. *Cetengraulis edentulus* and *Calamus*

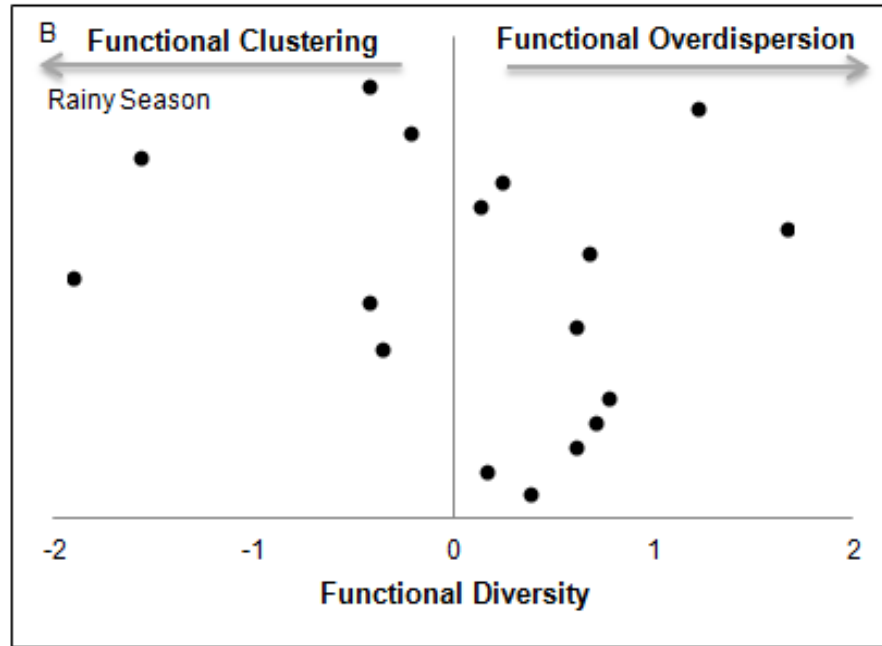
*pennatula* in the reefs; *Menticirhus litoralis* and *Sphyræna tome* in the lagoon area; and *Polydactillus virginicus* and *Lutjanus vivanus* in the estuarine regions).

The functional diversity measured for the dry and rainy seasons was different than that expected by chance (standardized effect size different from 0). As predicted, in the dry season, species are more diverse and functionally complementary (Figure 2 a). In contrast, the assemblages collected in the rainy season had higher levels of functional clustering (Figure 2 b).

**Figure 2a and 2b: Functional Diversity of assemblages for the 3 different regions (region 1 - influenced by reef formations, region 2 - influenced by lagoons and region 3 - influenced by estuary) in two strata depth during the dry and rainy seasons.**







Fonte: Autora da dissertação, 2014.

### 3.4.3 Environmental variables and functional diversity

The first two components of the PCA explained 54.22% of the variability, (36.35% in the first component and 17% in the second). The variables related to Factor 1 were temperature, turbidity, salinity and, negatively, oxygen. For Factor 2, depth and oxygen were positively associated (Table 3, Figure 3).

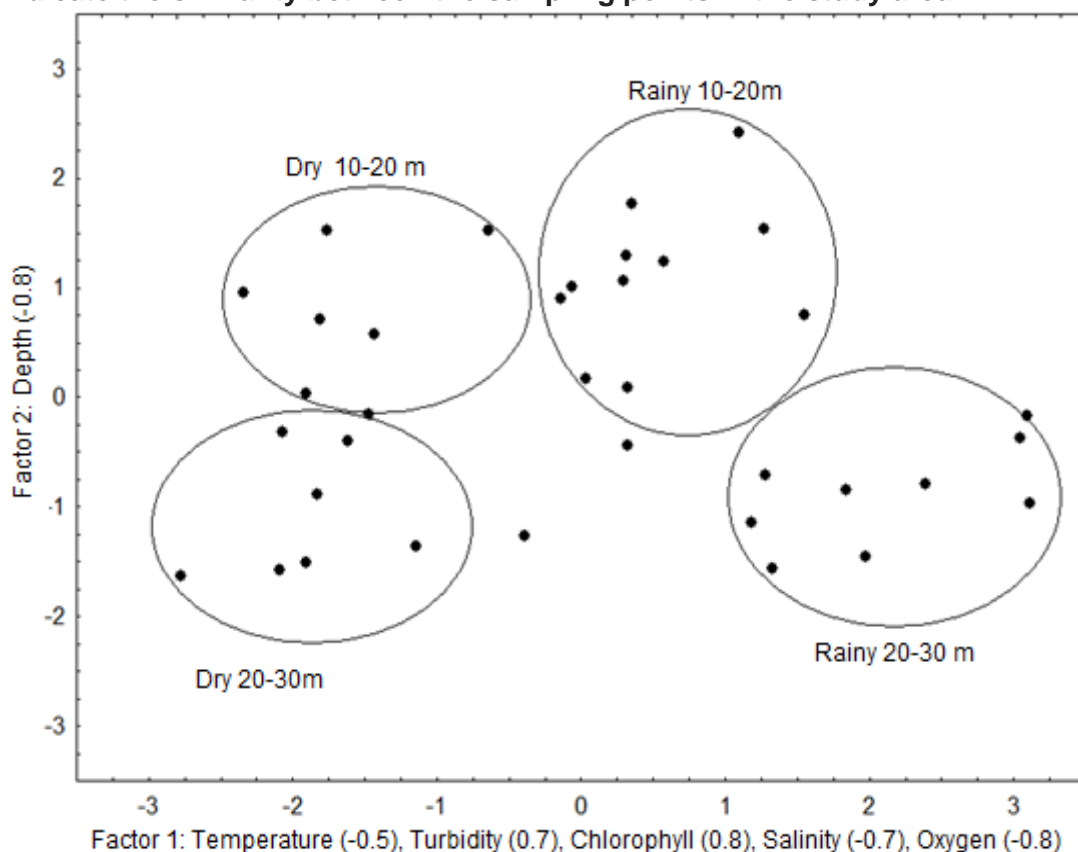
**Table 3: Mean and standard deviation (SD) of environmental variables for the four groups (season and depth) as demonstrated in the PCA.**

Group	FD	Depth (m)	Temp. (C°)	Turbid. (TU)	Chloro a	Salinity (SAL)	Oxygen (O <sup>2</sup> )
Shallow- rainy	0.28 ±0.75	13.33 ±4.92	27.92 ±0.30	0.40 ±0.23	1.65 ±0.87	36.51 ±0.67	1.18 ±0.88
Deep- Rainy	-0.74 ±1.23	26.67 ±5.00	27.80 ±0.36	0.69 ±0.42	2.16 ±0.58	34.91 ±0.85	0.96 ±0.06
Shallow- dry	0.12 ±0.67	14.29 ±5.35	28.42 ±0.31	0.05 ±0.22	1.06 ±0.58	37.24 ±0.08	3.47 ±1.14
Deep- Dry	-0.26 ±0.55	27.50 ±4.63	28.14 ±0.34	-0.01 ±0.40	0.26 ±0.30	37.15 ±0.26	3.58 ±1.07

Total	-0.13	20.00	28.03	0.32	1.35	36.39	2.10
	$\pm 0.91$	$\pm 8.28$	$\pm 0.38$	$\pm 0.42$	$\pm 0.96$	$\pm 1.08$	$\pm 1.48$

Fonte: Autora da dissertação, 2014.

Figure 3: PCA score of factors 1 and 2 explains 59.34% of the variability. The circles indicate the similarity between the sampling points in the study area.



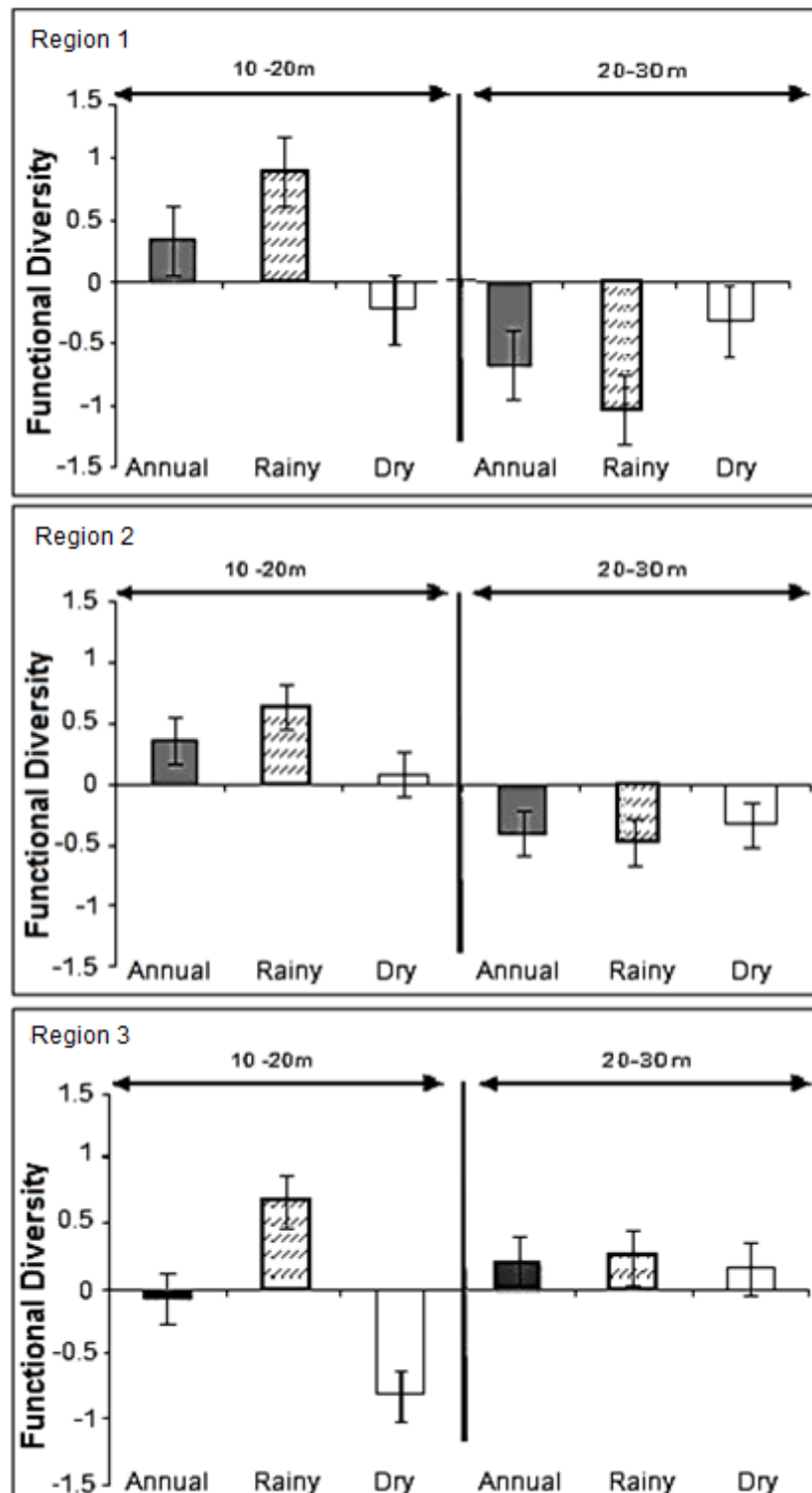
Fonte: Autora da dissertação, 2014

The PCA groupings can be interpreted in terms of seasonality and depth (Figure 3). FD is higher in shallow waters (10-20 m) and in the rainy season (Figure 4). The most significant environmental variables in the rainy season were chlorophyll, turbidity and temperature, while depth was more important in the dry season (Figure 4). However, the patterns of FD in region 3 (influenced by the São Francisco River estuary) are more variable than the other two regions. Indeed, this region maintains higher FD at greater depths in both rainy and dry seasons even though there appears to be a strong seasonal signal in the 10-20m depth zone (Figure 4). In

contrast, the reef and lagoon influenced environments are characterized by the predominance of environmental filter effects at greater depths.

Unique species and assemblages were associated with each stratum and depth zone (Table 4). The samples from the 10-20 m depth zone of the three study regions were composed of 75% estuarine species and 25% reef species in contrast to the 20-30 m isobaths, which were composed of 58% estuarine species and 42% of reef species. The region influenced predominantly by reefs (Region 1) and that influenced predominantly by lagoons (Region 2) had a higher number of unique species in the rainy season. However, the Region (3) influenced by the São Francisco estuary had a similar proportion of unique species during the two periods analysed.

Figure 4 - Functional Diversity of assemblages for the 3 different regions (region 1 - influenced by reef formations, region 2 - influenced by lagoons and region 3 - influenced by estuary) in two strata depth during the dry and rainy season.



Fonte: Autora da dissertação, 2014

**Table 4 - Unique species of each collected region at 10-20m and 20-30m depths during dry and rainy seasons. Ability to live in Brackish water from fishbase ([www.fishbase.com](http://www.fishbase.com)).**

	Region	Depth Zone		Season	
		10-20m	20-30m	Dry	Rainy
<i>Acanthurus bahianus</i>	2		x		x
<i>Aconthostracion polygonus</i>	1		x	x	
<i>Balistes capriscus</i>	1		x		x
<i>Balistes vetula</i>	3		x		x
<i>Bairdiella ronchus (br)</i>	3		x	x	
<i>Bothus ocellatus</i>	2		x	x	
<i>Bothus robinsi</i>	2		x	x	
<i>Calamus pennatula</i>	1		x		x
<i>Cephalopholis fulva</i>	3		x	x	
<i>Cetengraulis edentulus (br)</i>	1	X	x		x
<i>Chaetodipterus faber (br)</i>	3	X			x
<i>Cynoscion microlepidotus (br)</i>	1	X		x	
<i>Cynoscion virescens (br)</i>	1		x	x	
<i>Dactylopterus volitans (br)</i>	1		x		x
<i>Diplectrum formosum</i>	3	X			x
<i>Echeneis naucrates (br)</i>	1	X		x	
<i>Genyatremus luteus (br)</i>	3		x	x	
<i>Haemulon aurolineatum</i>	2		x	x	
<i>Haemulon plumieri</i>	1		x	x	
<i>Hemicaranx amblyrhynchus</i>	3		x	x	
<i>Isopisthus parvipinnis (br)</i>	3		x	x	
<i>Lutjanus analis (br)</i>	1		x	x	
<i>Lutjanus cyanopterus (br)</i>	3	X			x
<i>Lutjanus vivanus</i>	3	X		x	
<i>Menticirrhus litoralis (br)</i>	2	X	x		x
<i>Odontoscion dentex</i>	1		x		x
<i>Orthopristis ruber (br)</i>	2		x	x	
<i>Peprilus paru (br)</i>	2		x		x
<i>Polydactylus virginicus (br)</i>	3	X	x		x
<i>Scarus guacamaia</i>	1	X		x	
<i>Sphyraena tome</i>	2	X		x	
<i>Syacium papillosum</i>	1		x		x
<i>Trichiurus lepturus (br)</i>	2		x		x
<i>Ulaema lefroyi</i>	2		x		x

Fonte: Autora da dissertação, 2014.

### 3.5 Discussion

Mechanistic models of community assembly state that biotic and abiotic filters constrain species establishment through selection on their functional traits (Emerson and Gillespie, 2008; Lebrija-Trejos et al., 2010). In other words, how species within assemblages interact with each other and the environmental constraints imposed by them largely determine what species will be found within a given area. However, these two processes are predicted to have contrasting effects on the distribution of functional traits within a community: abiotic filters select species with similar suites of adaptations (traits) that allow them to thrive within the specific conditions of the local environment in a process known as niche/environmental filtering (Mouchet et al., 2010; Mouillot et al., 2007). Biotic interactions, especially inter-specific competition, prevent functionally similar species that overlap in their fundamental niche from co-existing in the same community in a process known as limiting similarity (Mayfield and Levine, 2010), thereby increasing the functional diversity (FD) of species within an assemblage (Herben and Goldberg, 2014; Krasnov et al., 2014; Mouillot et al., 2007).

From a conceptual perspective, FD could increase within an assembly due to either a loss of functionally similar species through limiting similarity or an influx of functionally distinct species through a change in abiotic conditions (the removal of environmental filters). In this study we hypothesized that FD would increase in coastal shelf ecosystems due to seasonal changes in abiotic conditions (salinity, turbidity, sediment load) associated with an increased influence of the terrestrial environment (so called 'estuarization'). Specifically, we predicted that predominantly estuarine fish species would be able to invade shallow coastal shelf assemblages during the rainy season, thereby increasing FD. A corollary of this is that FD would be lower during the dry season and in assemblages of deeper zones.

Our results provide strong support for an increase in FD in shallow coastal waters during the rainy season, indicating that tropical coastal fish assemblages in northern Brazil are strongly influenced by niche filtering (MacArthur and Levins, 1967; Mouillot et al., 2007) or, more accurately, the removal of niche filtering. Specifically, FD was generally higher in shallow areas than deep areas, and was higher during the rainy season than the dry season. This is consistent with the relaxation of niche filtering since deeper areas are further from the land and have a much greater

volume of water and are therefore less influenced by seasonal changes in terrestrial precipitation and associated run-off/discharge.

Although study Regions 1 (reef associated) and 2 (lagoon associated) showed broadly similar patterns, Region 3 (influenced by the São Francisco River) showed more variable results. In the shallower sample sites the rainy season was associated with high FD and the dry season with very low FD. However, the deeper sites showed no clear pattern and FD remained slightly higher than the null model prediction for both wet and dry seasons. Such inconsistent results for this region are not completely unexpected, given that the São Francisco River suffers from many anthropogenic impacts (dams and siltation) and dispersed sediment plumes and nutrients near to the river mouth (Manso et al., 1997; Martins et al., 2011). The river also has a very large drainage area with inputs from areas with very different precipitation patterns to those observed in northeast Brazil. The lack of strong seasonality in the biophysical characteristics of the area affected by the river is supported by studies on primary productivity which indicate that chlorophyll "a" concentrations on the adjacent shelf environment remain high throughout the year (Knoppers et al., 2006; Oliveira and Kjerfve, 1993).

Most of the species recorded were classified as estuarine species (66% of total). From the species that were unique to a region and depth range, estuarine species remain the most prevalent (61% of total). These species tend to have larger size, smaller eyes, lower weights and body heights. In tropical regions some fish species, especially juveniles, use the inner continental shelf as well as the estuaries (Longhurst and Pauly, 1987) although habitat usage may depend on a number of abiotic and biotic factors, particularly food availability.

### **3.6 Conclusion**

Investigating patterns of functional organization of assemblages is a powerful tool for understanding how ecological communities form and transform. Here, we provide strong evidence that seasonal changes in tropical coastal shelf fish assemblages are associated with alterations in environmental filters, causing increases in functional diversity in shallow regions that are strongly influenced by the terrestrial environment during the annual rainy season. However, despite these clear patterns our results should be treated with a degree of caution for the following

reasons: 1) the change in assemblage structure from dry to wet season was not solely accountable to the influx of estuarine adapted species and it would therefore be overly simplistic to interpret the increase in FD in shallow areas as only due to seasonal estuarization effects. Communities in transitional habitats such as the interface between land and sea are subject to rapid and often considerable changes in the abiotic milieu. Such variability is likely to have complex and non-linear impacts on species assemblages and a definitive analysis would require more intensive sampling at multiple spatial scales. (2) The more inconsistent results from study Region 3 suggest that large rivers may have specific and unexpected influences on the functional dynamics of fish assemblies – further research is required, especially with respect to the effects of anthropogenic alterations of flow regime on adjacent fish assemblages. (3) Finally, although functional trait analysis shows considerable promise, it is still at a very early stage of development. Various alternative measures of FD exist (Schleuter et al., 2010), and choice of index and/or traits may generate different results. Notwithstanding these limitations, our study clearly demonstrates the potential utility of a functional approach for better understanding the assembly of coastal fish communities.



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