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VICTOR EMMANUEL LOPES DA SILVA

PADRÕES E PROCESSOS QUE REGEM AS DIMENSÕES DA DIVERSIDADE DE PEIXES ESTUARINO-COSTEIROS DO ATLÂNTICO OCIDENTAL

MACEIÓ - ALAGOAS
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Tese apresentada ao Programa de Pós-Graduação em Diversidade Biológica e Conservação nos Trópicos do Instituto de Ciências Biológicas e da Saúde, Universidade Federal de Alagoas, como requisito para obtenção do grau de doutor em CIÊNCIAS BIOLÓGICAS na área da Biodiversidade.

Orientadora: Dra. Nidia Noemi Fabré
Coorientadora: Dra. Marina Dolbeth

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Tese apresentada ao Programa de Pós-Graduação em Diversidade Biológica e Conservação nos Trópicos, Instituto de Ciências Biológicas e da Saúde. Universidade Federal de Alagoas, como requisito para obtenção do título de Doutor(a) em CIÊNCIAS BIOLÓGICAS na área da Biodiversidade.

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“Para onde vão os trens, meu pai?

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Tu podes ir e ainda que se mova o trem,
tu não te moves de ti.”

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RESUMO

Durante as últimas décadas, ecologistas têm direcionados seus esforços para o desenvolvimento de estudos que visam a conservação de espécies e ecossistemas. Ainda assim, vivemos uma das maiores crises da biodiversidade, com taxas de extinções elevadas e processos de degradação de habitat cada vez mais rápidos. Tal problemática resulta, em parte, da constante negligência do conceito multidimensional de biodiversidade, que engloba não apenas quais e quantas espécies residem em uma determinada área, mas também suas características fenotípicas, histórias evolutivas e variabilidade de genes. A compreensão integrada dessas diferentes dimensões, além de seus padrões e quais processos os regem, é fator determinante para o desenvolvimento de estratégias efetivas de manejo e conservação, principalmente para ambientes de alta produtividade e grande importância ecológica, tais como os ambientes estuarino-costeiros. Sendo assim, o presente trabalho tem como objetivo desenvolver uma análise integrada dos componentes distintos da diversidade de peixes estuarino-costeiros em diferentes escalas espaciais. No primeiro capítulo discutimos como a diversidade de habitats e a sazonalidade de áreas tropicais atuam de forma sinérgica para manutenção da redundância funcional de áreas costeiras. O segundo capítulo, por sua vez, avalia a importância relativa de mosaicos costeiros para diferentes partes das comunidades, identificando as relações entre variáveis abióticas e guildas ecológicas. Por fim, o terceiro capítulo, faz uma análise regional das dimensões da biodiversidade de peixes estuarinos ao longo Atlântico Ocidental, visando a compreensão de processos e padrões que regem as comunidades ictiícas e sua participação no dinâmica natural de ambientes estuarino-costeiros.

Palavras-chave: estuários, peixes, biogeografia, biodiversidade

ABSTRACT

During the last decades, ecologists have focused their efforts on the development of studies aimed at the conservation of species and ecosystems. Even so, we are experiencing one of the greatest biodiversity crises, with high extinction rates and increasingly rapid habitat degradation processes. This problem results, in part, from the constant neglection of the multidimensional concept of biodiversity, which encompasses not only which and how many species reside in a given area, but also their phenotypic characteristics, evolutionary histories and gene variability. The integrated understanding of these different dimensions, in addition to their patterns and which processes drive them, is a determining factor for the development of effective management and conservation strategies, especially for environments of high productivity and great ecological importance, such as estuarine-coastal environments. Therefore, the present work aims to develop an integrated analysis of the distinct components of estuarine-coastal fish diversity at different spatial scales. In the first chapter we discussed how the diversity of habitats and the seasonality of tropical areas act synergistically to maintain the functional redundancy of coastal areas. The second chapter, in turn, assesses the relative importance of coastal mosaics for different parts of communities, identifying the relationships between abiotic variables and ecological guilds. Finally, the third chapter makes a regional analysis of the dimensions of estuarine fish biodiversity along the Western Atlantic, aiming at understanding the processes and patterns that govern ichthyic communities and their participation in the natural dynamics of estuarine-coastal environments.

Keyword: estuaries, fish, biogeography, biodiversity

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1. APRESENTAÇÃO

Abordagens funcionais têm emergido como uma das principais ferramentas no manejo e conservação de espécies e ecossistemas (POOL; GRENOUILLET; VILLÉGER, 2014; VILLÉGER et al., 2012, 2017). Isso deve-se ao fato de que componentes funcionais das assembleias, tais como riqueza, equitabilidade e divergência auxiliam na compreensão de diversos processos ecológicos, tais como fatores que afetam a estabilidade ecossistêmica, relações entre biodiversidade e serviços ecossistêmicos, e mecanismos de coexistência de espécies (DIAZ; CABIDO, 2001; TILMAN, 2001). Ainda assim, o conhecimento sobre a estrutura funcional de algumas áreas ainda é limitado, até mesmo para ecossistemas com alta produtividade e de alta importância ecológica. Um exemplo disso, embora não seja o único, é a baixa quantidade de informações que temos sobre a estrutura funcional de ambientes estuarino-costeiros (BAPTISTA et al., 2015; DOLBETH et al., 2016a; SILVA-JÚNIOR et al., 2017).

Estuários e habitats costeiros estão entre os ecossistemas mais produtivos da terra, contribuindo com diversos serviços ecológicos, econômicos e ecossistêmicos. Além de estarem diretamente relacionados com a manutenção de populações futuras de diversas espécies (BECK et al., 2003; DOLBETH et al., 2008), estes ambientes apresentam uma conexão direta com ecossistemas adjacentes (CLAUDINO et al., 2015), criando corredores que permitem o fluxo intenso de transição entres os ambientes marinhos, estuarinos e de água doce.

Essa dinamicidade complexa criada por essa conectividade ecossistêmica afeta a composição taxonômica e até mesmo funcional destas áreas. Por exemplo, o trabalho de Passos et al. (2016) discute que a extensão de condições estuarinas para áreas marinhas tem alterado a estrutura funcional de comunidades de peixes demersais nos trópicos, ressaltando a importância de uma melhor compreensão sobre a estrutura funcional de assembleias de peixes estuarinos e análises mais detalhadas sobre essa conexão entre estuários e áreas adjacentes.

Uma vez que a dinamicidade de ecossistemas estuarinos causa alterações constantes na composição específica das assembleias ictiícas (DA SILVA et al., 2018), entender o arranjo funcional destas comunidades parece ser um componente chave para o manejo e conservação eficaz das espécies e destes ambientes. Especificamente, uma análise dos traços que as espécies estuarinas possuem e como as funções são desempenhadas por estas espécies em tais ecossistemas é necessária para que possamos compreender os processos ecossistêmicos. Porém, para a caracterização de padrões na estrutura destas assembleias é necessária uma compreensão prévia e ampla dos fatores que podem influenciar a dinâmica funcional das espécies ictiícas. Sendo assim, o estudo integrado das diferentes dimensões da biodiversidade de peixes em ambientes estuarino-costeiros deve ser realizado em diferentes escalas espaciais.

Por exemplo, o trabalho de Henriques et al. (2017) mostra que barreiras biogeográficas, tais como correntes oceânicas e condições climáticas distintas (ex.: temperatura e precipitação) afetam não apenas a composição e riqueza de espécies, mas também a distribuição dos seus traços funcionais. Já em escalas mais finas (regionalmente e localmente falando) uma outra gama de fatores, tais como forma do estuário, tipo de conectividade com ambientes costeiros e variações sazonais em salinidade e temperatura atuam mais ativamente na estruturação funcional das comunidades estuarinas (DOLBETH et al., 2016a; SILVA-JÚNIOR et al., 2017). Isso ocorre porque a transição entre escalas resulta em passagens hierárquicas de reino para províncias biogeográficas, que por sua vez são definidas por características distintas de produtividade, vazão, entre outras condições ambientais.

Porém, é importante ressaltar que não apenas fatores abióticos estão atrelados com os processos que influenciam a estrutura funcional destas assembleias. A história evolutiva das espécies pode ter um papel determinante na distribuição de traços e grupos funcionais, influenciando assim as funções ecossistêmicas desempenhas por estas espécies (PAVOINE; BONSALL, 2011). Tal característica deve-se ao fato que sinais filogenéticos podem ter uma estreita relação com a conservação de traços de espécies durante sua história evolutiva, moldando a estrutura taxonômica e funcional existente (FLYNN et al., 2011). Além disso, processos de especiação e dispersão são capazes de introduzir novas espécies a comunidades já estabelecidas, podendo alterar a dinâmica das comunidades e a funcionalidade de todo o ecossistema, além de criar uma conexão entre diferentes escalas espaciais (VELLEND, 2010).

A diversidade de fatores que influenciam as diferentes dimensões da diversidade faz com que seja necessário um estudo que considere diferentes escalas espaciais (ex.: global e regional) e incluam em suas análises além de fatores abióticos (ex.: condições ambientais, estrutura do estuário e etc) as relações filogenéticas entre as espécies, fornecendo assim um conjunto de informações que nos permita direcionar esforços para a conservação das espécies e do ecossistema estuarino como um todo. Sendo assim, o presente trabalho tem como objetivo analisar as dimensões da diversidade de peixes em ambientes estuarino-costeiros em diferentes escalas espaciais, visando a compreensão de padrões e os processos que regem não apenas a estruturação das comunidades nessas áreas, mas também a funcionalidade ecossistêmica desses ambientes.

2. REVISÃO DA LITERATURA

2.1. Ambientes estuarino-costeiros e assembleias ictiícas

Ambientes estuarino-costeiros são zonas de transição entre o ambiente marinho e de água doce, onde a mistura de massas d'água de diferentes densidades causa grandes variações dos parâmetros físicos e químicos destes habitats criando um ecossistema complexo e bastante dinâmico (BIANCHI, 2007). Esta complexidade estrutural associada ao influxo contínuo de nutrientes proveniente de ambientes aquáticos continentais confere a estes ecossistemas altos níveis de produtividade e abrigo para indivíduos juvenis (AZEVEDO; BORDALO; DUARTE, 2014; SCHELSKE; ODUM, 1962), sendo utilizados por diversas espécies em pelo menos uma parte do seu ciclo de vida. Além disso, estudos têm evidenciado que tais ecossistemas estão diretamente relacionados com a sobrevivência e manutenção de populações futuras, uma vez que várias espécies de peixes (BECK et al., 2003; DA SILVA et al., 2018), crustáceos (MARTINS; RODRIGUES; KINAS, 2014) e outros organismos, tais como aves e anfíbios (BRANCO, 2000; GROSE; HILLEBRANT; CREMER, 2013) dependem desses ambientes para a alimentação, reprodução e/ou crescimento (NAGELKERKEN et al., 2015).

Por serem ambientes dinâmicos, as comunidades biológicas que habitam tais ambientes usualmente sofrem constantes mudanças em sua estrutura. Isso ocorre porque diversos fatores bióticos e abióticos influenciam a composição e abundância de espécies nestes ecossistemas, tais como interações intra e interespecíficas (ELLIOTT et al., 2007), salinidade (BARLETTA et al., 2005), temperatura (HARRISON; WHITFIELD, 2006), turbidez (OOI; CHONG, 2011) e disponibilidade de alimento (GRENOUILLET; PONT; SEIP, 2002). Contudo, a estrutura básica de alguns grupos se mante relativamente estável, apesar das mudanças recorrentes que ocorrem na composição específica. Por exemplo, assembleias de peixes estuarinos geralmente são compostas por um conjunto de espécies de água doce, marinhos migrantes e residentes que utilizam tais ecossistemas em pelo menos uma parte do seu ciclo de vida (SELLESLAGH et al., 2009).

Os peixes são um grupo de grande particularidade em estuários e habitats costeiros, pois muitas espécies marinhas e de água doce, incluindo espécies de alto valor econômico, utilizam essas áreas como berçários e/ou criação (BECK et al., 2003). Historicamente, a estrutura de assembleias ictiícas destas áreas tem sido alvo de diversos estudos ecológicos (ABLE, 2005; ELLIOTT; MCLUSKY, 2002), o que tem ajudado na compreensão de processos e fatores que afetam a composição especifica destas assembleias no tempo e espaço (BARLETTA et al., 2008; BLABER; GRIFFITHS; PILLANS, 2010; MÉRIGOT et al., 2017). Por exemplo, diversos trabalhos têm evidenciado que os fatores estruturantes da ictiofauna estuarina são variados, tais como as características físicas do próprio estuário como tamanho, profundidade e grau de conectividade com o ambiente marinho (RUEDA; DEFEO, 2003), os padrões climáticos regionais, principalmente as flutuações nas taxas de pluviosidade e temperatura (DA SILVA et al., 2018) e condições locais, como nível de produtividade e variação da salinidade (BARLETTA et al., 2005). Os peixes respondem a este conjunto de fatores por aclimatação ou migração sazonal, fazendo com que as assembleias ictiícas sejam marcadas por constantes mudanças em sua estrutura taxonômica com um número grande de espécies que passam um curto período de tempo nestes ambientes, e um número reduzido de espécies que apresentam permanência anual (ELLIOTT et al., 2007; GIBSON et al., 1996; PATERSON; WHITFIELD, 2000).

Contudo, ainda que a produção científica sobre a estrutura de assembleias de peixes estuarinos seja relativamente extensa, lacunas em alguns campos de conhecimento ainda existem, fazendo com que exista uma falta de informação que é crucial para a conservação destes ecossistemas como um todo (BLABER; BARLETTA, 2016). Por exemplo. apenas alguns trabalhos recentes têm utilizados abordagens que integrem o conhecimento taxonômico com a funcionalidade ecossistêmica, tal como a caracterização funcional de assembleias de peixes estuarinos (DOLBETH et al., 2016b; HENRIQUES et al., 2017; MÉRIGOT et al., 2017; SILVA-JÚNIOR et al., 2017). Menor ainda é o número de estudos que especializam tais análises, uma vez que estuários e habitats costeiros podem estar conectados em um mosaico de habitat que funciona de forma interdependente. Uma vez que a dinamicidade destes ecossistemas causa alterações constantes na composição específica das assembleias, entender as funções desempenhadas pelas espécies destas comunidades parece ser um componente chave para o manejo e conservação eficaz das espécies e destas regiões, já que mudanças funcionais na estrutura das assembleias podem afetar diretamente a funcionalidade dos ecossistemas.

Um bom exemplo é o trabalho recente de Passos et al. (2016) que mostra que extensão das condições estuarinas para o ambiente marinho influencia até mesmo a estrutura funcional de áreas costeiras adjacentes, criando corredores que permitem a migração de espécies estuarinas com traços funcionais distintos para áreas mais profundas. Isso ocorre porque muitos estuários possuem uma conexão direta com o ambiente marinho. O problema é que diversos autores têm pontuado que as atuais mudanças que sistemas naturais têm sofrido no mundo todo podem estar afetando negativamente a conectividade biológica entre diferentes ecossistemas, colocando em risco a diversidade de comunidades biológicas e a sobrevivência de populações futuras de muitas espécies (SELLESLAGH; AMARA, 2008; SHEAVES, 2005). Parte do problema resulta da falta de um conhecimento mais aprofundado e detalhado de como está conexão ocorre e é mantida (DE JONGE; ELLIOTT; BRAUER, 2006). Por exemplo, Vasconcelos et al. (2011) em seu estudo discutem como a abordagem tradicional de estruturação e quantificação das comunidades biológicas utilizada em diversos estudos para se avaliar a conectividade entre ecossistemas não fornece informações suficientes sobre os mecanismos que permitem que essa conectividade exista, sendo necessária a implementação de abordagens ecossistêmicas e funcionais em tais trabalhos.

2.2. Abordagens funcionais e filogenéticas

Nas últimas décadas, abordagens funcionais têm emergido como uma das principais ferramentas de estudos ecológicos que visam o manejo e conservação de espécies e ecossistemas (KANG et al., 2015; TERESA; CASATTI; CIANCIARUSO, 2015; VILLÉGER; GRENOUILLET; BROSSE, 2013). Isso ocorreu porque abordagens baseadas em características comportamentais, fisiológicas ou morfológicas que impactam a adaptabilidade dos indivíduos (VIOLLE et al., 2007) têm um alto poder preditivo sobre o funcionamento dos ecossistemas, a estrutura de comunidades biológicas e relações espécie-ambiente (MESSIER; MCGILL; LECHOWICZ, 2010; TILMAN, 2001). Por exemplo, a diversidade de funções desempenhadas pelas espécies, conhecida como diversidade funcional, tem sido de grande importância para a compreensão das relações entre biodiversidade e serviços ecossistêmicos, como também dos mecanismos de coexistência de espécies (DIAZ; CABIDO, 2001; TILMAN, 2001).

Historicamente, diversas hipóteses foram formuladas na tentativa de se compreender a relação entre diversidade de espécies e o funcionamento de um determinado ecossistema (KANG et al., 2015). Tais hipóteses, usualmente, são atreladas principalmente a participação das espécies na cadeia trófica (KANG et al., 2015; WANG; BROSE, 2018), uma vez que a transferência de energia é um componente principal da funcionalidade ecossistêmica. Por exemplo, uma das teorias mais conhecidas e estudadas é a hipótese da diversidade-estabilidade postulada por MacArthur (MACARTHUR, 1955) que relaciona alta diversidade de espécies com máxima estabilidade ecossistêmica. Para MacArthur (1955), a estabilidade de sistemas naturais é alcançada pelo aumento no número de espécies, uma vez que tal incremento faz com que um maior número de nichos tróficos disponíveis no ecossistema seja ocupado. Ou seja, quanto mais funções são desempenhadas pelas espécies mais resiliente será o ecossistema. Contudo, trabalhos posteriores mostraram que a relação entre diversidade e estabilidade ecossistêmica é bem mais complexa, uma vez que fatores como a capacidade que a comunidade tem de suportar diferentes espécies e grupos funcionais são bem mais significativos na determinação dos processos e estabilidade dos ecossistemas do que o apenas a diversidade de espécies (MCCANN, 2000).

Embora muitos estudos tenham mostrado uma relação positiva entre a riqueza de espécies e a diversidade de funções (DIMITRIADIS; KOUTSOUBAS, 2011), um debate acerca das similares entre diferentes espécies emergiu nos anos 90, fazendo com que novas perspectivas nascessem dentro do estudo das relações entre espécies e funções. Com isso, entender padrões sobre a estrutura funcional de comunidades biológicas e sua relação com os ecossistemas tem cada vez mais se tornado o objetivo de diversos estudos, na tentativa de elucidar questões cruciais no ramo da ecologia (BELLWOOD; HOEY; CHOAT, 2003; TILMAN et al., 1997; UMAÑA et al., 2017). Neste contexto não é surpreendente que tenha acontecido um aumento expressivo na produção científica acerca da estrutura funcional de diversos grupos em ecossistemas variados, além do desenvolvimento de novas métricas (BOTTA-DUKÁT, 2005; PETCHEY; GASTON, 2002, 2006). Ainda assim, lacunas de conhecimento sobre alguns grupos de espécies, tais como os peixes, são comuns e geralmente dificultam o desenvolvimento de medidas eficientes de conservação.

2.3. A estrutura funcional de comunidades estuarino-costeiras

Embora estuários sejam um dos ambientes mais produtivos do mundo, contribuindo com diversos serviços ecossistêmicos (HARLEY et al., 2006), existem poucos trabalhos que utilizam abordagens funcionais para avaliar as comunidades biológicas estuarinas e sua relação com o ecossistema (DOLBETH et al., 2016a; MICHELLI; HALPERN, 2005; SILVA-JÚNIOR et al., 2017). Uma constante dificuldade para a realização de tais estudos com comunidades ictiícas é a atual quantidade limitada de informação sobre traços funcionais de peixes (ALBOUY et al., 2011; SIBBING; NAGELKERKE, 2001). Por exemplo, não existe uma classificação detalhada sobre quais traços funcionais das assembleias ictiícas respondem a variações do ambiente (traço resposta), e quais são os atributos que interferem na dinâmica ecossistêmica – (traço efeito) (VIOLLE et al., 2007). Estas informações são de importância análises mais detalhadas sobre a variabilidade de respostas que ocorrem dentro de um conjunto de espécies que desempenham funções similares (grupo funcional), e consequentemente são necessárias para a compreensão das relações entre as comunidades e os serviços ecossistêmicos (LALIBERTÉ et al., 2010).

Os poucos trabalhos existentes sobre a estrutura funcional de assembleias de peixes estuarinos têm fornecido dados importantes para entendimento das relações espécies-ambiente e sobre resiliência ecossistêmica. O estudo de Baptista et al. (2015) ao analisar a mudança na estrutura funcional nas comunidades ictiícas de um estuário em Portugal durante 30 anos revelou que ao longo do tempo, embora diferentes espécies transitaram pelo estuário, a funcionalidade ecossistêmica se manteve estável graças a alta redundância funcional entre as espécies que habitam tais ambientes. Ou seja, apesar das constantes alterações na composição específica, as funções desempenhadas pelas espécies ictiícas tendem a serem mantidas para promover resiliência ecossistêmica. Padrões similares foram encontrados em trabalhos desenvolvidos em estuários no nordeste do Brasil, onde estuários com baixa redundância funcional se mostram mais sensíveis a impactos naturais e/ou antropogênicos (DOLBETH et al., 2016a).

Porém, qual os fatores que afetam a estrutura funcional de peixes estuarinos e o que pode causar redundância? Assim como na estrutura taxonômica, uma variedade de fatores pode influenciar a composição funcional de assembleias ictiícas, tais como ações antropogênicas (DOLBETH et al., 2016a), características geomorfológicas do estuário (HENRIQUES et al., 2017) e variações nas condições ambientais locais (PASSOS et al., 2016). O estudo recente de Henriques et al. (2017) merece um destaque pois foi o primeiro a incluir barreiras biogeográficas como variável explicativa da distribuição funcional das assembleias ictiícas. De fato, os autores mostram que existe uma vasta amplitude de fatores que estão diretamente relacionados com a estruturação funcional dos estuários, tais como variações de salinidade e produtividade, tamanho do ecossistema estuarino, conectividade hidrológica com áreas adjacentes, entre outros.

Contudo, embora características relacionadas com a divisão das regiões biogeográficas marinhas (correntes oceânicas, variação climática, e etc

(SPALDING et al., 2007) – assim como a existência de filtros ambientais – ex.: variação em salinidade, produtividade e etc. – sejam fatores importantes para a estruturação das assembleias ictiícas, um componente que em muitos estudos é negligenciado é a própria história evolutiva das espécies. A história filogenética das espécies pode ter uma forte relação com as funções desempenhadas nos ecossistemas (FLYNN et al., 2011), e em muitos casos atributos importantes para a montagem e interação das assembleias são usualmente conservados durante a história evolutiva das espécies. Sendo assim, para uma melhor compreensão dos fatores estruturantes de comunidades de peixes estuarinos é necessária uma análise que englobe diferentes escalas de tempo e espaço, além da inclusão de análises filogenéticas na tentativa de elucidar se a estrutura funcional destas assembleias é produto da história evolutiva das espécies, de filtragem ambiental ou uma conjunção de ambos.

2.4. Diversidade filogenética

A diversidade filogenética ganhou espaço em estudos ecológicos principalmente no início da década de 1990 com a crescente necessidade de se estabelecer prioridades para a conservação (CIANCIARUSO; SILVA; BATALHA, 2009; MAY, 1990). Tal abordagem incorpora em suas análises as relações filogenéticas das espécies, partindo da premissa que comunidades com espécies filogeneticamente mais distintas são mais biodiversas que aquelas que possuem espécies com parentescos próximos (MAGURRAN, 2004; WILLIAMS; HUMPHRIES; VANE-WRIGHT, 1991). Particularmente, esta análise reconhece que árvores filogenéticas refletem as diferenças fenotípicas, genéticas e comportamentais entre diferentes linhagens evolutivas (TUCKER et al., 2017). Sendo assim, espera-se que extinções de espécies não-aparentadas gerem uma maior perda de informação filogenética na comunidade do que a extinção de uma espécie com parentescos próximos, fazendo com que a identificação de áreas com maior diversidade filogenética seja uma estratégia eficaz para a conservação das espécies e dos ecossistemas como um todo (MOUQUET et al., 2012; POLASKY et al., 2001).

No geral, as medidas de diversidade filogenética se mostram bastantes eficientes na compreensão dos processos de estruturação de comunidades, permitindo que as interações que levam a coexistência de espécies sejam mais bem compreendidas (WEBB et al., 2002). Isso deve-se, principalmente, ao fato de que tais interações podem ser resultado de uma variedade de fatores, incluindo os processos evolutivos passados e contínuos (CHASE, 2003; WEBB et al., 2002). No entanto, embora sua aplicabilidade seja abrangente, tal ferramenta ainda é pouco utilizada, principalmente no ramo da zoologia, onde existe uma grande escassez de informações sobre a diversidade filogenética de comunidades naturais (CIANCIARUSO; SILVA; BATALHA, 2009).

Um dos grandes desafios, por exemplo, é a definição das diferentes características entre espécies que pode explicar padrões de estruturações de comunidades (MOUQUET et al., 2012). Embora diversos trabalhos tenham utilizado a diversidade filogenética para identificar os processos ecológicos que determinam padrões de distribuição e diversidade de espécies (JETZ et al., 2012), Tucker et al. (2017) discute que o uso de análises filogenéticas em ecologia de comunidade e em estudos de conservação ainda é bastante subestimado. Por exemplo, a integração de análises filogenéticas com abordagens funcionais parece ser de extrema importância para a compreensão de regras de montagem de comunidades, principalmente porque as relações entre atributos funcionais, hábito alimentar e funções desempenhadas pelas espécies podem ser produto das afinidades filogenéticas entre espécies (DINIZ-FILHO et al., 2011; PAVOINE; BONSALL, 2011). De fato, a diversidade filogenética tem sido até mesmo utilizada como um *proxy* em estudos de ecologia funcional utilizando a similaridade/dissimilaridade entre espécies como ferramenta para identificar funções (MOUQUET et al., 2012; WEBB et al., 2002).

Estudos que combinam abordagens funcionais e filogenéticas têm mostrado alto potencial para identificação e priorização de espécies-chave, e para predições de respostas e da suscetibilidade das comunidades biológicas frente as mudanças globais (LAVERGNE et al., 2010; THUILLER et al., 2011), fornecendo informações cruciais para a conservação de ecossistemas e espécies. Além disso, a união de ambas as abordagens tem permitido a identificação dos processos de estruturação de assembleias, mostrando que filtros ambientais e a história biogeográfica podem atuar de formas distintas na distribuição de diferentes grupos (LEIBOLD; ECONOMO; PERES-NETO, 2010).

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3. CAPÍTULO I: Assessing tropical coastal dynamics across habitats and seasons through different dimensions of fish diversity[1]

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Abstract

Coastal habitat mosaics are among the most productive ecosystems around the globe, with many ecological and social-economic services provided. Their natural challenging conditions have always been a subject of concern for ecologist and conservationist, with a particular interest in understanding how its spatial and temporal dynamics influence ecosystem functioning. In this context, we aimed to assess tropical coastal dynamics using an integrative approach, measuring the different facets of fish diversity across space (habitats) and time (seasons). Three different estuarine systems and their adjacent areas in the southwestern Atlantic were monthly sampled between July 2017 and June 2018, in a sampling design

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that encompassed three different coastal mosaics with three habitat types (mangroves, seagrass and sandy beaches), and both seasons of the studied region (dry and rainy). Taxonomic, phylogenetic, and functional diversity were then evaluated with equivalent diversity measures to allow comparisons between them. Different patterns of species occurrence and distribution were found between habitats and seasons, which resulted in different effects on the abundance-weighted diversity dimensions. Although taxonomic diversity of habitats was greater during the rainy season (p=0.03), a seasonal increase in phylogenetic diversity was only observed in the sandy beach habitat (p=0.04). In contrast for the functional diversity, no significant differences were found among habitats in both seasons (p=0.15), indicating high levels of redundancy. Our results showed that patterns in the occurrence and abundance of tropical fish species among habitats that comprise a coastal mosaic have different effects on distinct diversity dimensions. More precisely, for tropical coastal systems with marked seasonality, both habitats and season appear to play a synergic role in the maintenance of ecosystem functioning by enhancing functional and phylogenetic redundancy.

Keywords: biodiversity dimensions; Fish Ecology; tropical estuaries

3.1. Introduction

Identifying priority habitats for conservation has always been one of the main goals of ecologists and conservationists worldwide (Wilson et al., 2006; Xu et al., 2019). The increasing number of threats to species and greater impacts on ecosystems have stimulated the development of different and complex prioritization strategies to identify areas of interest for protection and conservation (Pereira et al., 2012). However, despite all the work done, indicators still show huge losses of biodiversity and ecosystem services across many scales (Butchart et al., 2010; Velazco et al., 2019), with current extinction rates and habitat degradation often compared to the five previous mass extinction events in the last 600 million years (Stork, 2010).

According to Ceauşu et al. (2015), many factors play a significant role in the loss of species and ecosystem services. Nevertheless, one major issue lies in how current methodologies to prioritize conservation measurements are designed and implemented. To date, most conservation approaches are still typically based on one single component of biodiversity (Doxa et al., 2016), neglecting its multidimensional concept that includes species, evolutionary entities, functional traits and genetic diversity of taxa that inhabit a particular region (Mazel et al., 2014). So, identifying successful strategies for ecosystems' conservation implies embracing all biodiversity facets since their protection is critical for maintaining the ecosystems' functions and their essential services to humans (Pollock et al., 2017). Nevertheless, the poor understanding of how diversity dimensions are related to each other may result in conservation actions proposed only through species-based indicators, which encompass species richness and their vulnerability, but neglect their evolutionary and functional information (Brum et al., 2017; Ouchi-Melo et al., 2018).

In coastal areas, for example, only a few recent studies have used integrative approaches to analyze different diversity components (Dolbeth et al., 2016; Henriques et al., 2017b; Mérigot et al., 2017). The high structural complexity of these areas makes them one of the most intricate and productive ecosystems on earth, providing multiple ecological and economic services, such as their well-established nursery function for many species (Elliott and Whitfield, 2011; Nagelkerken et al., 2000). The planning and management of coastal ecosystems have always been complex due to their challenging natural conditions and great structural complexity (Blaber and Barletta, 2016). For instance, habitat diversity found within these areas creates a coastal ecosystem mosaic that is often credited as a critical component of higher productivity levels and unique diversity profiles (Eggleston et al., 1999; Ferreira et al., 2019; Nagelkerken et al., 2015; Sheaves, 2009). Each habitat that comprises the coastal mosaic has its own dynamics and may have different roles for species in the same community (Nagelkerken et al., 2015). However, the effects of this habitat heterogeneity on ecosystem functioning and filtering mechanisms are still poorly understood (but see Dolbeth et al. 2013, 2016), especially when considering seasonal changes (Blaber and Barletta, 2016).

In tropical regions, for example, seasonality driven by rainfall regimes tends to cause pronounced changes in environmental conditions and habitats' structure of coastal areas (Passos et al. 2016), having a direct impact in the shaping and structuring of fish assemblages. The greater inputs of freshwater and sediments during rainy months modify productivity levels and environmental conditions, creating additional seasonal changes in salinity, turbidity and dissolved oxygen levels, which affect species and habitats (Barletta-Bergan et al., 2002; Neto et al., 2014). In seagrass beds, their total coverage and biomass tend to decrease with higher rates of rainfall and greater water turbidity (Koch et al., 2007), which may cause a few fish species to migrate to adjacent areas in their search for shelter (Nagelkerken et al., 2015). Estuarine and coastal sandy beaches' dynamics also change seasonally, with stronger wave action during the rainy season that produces a constant remineralization process of organic matter and makes a greater quantity of nutrients in the water column available, attracting new species to this habitat (Santana et al., 2013).

Few studies have shown that seasonal changes in species composition appear not to affect the functioning of these areas due to high functional redundancy among fish species (da Silva and Fabré, 2019; Dolbeth et al., 2016). Yet, these did not consider habitat-specific approaches nor how diversity dimensions relate to each other through space and time to understand their consequences on ecosystem functioning. Therefore, the present study aimed to understand the relationship between diversity dimensions of fish assemblages across habitats and seasons of costal mosaic systems, to provide subsidies for effective management and conservation actions for species and the ecosystem as a whole. Specifically, we conducted an integrative approach to assess the individual and synergic effects of temporal and spatial changes on species composition, phylogenetic lineages, and the functional diversity of fish species of three tropical coastal mosaics and their main habitats.

3.2. Materials and methods

3.2.1. Study area, sample design and fish survey

Sampled areas were chosen based on their ecological and socioeconomic importance for the region (Oliveira and Kjerfve, 1993; Paulino et al., 2020). Three distinct systems of the southeastern Atlantic region were included in this study (Fig. 1). The region is characterized by a tropical, semi-humid climate with two well-defined seasons driven by rainfall: a dry season between October and April, and a rainy season from May to September. The first two sampled areas are located within one of the most important marine protected areas (MPA) of Brazil – the Área de Proteção Ambiental Costa dos Corais (APACC), with 400,000 ha of extension that host approximately 120 km of mangroves, sandy beaches, coral reefs, and other ecosystems. The third habitat mosaic is located on the Mundaú-Manguaba Estuarine Lagoon Complex, one of the most productive estuarine systems in northeastern Brazil (Oliveira and Kjerfve, 1993).

All three areas have a variety of habitats within their extensions which present distinct habitat configurations (Fig. 1). Among them, three typical habitat types were sampled during the study period: mangroves, seagrass beds and sandy beaches. Previous studies have analyzed features of these habitat types individually throughout the region, showing that despite being displayed in different habitat configuration in sampled systems, each habitat type has a specific dynamic, with only small changes in environmental conditions occurring from one system to another (Azevedo-Farias et al., 2021; Barros and Rocha-Barreira, 2014; da Silva et al., 2018; Paulino et al., 2020; Teixeira, 1997). Mangrove sites were set in regions close to the estuaries' banks covered with mangrove forest dominated by Rhizophora mangle, Avicennia schaueriana, and Laguncularia racemose. Seagrass stations (mainly comprised of Halodule wrightii) were all selected in relation to their proximity to the estuaries' mouths. Sandy beach stations were all established in the shallow waters adjacent to the estuaries' mouth (mean depth ≤ 1.5 m).

Two sampling stations per habitat type were set in each area, resulting in 18 sampling stations that were surveyed monthly from July 2017 to June 2018. In each sampling station, we conducted two standardized surveys per month using a beach seine 12 m long and 3 m high with a mesh size of 12 mm and opposite knots, comprising a total of 438 samples. Each sampling procedure lasted for five minutes to minimize impacts on local communities (De Araujo et al., 2008) and all collected fishes were taken to the laboratory for identification at species level following regional taxonomic keys.

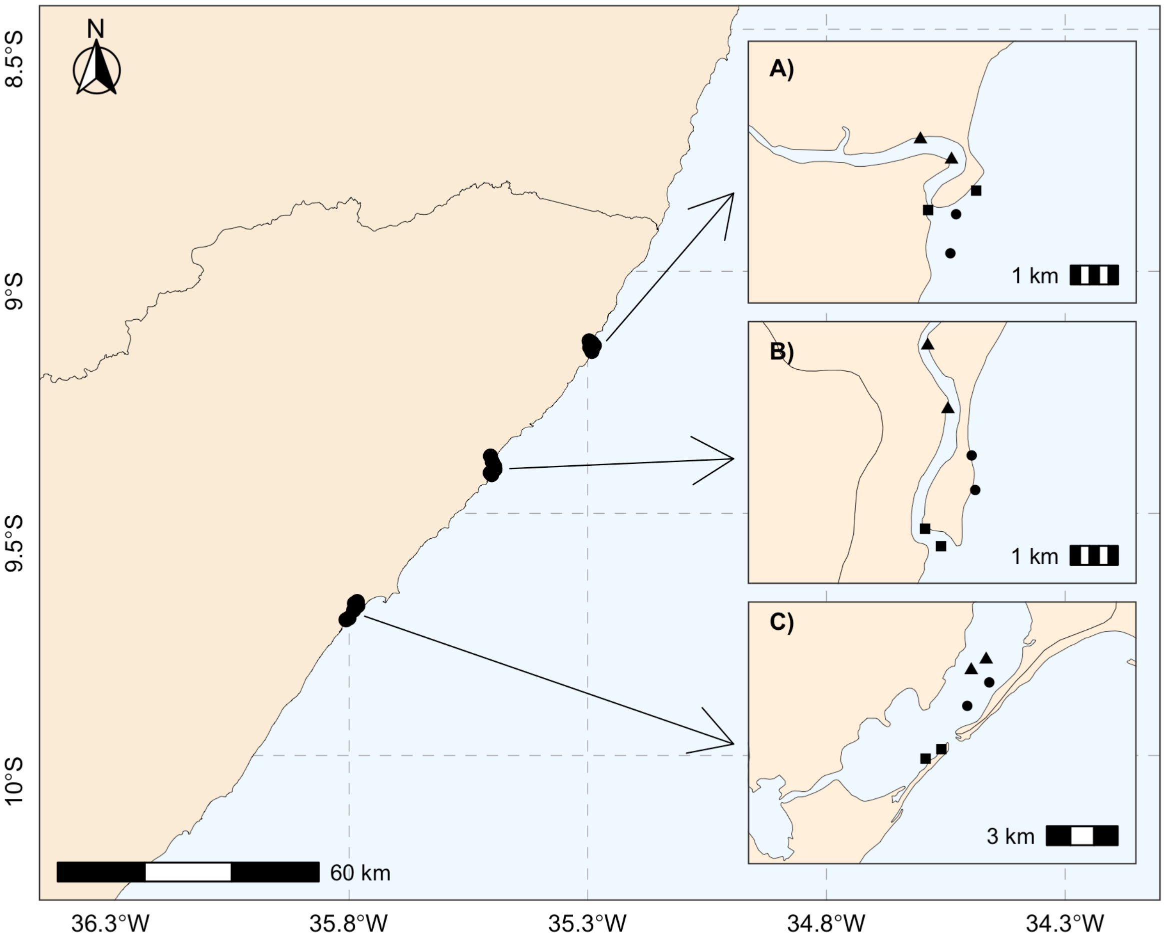

Figure 1. Study area, showing the three sampled estuarine systems: Manguaba river estuary (A), Santo Antônio river estuary (B) and Pontal estuary (C). Sampling stations are represented according to habitat type: mangrove (▲), seagrass beds (●) and sandy beach (■).

3.2.2. Functional traits and species phylogeny

A combination of seven traits that describe well-known functions performed by fish species was selected for this study (see Table 1 for information on traits). Selected traits are mainly related to fish diet and movement, having a solid relationship with species performance, such as detection and capture of food items, swimming efficiency, and metabolic allocation of energy in the body (Henriques et al., 2017b). Information was mainly retrieved from published datasets (Beukhof et al., 2019) and online databases such as FishBase (Froese and Pauly, 2020). For species that were not included in these databases, we searched trait information on available literature.

Table 1. Functional traits used to estimate the functional diversity of fish species along the sampled systems.

Trait	Ecological meaning	Reference
Maximum body size	Reflects position in the food web, metabolic rates, dispersal ability, mobility and home range	Henriques et al., (2017b)
Body shape	Indicates swimming performance, and patterns in habitat use	Ribeiro et al., (2016)
Habitat association	Relates to the use of water-column, and adaptations to habitats	Beukhof et al., (2019)
Salinity preference	Reflects the physiological ability to deal with osmotic stress in brackish estuarine waters	Henriques et al., (2017b)
Trophic guild	Relates to the position in the food web, and shows the influence of a species on abundance of others	Henriques et al., (2017b)
Feeding mode	Reflects feeding strategies and it is also associated to species diet	Floeter et al., (2018)
Reproductive guild	Indicates dispersal ability, colonization potential, and population growth	Lefchech &Duffy, (2015)

Phylogenetic analyses of species were carried out based on the current taxonomy of fishes (Betancur-R et al., 2017). A total of 100 trees were retrieved using the package “fishtree” in the software R statistics (Chang et al., 2019), which provide access to sequences, phylogenies, fossil calibrations and diversification rate estimates for ray-finned fishes from the Fish Tree of Life website (https://fishtreeoflife.org). All 100 phylogenetic topologies were used to build a final Majority-Rule Consensus Tree using the package “phytools” (Revell, 2020).

3.2.3. Data analysis

Differences in species composition between ecosystems and among habitats and seasons were tested by permutational analysis of variance (PERMANOVA), considering a 3-way mixed design with habitats (with 3-levels) nested in estuaries (with 3-levels) and crossed with seasons (with 2-levels) (Anderson et al. 2008). Significant results were further investigated by a post-hoc test using the function “pairwise.adonis” in the pairwiseAdonis package (Martinez Arbizu, 2020). The dimensions of diversity were then evaluated for each habitat and season with equivalent diversity measures to allow comparisons between them (de Bello et al., 2009). Fish taxonomic diversity was estimated through the Simpson’s index (D’), whereas the phylogenetic and functional diversities were assessed by Rao’s quadratic entropy (RaoQp and RaoQf). All indexes were used for partitioning diversity into their α and β components, considering all sampling sites in each habitat and season. The partitioning of diversity assumed an additive relationship between the α and β components, with α representing the within-community of each site, and β-diversity evaluating the degree of change in species composition among communities (Lande, 1996; Whittaker, 1972). Differences in the α-component of all dimensions between habitats and season were evaluated using the Scheirer-Ray-Hare extension of the Kruskal-Wallis test (Sokal and Rohlf, 1995).

Additionally, we performed principal coordinate analyses (PCoAs) using species data to provide specific typologies of each diversity dimension for habitats and seasons (Weithoff, 2003). As each diversity dimension considers different data types, PCoAs were carried out using distinct similarity matrix for each dimension. For the taxonomic space, a Bray-Curtis distance was applied to a species-abundance matrix, which included the total abundance of species in all samples per habitat and season. The phylogenetic space was produced from the reconstructed phylogenetic topology of species using the cophenetic distance (Munch and Stefanou, 2019; Sobral et al., 2016), and for the functional space, we used the Gower distance in a species-traits matrix, which incorporated data of all species and traits (Pavoine et al., 2009). The first two PCoA axes were used to create bidimensional spaces for each diversity dimension, and spaces were used to identify species and/or groups responsible for significant changes across habitats and seasons.

All diversity measures were carried out within the R software (R Core Team 2012), using the ‘Rao’ function of de Bello et al. (2010).

3.3. Results

A total of 2,668 individuals, distributed in 86 species of 30 families, were collected during the study period. In terms of species richness, the most representative habitat during the dry season was the seagrass (42 species), followed by mangroves (36) and sandy beaches (29). This pattern shifted in the rainy season, with sandy beach areas (44) being richer than seagrass beds (40) and mangroves (34). Although all three areas had a similar species composition (Table 2, PERMANOVA, $p>0.05$), different patterns of species occurrence and distribution were found between habitats and seasons. For instance, species composition was significantly different among habitats during the dry season, with each habitat having its own pool of species (Table 2, PERMANOVA, $p=0.01$). In the rainy season, however, sandy beach and seagrass habitats shared a similar species composition (post-hoc test, $p=0.53$) which was significantly different from the one found in mangrove areas (post-hoc test, $p=0.01$).

The seasonal and spatial patterns on species richness also resulted in different effects on the abundance-weighted diversity dimensions. Although α-taxonomic diversity of all habitats was greater during the rainy season in comparison to the dry season (Fig. 2a, Scheirer-Ray-Hare test, p=0.03), a seasonal increase in α-phylogenetic diversity was only observed in the sandy beach habitat (Fig. 2b, Scheirer-Ray-Hare test, p=0.04). In contrast for the α-functional diversity, no significant differences were found among habitats in both seasons (Fig. 2c, Scheirer-Ray-Hare test, p=0.15). When diversity was partitioned, the β-component of taxonomic diversity was consistently greater than the α-component, indicating a high turnover of species in all habitats and seasons (Fig. 3). However, these changes in species composition did not greatly impact the β-phylogenetic and β-functional components of diversity (Fig. 3), demonstrating high phylogenetic and functional redundancy among species for all habitats.

Table 2. Three-way permutational analysis of variance (PERMANOVA) with 1,000 permutations for estuarine fish species data. The analysis was carried out considering a mixed design with habitats nested in estuaries and crossed with seasons.

Source	df	SS	MS	Pseudo-F	p
Ecosystem	2	0.851	0.425	1.124	0.219
Habitat	2	1.753	0.876	2.315	0.001
Season	1	0.705	0.704	1.980	0.004
Habitat (Estuary)	4	2.903	0.725	1.917	0.001
Habitat × Season	3	1.555	0.518	1.369	0.013

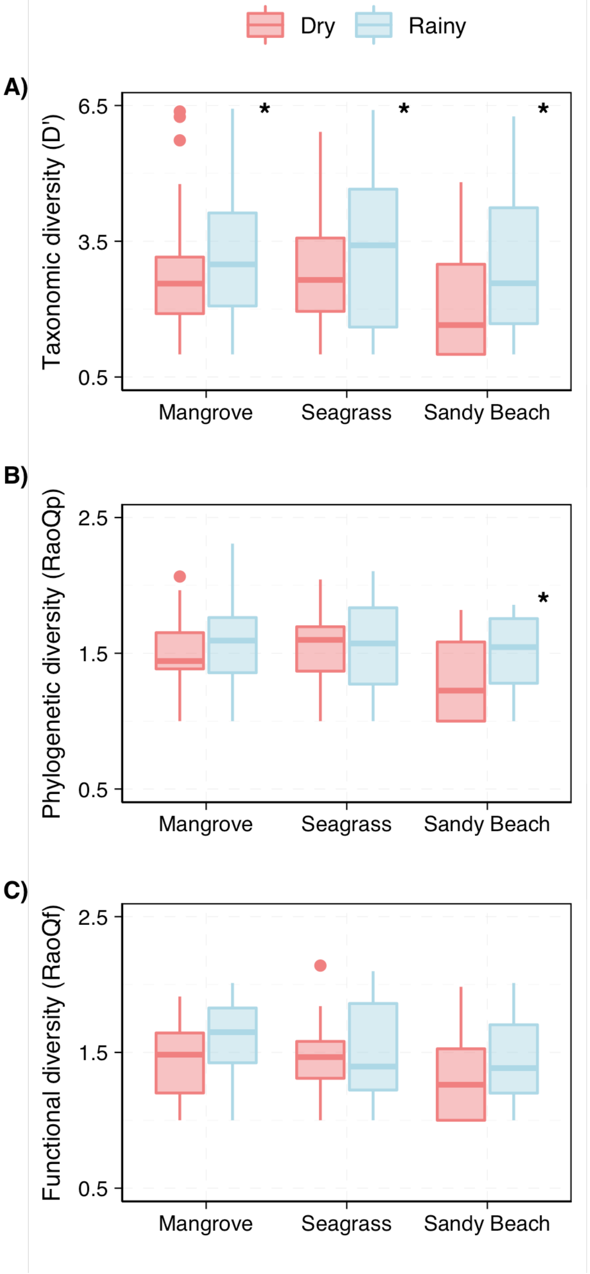

Figure 2. Variability in the α-component (abundance-weighted) of each diversity dimension of fish species for habitats and seasons of three tropical estuaries. The * represents a statistically significant difference between seasons.

A few insights into these relationships could be assessed by analyzing the position of studied species in the taxonomic, phylogenetic and functional spaces (Fig. 4). In seagrass beds, there were seasonal changes in species composition that resulted from both the occurrence of species in the rainy season that were typically common to mangrove and sandy beaches habitats (i.e., Mugil curema and Diapterus aurautus) and the addition of new marine species that were unique to this habitat (i.e., Acanthurus coeruleus and Archosargus rhomboidalis). For sandy beach areas, the increase of α-taxonomic and α-phylogenetic diversity during the rainy season was caused by the occurrence of species with a more estuarine habit, such as Trinectes paulistanus, Symphurus tessalatus, Mugil liza and Cathorops spixii, as well as the occurrence of species that were unique to the seagrass beds during the dry season.

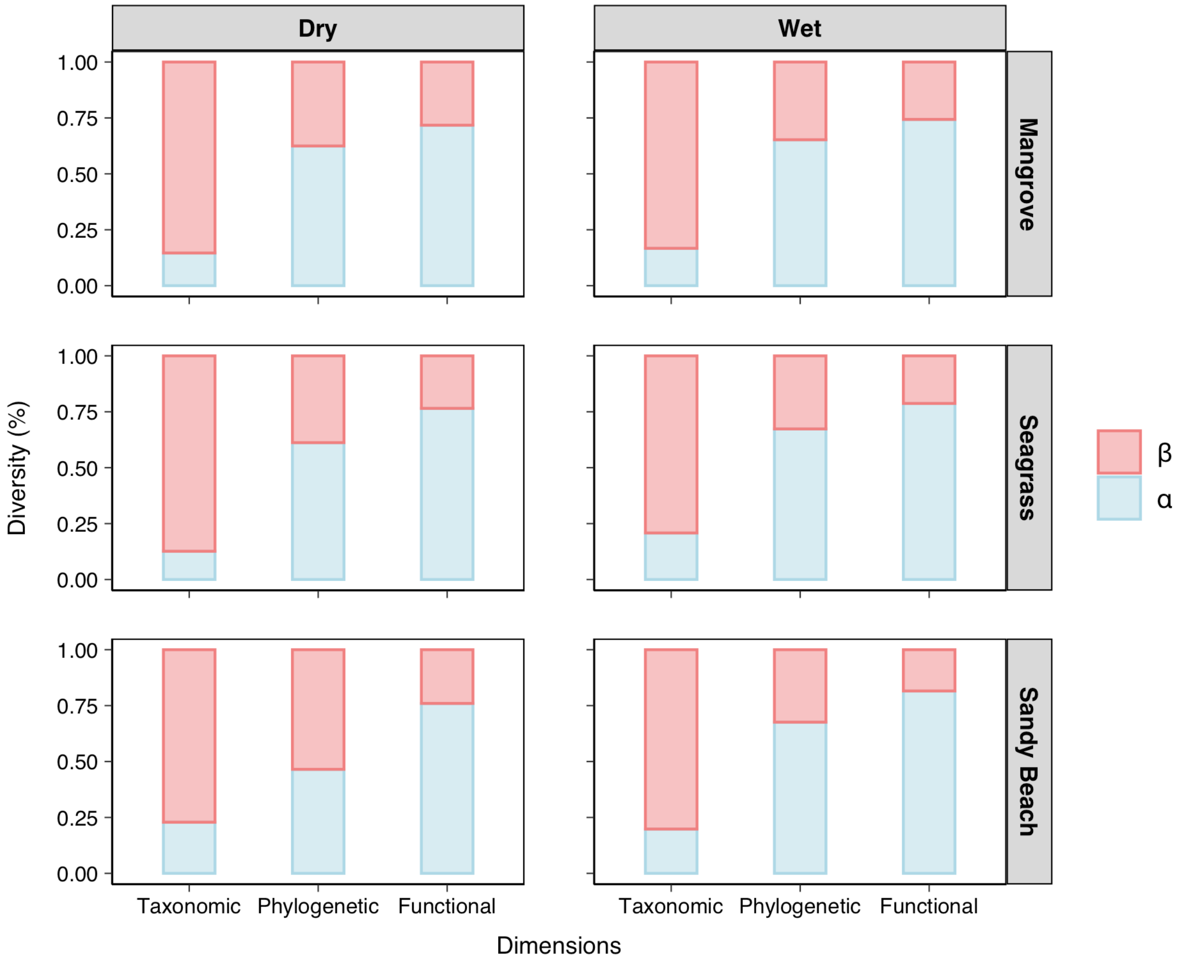

Figure 3. α and β components of the three diversity dimensions of tropical fish assemblages among habitats and seasons of three estuarine systems.

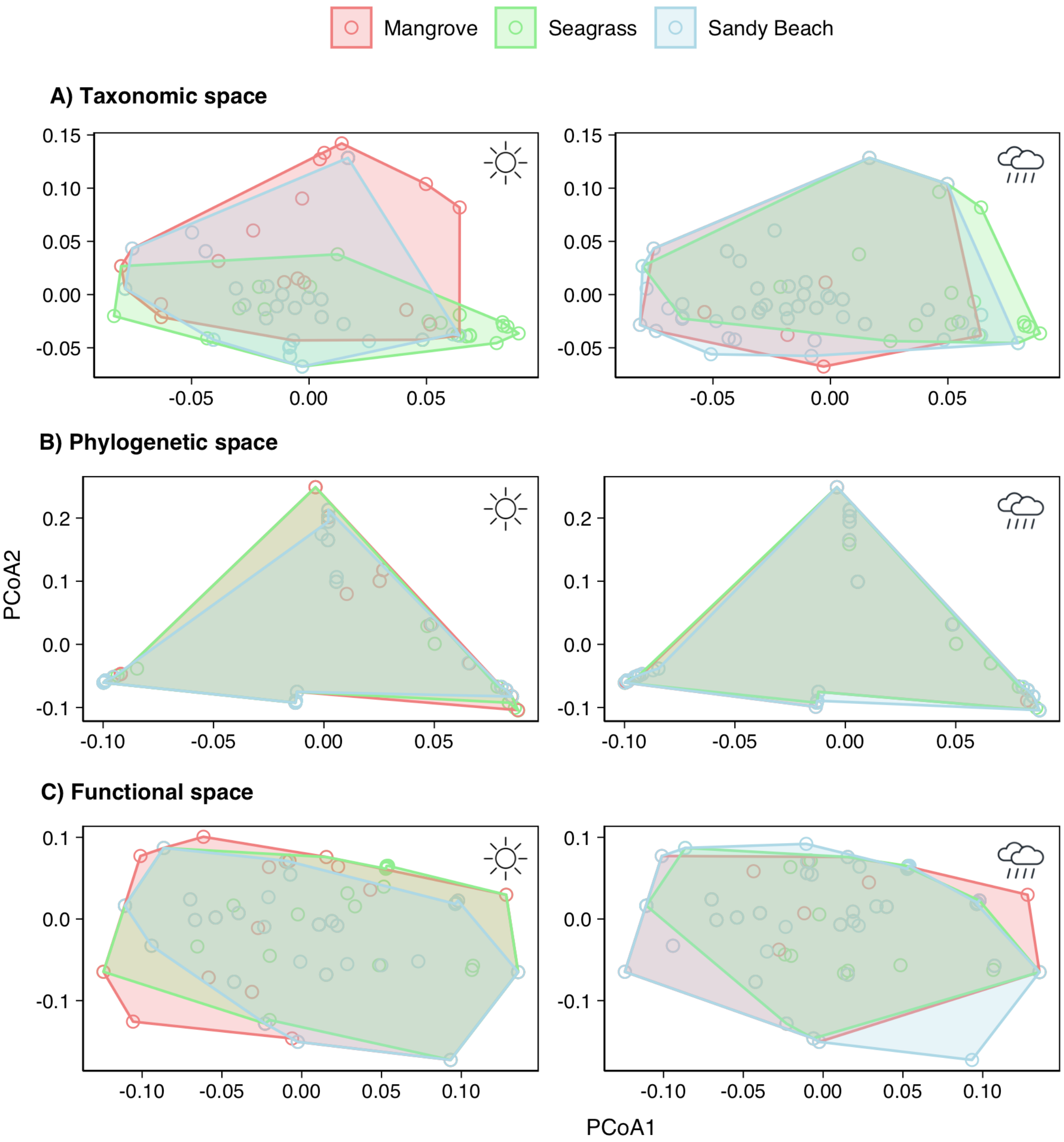

Figure 4. Taxonomic (A), phylogenetic (B) and functional (C) spaces occupied by fish assemblages of three tropical estuarine systems across different habitats (mangrove = red; seagrass = green; sandy beach = blue)) and seasons (dry = sun symbol; wet = rain symbol).

3.4. Discussion

Habitat diversity within tropical coastal areas has always been credited as a key component of the higher taxonomic diversity profile of these ecosystems (Eggleston et al., 1999; Ferreira et al., 2019; Nagelkerken et al., 2015). However, the effects of habitat heterogeneity on ecosystem functioning and filtering mechanisms are still poorly understood, primarily due to the highly complex dynamics of habitat mosaics. Our results add to the current knowledge of estuarine and coastal ecology by showing that patterns in the occurrence and abundance of tropical fish species have different effects on distinct diversity dimensions. More precisely, for tropical systems with marked seasonality, both habitats and season appear to play a synergic role in the maintenance of ecosystem functioning by enhancing functional and phylogenetic redundancy.

3.4.1. Species composition among coastal habitats and seasons

Overall, despite differences in the distribution of habitats and in the morphology of studied systems, habitat configuration had no significant effect in structuring fish assemblages, with a similar specie composition being found in all three sampled systems. Although it would be expected that habitat configuration would play a significant role in shaping biological communities, studies have shown that this effect is weaker at smaller scales and often independent of system geo-morphology (Dorenbosch et al., 2007, 2004). However, distinct pattern of habitat use by species was observed for each season. During the dry season, habitats had their own species composition, with significant differences between assemblages depending on the characteristics of each habitat. In this season, habitats have distinct environmental conditions, being able to maintain their own individual features and dynamics (Sales et al., 2016). Therefore, environmental filtering selects a different set of species depending on individuals' physiological adaptations, such as osmoregulatory capacity and diet requirements (Barletta et al., 2005). For example, sandy beach and seagrass areas tend to have higher and more stable salinity levels than mangroves during the dry season months (da Silva et al., 2018). These conditions are more suitable for species with preference for higher salinity environments, such as marine straggler fishes (da Silva and Fabré, 2019; Potter et al., 2015) that find additional food sources and shelter in these areas. Since salinity is a key structuring factor of coastal fish assemblages, its great variability among habitats favors the presence of some species while limiting the occurrence of others (Barletta, 2004; Hajisamae and Yeesin, 2014).

On the other hand, the rainy season was characterized by changes in species composition that caused an increase in α-taxonomic diversity for all habitats and enhanced similarity among them. During the rainy season, tropical estuarine habitats typically receive great inputs of freshwaters and sediments, which extend the estuarine condition to all habitats and the coast (Longhurst and Pauly, 1987). This process called “estuarization” alters productivity levels and environmental conditions, such as salinity, turbidity and dissolved oxygen (Krumme et al., 2012; Neto et al., 2014; Passos et al., 2016), affecting the habitats’ structure and their fish assemblages (Sales et al., 2016). For instance, seasonal changes in species composition of seagrass habitats can be associated with the life cycle of tropical seagrass species, highly sensitive to variations in water physical-chemical parameters (Barros and Rocha-Barreira, 2014). Seasonal fluctuations in turbidity and salinity can cause seagrass loss and decrease its total biomass, changing habitat features and availability, which will inevitably affect fish species (Koch et al., 2007; Preen and Marsh, 1995).

Moreover, the estuarization of costal habitats enhanced by rainfall appears to cause a temporary spatial homogenization, allowing changes in species composition by facilitating the transit of existing species among habitats, as well as the occurrence of new species in the same area. This assumption can be supported by the similarity in species composition of seagrass and sandy beach areas during the rainy season in all three sampled areas. The seasonal reduction of seagrass biomass caused by greater rainfall rates reduces habitat complexity and increases structural similarity to sandy beach areas, enabling the selection of a similar set of species in both habitats. In addition, their dynamics suffer similar pressures with intensifications of rainfall and freshwater supply, such as decreases in salinity levels and greater wave actions that promote a constant organic matter remineralization (Lacerda et al., 2014; Rodrigues and Vieira, 2013). Furthermore, another evidence of habitat homogenization by estuarization is the occurrence of a few estuarine species that were typically found in mangrove habitats inhabiting the sandy beaches and seagrass beds during the rainy season, even though mangroves were able to maintain their own species composition during both seasons.

3.4.2. Relationship between diversity dimensions throughout the estuarine dynamics

Although rainfall regime appears to play a significant role in structuring tropical fish assemblages among estuarine and coastal habitats, the great species turnover (high β-taxonomic diversity) found in our study was followed by a trait-convergence pattern. Specifically, we found that species' functions were similar for all habitats (low β-functional diversity), regardless of the increases in taxonomic diversity and changes in species composition. High functional redundancy along with great diversity of species are typically credited as key components of resilience and stability (Baptista et al., 2015; Casatti et al., 2015), as ecosystems are able to maintain key functions even in the face of species migrations or extinctions (Teichert et al., 2017). However, there is more to the concept of redundancy than just assuming that species are functionally similar, with many authors arguing that a subtle level of complementarity may be hidden behind an apparent redundancy (Blüthgen and Klein, 2011). For instance, great levels of niche differentiation among redundant species have been shown to provide a portfolio effect within the estuarine ecosystem by promoting stable coexistence of competitive species and maximizing resource use (da Silva and Fabré, 2019).

While the mechanisms behind this niche differentiation are still poorly understood, the phylogenetic history of species appears to be closely associated with this diversification (Blüthgen and Klein, 2011; Elmqvist et al., 2003). In our results, for example, functional diversity of sandy beaches remained stable despite an increase in both, the taxonomic and phylogenetic diversity during the rainy season, even with the addition of phylogenetically distinct species. This result again shows the prevalence of functionally redundant species among estuarine and coastal habitats and illustrates how phylogenetic lineages may play a significant role in maintaining that functional redundancy. Although an increase in the diversity of functions is expected with the rise of phylogenetic diversity (Cadotte et al., 2010), species in the same functional group (a set of taxa that perform a similar function) may differ in the way they perform a particular role depending on life history features (Elmqvist et al., 2003). Indeed, it is expected that the presence of phylogenetically distinct species in the same functional group ensures the continuity of functions even when faced with disturbances, by providing a certain degree of complementary between species (Jonsson et al., 2002). Therefore, it is possible that the addition of fishes with a more estuarine habit in sandy beaches during the rainy season may have enhanced redundancy by increasing niche differentiation among assemblages.

3.4.3. Limitations, current concerns, and implications for conservation

Although we acknowledge that our study may have some limitations due to the use of only one sampling gear to estimate species composition, the presence and dominance of juveniles and small-sized fishes throughout the coastal habitats in this region often result in similar diversity profiles among different applied sampling methods (Henriques et al., 2017a; Vasconcelos et al., 2015). The main purpose of our study was to retrieve a representative sample of fish assemblages that have a significant contribution to the functioning of coastal habitat mosaics, and as each studied habitat is mainly used by juveniles and small-sized species as feeding areas and shelters, we believe that our study covers a significant portion of species found in the area.

Our study suggests that habitats and seasons are all involved in a synergic process that is directly linked to the maintenance and management of ecosystem functioning. More precisely, we found that both habitats and seasons have a significant role in structuring the three dimensions of fishes' diversity, with a clear seasonal pattern that appears to enhance redundancy of functions among habitats. Consequently, conservationists should use integrative approaches that take in consideration both factors when defining management actions in order to conserve tropical estuarine and coastal systems as a whole. Nevertheless, it is important to highlight that there are many current threats to the ecological integrity of these environments, which can put this dynamics at risk (Blaber and Barletta, 2016). Climate change, for example, has great potential to increase rainfall in these areas at unprecedent rates, especially during the dry season, which would impact freshwater runoff and sediment supplies and eventually cause a homogenization of ecosystems (Bernardino et al., 2015; Marengo et al., 2010). Although a temporary homogenization appears to be a key component of estuarine ecosystem functioning by enhancing habitat connectivity and facilitating species movements, the permanent homogenization would impact the individual integrity of habitats, by changing habitat features and conditions and affecting species that inhabit these areas (Gartner et al., 2013). For example, estuarine-dependent fishes tend to use different habitats as they grow to complete their life cycle. Thus, a permanent homogenization would affect these species dynamics and interfere in their development process (Nagelkerken et al., 2015, 2008).

Furthermore, the increasing number of threats posed by human-induced impacts are also of great concern, especially for the tropical region where estuaries and coastal areas are suffering unprecedented levels of anthropogenic pressures (Blaber and Barletta, 2016). River damming has reduced water and sediment flows, changing productivity levels and affecting estuarine habitats' structure (Lacerda et al., 2007). Urbanization of nearby areas has changed the overall estuarine landscape, causing species loss and reducing fishery production (Pereira et al., 2010). In addition, habitat degradation in these ecosystems has been greater than ever, with the ongoing transformation of mangrove areas into shrimp farms, the shrinking of seagrass coverage due to poor water quality and increasing beach pollution (Arthington et al., 2016). Our results showed how important the seasonal dynamics and habitat diversity are for coastal areas. So, conservation actions should focus on the integrated protection of all habitats that comprise the coastal mosaic, such as sandy beaches, mangroves and seagrass beds, to sustain the complexity of inshore coastal areas that are highly productive for coastal fisheries and fundamental to maintain coastal livelihoods.

3.5. Acknowledgements

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4. CAPÍTULO II: Relative importance of habitat mosaics for fish guilds in the northeastern coast of Brazil[2]

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Abstract

The identification of patterns in habitat use by fish guilds may provide an integrated perspective of coastal mosaics. Thus, we used multivariate analyses to assess the relative importance of habitat types for fish guilds based on density and species composition throughout a seasonal event in the northeastern coast of Brazil. Our results showed a great variability of responses found for each functional group, with species composition of guilds that are estuarine-related being affected by habitat types (p=0.001) and seasons (p=0.008), whereas the facultative estuarine users showed no significant relationship with both variables (p=0.95). Specific habitat association patterns were not found for guilds, though solely estuarine species (p=0.041) and marine straggler fishes (p=0.027) were related to environmental conditions that varied greatly with seasonality (i.e., rainfall and salinity rates), indicating that temporal changes in the region allow species from different guilds to explore the whole coastal mosaic at different scales of space and time. For this reason, we highlight that the integrated protection of beaches, mangroves and seagrass compose an imperative strategy to sustain the complexity of inshore coastal areas that are highly productive for coastal fisheries and fundamental to maintain coastal livelihoods.

Keywords: seagrass, mangrove, reef fishes, coastal fisheries

4.1. Introduction

Fishes are among the most diverse and dynamics groups within the estuarine and coastal biota (Elliott et al. 2007), with assemblages being mainly comprised of marine, freshwater, and brackish species that spend at least one part of their life cycle in those areas. These estuarine and coastal species are one of the main components of ecosystems' functioning and resilience (Baptista et al. 2015; da Silva and Fabré 2019), as they perform a wide range of functions throughout their life history cycle, including the control and the transport of organic matter between different environments (Lebreton et al. 2011). Hence, it is not a surprise that ecologists have always tried to understand the drivers and patterns of temporal and spatial occurrence of fishes in these ecosystems (Barletta-Bergan et al. 2002; Henriques et al. 2017; da Silva et al. 2018).

However, studies describing how fish species use estuaries and coastal zones are often challenging due to the highly complex dynamics of these areas. For instance, the constant changes in the environmental conditions and productivity levels of these areas tend to create a wide range of responses from species in the same assemblage due to distinct physiological limitations, such as specific osmoregulation mechanisms (Whitfield et al. 2012; Telesh et al. 2013) and different dietary requirements (Whitfield 2017). This variability of responses along with other factors such as the great structural complexity found within have a direct impact on how species use the whole coastal space (Gillanders et al. 2003; Wasserman and Strydom 2011).

Indeed, the structural complexity of coastal areas has always been one of their main features, being well represented by the great diversity of habitat types, which may include mangroves, seagrass beds, saltmarshes, mudflats, and coastal sandy beaches (Pihl et al. 2007). Each one of these habitat types has its own characteristics and dynamics, creating a highly complex mosaic that shapes assemblages in many different ways, having distinct influences on ecosystem functioning (Pihl et al. 2007). For example, the nursery role of seascapes has been recently re-evaluated using a spatial perspective, and authors showed that the nursery value of habitats that comprise the coastal mosaic may vary between species and throughout fish development (Nagelkerken et al. 2015). In tropical regions, though mangroves and seagrass beds have always been credited as fundamental areas for fishes (Mumby et al. 2004), many studies have shown that species which are dependent on these habitats may also use other environments (i.e., sandy beaches and mudflats) throughout their life history (Gillanders et al. 2003; Vasconcelos et al. 2010; da Silva et al. 2018). Indeed, the diversity of habitat types appears to enhance the effectiveness of coastal areas as nurseries, since only a few species are confined to a single nursery ground, with mobile species connecting adjacent habitats through migrations to seek shelter and/or food resources (Nagelkerken et al. 2008; Nagelkerken et al. 2015).

Thus, the coastal habitat mosaic concept (Sheaves 2009) emerged as a more developed approach to evaluate the functioning of these ecosystems by incorporating the linkages among habitat types and the different stages of fishes' life cycle (Barbour et al. 2014; Nagelkerken et al. 2015). According to this concept, species migrate between adjacent areas as they grow, with the individual response of fishes depending on their relationship with habitats (Barbour and Adams 2012). In other words, from a spatial perspective, there may be a considerable variability in the value of habitat types for different species in the same community, as each habitat has its distinct features and dynamics, thus contributing disproportionally for distinct parts of the assemblage (Nagelkerken et al. 2015). Although this habitat mosaic concept has been largely applied to explain use and movements of single populations, for example, the migratory patterns of Lutjanidae, Haemulidae, Carangidae and other species with commercial value (Honda et al. 2013; Murray et al. 2018; Reis-Filho et al. 2019), a community perspective of this concept is still poorly explored.

Part of this lack of information based on community studies might be due to the many challenges faced by ecologists when trying to describe habitat use for the whole fish biota. Comparisons of fauna composition among different habitat types are very difficult (Nagelkerken et al. 2000), and the high dynamism of ecosystems makes the development of such studies even harder. In the tropics, for instance, seasonality driven by rainfall regimes causes not only changes in fish assemblages, but also in habitat’s structure (Passos et al. 2016), with seagrass coverage decreasing and sandy beach dynamics drastically changing from one season to another (Koch et al. 2007; Santana et al. 2013). A comprehensive understanding of how fish assemblages use coastal mosaics should take in consideration all these factors, since this type of information is required for the proper management and conservation of ecosystems and species (Sheaves et al. 2014; Potter et al. 2015).

In this context, one of the easiest and most effective strategies to evaluate habitat usage might be through the classification of species into guilds based on their functional attributes (Elliott et al. 2007). The guild approach provides a more comprehensive overview of species, allowing us to assess their ecological and functional role in ecosystems as it is often derived from species’ morphology, feeding habit, reproductive mode, or habitat use (Elliott et al. 2007; Potter et al. 2015). For example, the estuarine-use functional guild proposed by Elliott et al. (2007) and later developed by Potter et al. (2015) has been successfully used to understand spatial and temporal changes of fish assemblages (Ferreira et al. 2019), as well as to identify changes in the food web structure and energy flow of estuarine systems (Harrison and Whitfield 2008). This is possible because the categorization of species into guilds is based on many biological information regarding physiological adaptations and migratory patterns (Elliott et al. 2007). Nevertheless, habitat-specific studies using this guild approach are still rare in the current literature (Aguilar-Medrano et al. 2020), resulting in information gaps that are extremely concerning as habitat loss and degradation of costal habitats are increasing, especially in tropical regions (Blaber and Barletta 2016).

The identification of patterns in habitat use of fish guilds may provide an integrated perspective of coastal mosaics. Thus, the aim of this work was to assess the relative importance of habitat mosaic types for fishes, based on density and guild's composition, during a seasonal event in the northeastern coast of Brazil. We hypothesized that changes in the density of individuals and species composition of guilds would be associated to habitats and seasons. Our data not only will expand the current knowledge regarding the habitat use patterns of fish assemblages in tropical regions but will also provide a more integrated perspective that recognizes the value of the entire coastal habitat mosaic.

4.2. Material and methods

4.2.1. Study area and sample design

This study was conducted in three coastal areas located in the northeastern coast of Brazil in the southeastern Atlantic (Fig. 1), characterized by a tropical, semi-humid climate with two well-defined seasons: a dry season from September to February, and a wet season between March and August. The Manguaba river (9°9′28″S; 35°17′42″W) and Santo Antônio river estuaries (9°24′18″S; 35°30′25″W) are located within one of the most important marine protected areas (MPA) of Brazil – the Área de Proteção Ambiental Costa dos Corais (APACC). The APACC is the largest coastal MPA in the region with 400,000 ha of extension, hosting about 120 km of mangroves, sandy beaches, and coral reefs. The third sampled area has a bar-built conformation (Levinson 2010) and is located on the Mundaú-Manguaba Estuarine Lagoon Complex (9°39′57″S; 35°44′6″W), which is one of the most productive coastal systems in the northeastern Brazil (Oliveira and Kjerfve 1993).

In each area, six sampling stations were established along its extension, with two stations per habitat type (mangrove, seagrass, and sandy beach), resulting in a total of 18 sampling points (Fig. 1). Mangrove stations were located in regions close to the estuary's banks covered with mangrove forest dominated by *Rhizophora mangle*, *Avicennia schaueriana*, and *Laguncularia racemose* (da Silva et al. 2018). In the Manguaba river and Santo Antônio river estuaries, seagrass stations were located in beds (mainly represented by *Halodule wrightii*) nearby the estuaries' mouths, while in the Pontal estuary, stations were set in beds found inside the channels' system that builds the estuarine complex. All sandy beach stations were established in the shallow waters (mean depth ≤ 1.5 m) adjacent to the estuaries' mouth.

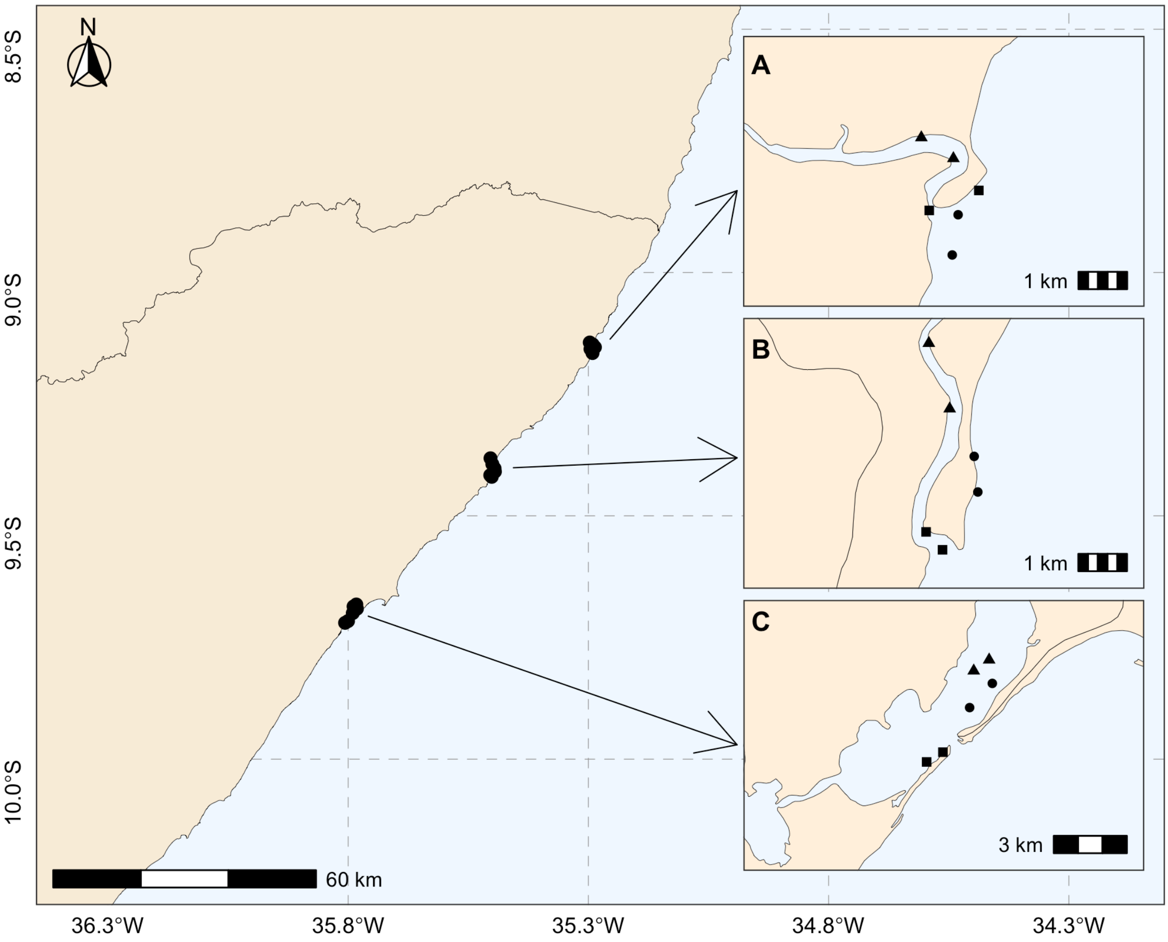

Fig. 1 Location of sampling sites for each habitat type: mangrove (▲), seagrass beds (●) and sandy beach (■) in the Manguaba river estuary (A), the santo Antônio river estuary (B) and the Pontal estuary (C).

4.2.2. Fish surveys and environmental information

From July 2017 to June 2018, we conducted monthly surveys covering the wet and dry seasons. Before fish sampling, we recorded the environmental conditions of each station (i.e., salinity, temperature, dissolved oxygen, and pH) with a Hanna HI 9828 multi-parameter water quality portable meter. After that, we conducted two standardized surveys in all sampling stations, using a beach seine 12 m long and 3 m high with mesh size of 12 mm and opposite knots. A total of 432 hauls were conducted for five minutes each in order to minimize impacts to local fish communities (de Araujo et al. 2008), with the initial and final geographic coordinates hauls recorded to estimate the sampled area (m^2). All collected fishes were taken to the laboratory and identified to species level following regional taxonomic keys (i.e. Figueiredo and Menezes 1978; Menezes and Figueiredo 1985). The identified species were later classified into their respective estuarine-use functional guilds (Potter et al. 2015), based on published data (Table 1). We also retrieved monthly data on rainfall (in mm) for each estuary from the Alagoas State Secretariat for the Environment and Water Resources (http://www.semarh.al.gov.br/) to represent the component seasonality in our study, and measured the distance of each sampled habitat from the estuary's mouth, using its coordinates recorded during sampling procedures.

Table 1 Estuarine-use functional guilds used to classify fish species collected in the present study following Potter et al. (2015)

Guild	Ecological characterization
Solely estuarine (SE)	Species which their lifecycle occurs only in estuarine environments
Estuarine and marine (E&M)	Species that can complete their lifecycle in either estuaries or in the marine environment
Marine estuarine dependent (MED)	Species whose juvenile individuals mandatorily requires estuarine shelters during his first life stages
Marine estuarine opportunist (MEO)	Species that occasionally may enter in estuarine areas, generally using these environments as alternative nursery areas, but may vary the distribution in adjacent areas

Guild	Ecological characterization
Marine straggler (MS)	Species that may enters estuaries sporadically in fewer numbers than MEO and are more common in areas which salinity do not variate considerably

4.2.3. Data analysis

Fish densities of identified guilds were estimated for each haul as the total number of collected individuals in the guild divided by the product of the swept area and the seine size (m^2) (Johnson et al. 2008). Variability in overall density of fish species was evaluated by a three-way ANOVA using guilds, habitats, and seasons as factors. To do so, datasets were previously log-transformed (log n+1) to reduce data aggregation and meet the assumptions of a parametric test. Normality and homoscedasticity of residuals were then analyzed by the Shapiro-Wilk and Levene's tests, respectively.

Furthermore, Bray–Curtis similarity matrices were constructed from the density data (#/m^2) for each guild and used to evaluate the effect and relative importance of habitat types and seasons on guilds' composition by two-way permutational multivariate ANOVAs (PERMANOVAs). The PERMANOVA is a nonparametric distance-based ANOVA that uses permutation procedures to test hypotheses and works by assigning components of variation (COV) of differing magnitudes to the main factors and interactions between them. The greater is the COV, the stronger is the influence of a particular factor or interaction term on the structure of the data (Anderson 2017).

To further investigate patterns identified through the PERMANOVAs analysis, a similarity percentage analysis (SIMPER) was later carried out to identify species that were responsible for the dissimilarity between factors in guilds that had a significant effect. We also carried out a non-parametric BEST procedure with the Spearman's rho rank correlation to identify whether or not guilds' composition could be explained by environmental conditions (Peterson et al. 2013). This approach uses the "bioenv" function from the "vegan" package to search for the best possible combination of environmental variables that gives a correlative explanation for the composition of guilds (Clarke and Ainsworth 1993).

Finally, the function “envfit” from the ‘vegan’ package was used to assess impacts of environmental factors on guild composition. This function performs an overlap between vectors representing environmental factors and NMS ordination plots, while testing for statistical significance with 999 random permutation tests (Smith et al., 2017). All statistical analyses were carried out in the R statistics software using the vegan package at a significance level of $p<0.05$ (R Core Team 2013).

4.3. Results

A total of 2,542 individuals, from 86 species and 30 families, were collected. Species were classified into five estuarine-use functional guilds (EUFG), with the marine straggler guild being the most representative in terms of species richness (22 species), followed by the marine estuarine opportunists, with 19 species, the solely estuarine and the estuarine and marine guilds (both with 17 species each), and the guild with less representants in terms of species was the marine estuarine with only 11 species.

Overall density of individuals varied greatly between the EUFGs (Table 2, three-way ANOVA, F=22.63, p=0.001), but the solely estuarine and the marine estuarine dependent guilds had the highest values registered throughout the study period (Fig. 3). Moreover, though habitat types and season had individual effects in the overall density of individuals, neither an interaction between them (F=0.897, p=0.411), nor a relationship with guilds was found (F=1.061, p=0.394). In fact, a similar pattern in the density of individuals among guilds and across habitat types was found for both seasons (Fig. 2).

Table 2 ANOVA results for the variability in the overall density of individuals across estuarine-use functional guilds, habitats, and seasons

Variable	df	Sum of Squares	F-value	p
Guild	4	52.95	22.636	0.000
Habitat	2	8.03	6.866	0.001
Season	1	4.71	8.054	0.005
Guild × Habitat	8	6.47	1.384	0.211
Guild × Season	4	2.17	0.927	0.451
Habitat x Season	2	1.05	0.897	0.411
Guild × Habitat × Season	8	4.95	1.061	0.394

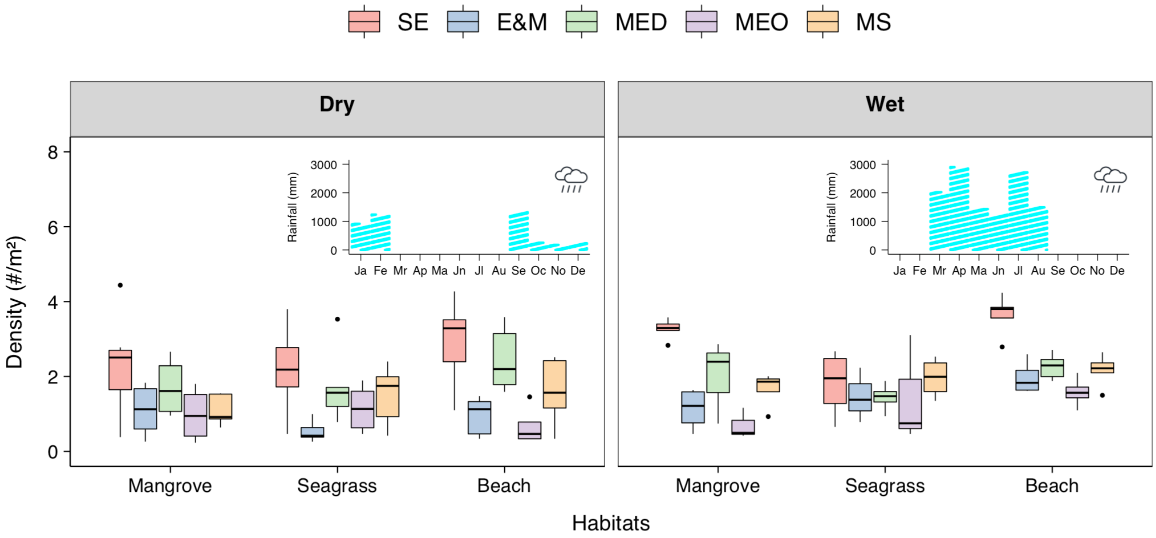

Fig. 2 Variability in the density of individuals of identified estuarine use functional guilds across habitats and seasons. Plot also shows rainfall data (in mm) for each month to highlight differences between seasons. SE – solely estuarine; E&M – estuarine and marine; MED – marine estuarine dependent; MEO – marine estuarine opportunist; MS – marine straggler

In relation to guilds' composition, each EUFG showed a distinct arrangement of species in relation to spatial and temporal variables (Table 3). Habitat type had a significant effect on the structuring of the guilds that show a certain degree of dependency with the estuarine environment, such as the solely estuarine (PERMANOVA, Pseudo-F=3.37, p=0.001), the estuarine and marine (Pseudo-F=, p=0.016) and the marine estuarine dependent guilds (Pseudo-F=1.85, p=0.006). Seasons showed a similar pattern, being also associated to EUFGs that are dependent on estuaries, except for the marine estuarine dependent guild (Pseudo-F=1.16, p=0.221). Additionally, an interaction between habitat types and seasons was also found for the solely estuarine species (Pseudo-F=-2.5, p=0.034). On the other hand, the species composition of marine estuarine opportunist and marine straggler individuals showed no significant relationship with habitats and seasons, even though the marine stragglers species were significatively correlated to the distance of habitat types from the estuary's mouth, as well as to changes in rainfall and salinity rates (Fig. 3, Table 4, BEST procedure, ρ=0.255, p=0.027).

To better understand the effects of habitat types and seasons on the composition of EUFGs, we analyzed the usage pattern of species for each guild. In the solely estuarine guild, though species tended to use the three available habitats, seasonal changes in the density of species shaped the overall structure of the guild. For example, *Sphoeroides testudineus* (responsible for 35.1% of total dissimilarity, SIMPER) was the most abundant species during the wet season in all habitat types but especially in the sandy beach area, whereas the second most abundant species, *Atherinella brasiliensis* (15%) had the highest values registered during the dry season for all three habitat types (Table S1). The occurrence and abundance of species in this guild were also correlated to habitats' distance from estuary's mouth, and a set of environmental variables – rainfall, pH, turbidity – that varied greatly throughout the estuarine dynamics (Fig. 3, Table 4, BEST procedure, ρ=0.291, p=0.041).

Table 3 PERMANOVA results for the density of estuarine-use functional guilds, obtained through the Bray–Curtis similarity matrix, showing the partitioning of multivariate variation and tests by habitats and seasons, as well as their interaction. SE – solely estuarine; E&M – estuarine and marine; MED – marine estuarine dependent; MEO – marine estuarine opportunist; MS – marine straggler

		Estuarine-use functional guild									
Source	df	SE		E&M		MED		MEO		MS	
		F	p	F	p	F	p	F	p	F	P
Habitat	2	3.37	0.001	1.51	0.016	1.85	0.006	1.03	0.134	1.25	0.11
Season	1	1.81	0.008	1.57	0.033	1.16	0.221	0.91	0.326	1.28	0.134
Habitat × Season	2	-2.5	0.034	-2.2	0.687	-1.9	0.698	-1.4	0.475	-1.5	0.959

For the estuarine and marine guild, species showed preference for a particular habitat, such as the mugilids *Mugil liza* and *M. rubrioculos* which were only found in the sandy beach areas. Even when species used more than one habitat, a clear habitat preference was found. For instance, *Lycengraulis grossidens* (26.8%) had the highest density values registered in the sandy beaches, whereas *Diapterus rhombeus* (13.7%) was more common to mangrove areas. In the marine estuarine dependent guild, species, such as *Eucinostomus gula* (24%), *Mugil curema* (17.4%), and *E. argenteus* (11%) used all three habitat types in both seasons, but the highest densities were recorded in the dry season with a slightly decrease occurring during the wet season (Table S1).

Table 4 Multivariate correlations between the environmental variables and estuarine-use functional guilds, displaying the top model from the BEST output for each guild, as well as its strength (ρ) and significance (p-value). SE – solely estuarine; E&M – estuarine and marine; MED – marine estuarine dependent; MEO – marine estuarine opportunist; MS – marine straggler

Guild	Best model	Correlation (ρ)	p-value
SE	Rainfall + pH + Turbidity + Dist.Mouth	0.291	0.041
E&M	Temperature + Dissolved oxygen	0.123	0.214
MED	pH	0.099	0.924
MEO	Rainfall + pH + Turbidity	0.192	0.629
MS	Rainfall + Salinity + Dist.Mouth	0.255	0.027

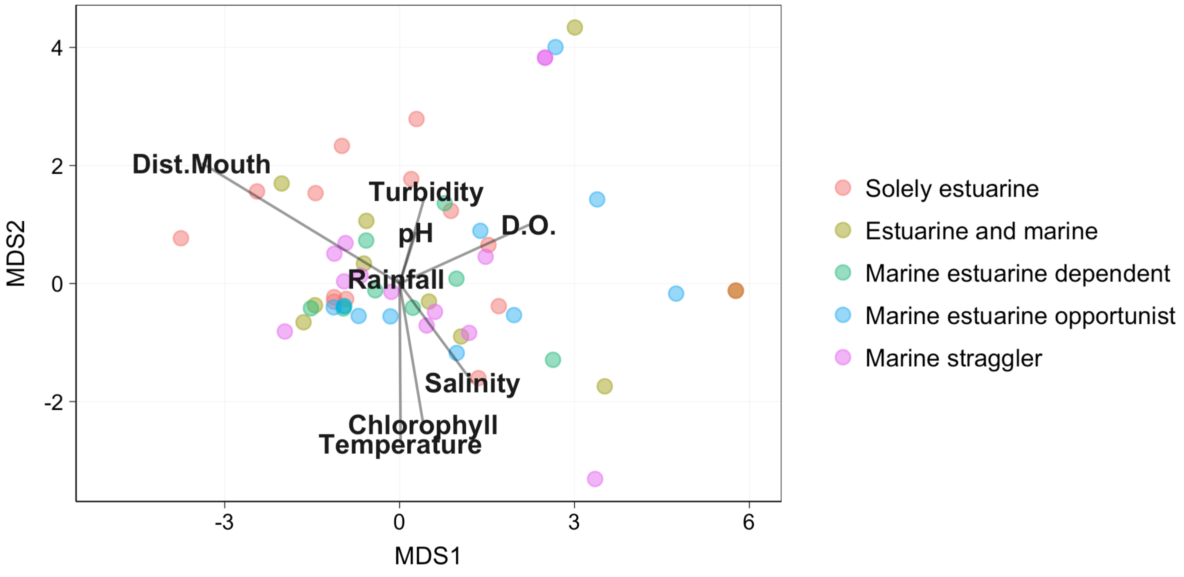

Fig. 3 Non-metric multidimensional scaling (NMS) ordination plots showing guild composition in relation to environmental factors.

4.4. Discussion

The results reported herein reinforce the importance of coastal mosaics for both, species composition and overall density of tropical fish species, highlighting that the relative importance of habitat types has seasonal variation for ecological guilds. Specifically, we found that the habitat mosaic along with the seasonal changes that occur throughout the coastal dynamics have different influences on distinct species found within the same assemblage, expressed by the great variability of responses found for each analyzed guild.

Marine estuarine dependent and solely estuarine species showed the greatest densities of individuals in all habitat types during both seasons, which was not a surprise as these guilds are typically reported as the main components of estuarine and coastal fish assemblages (Mumby 2006; Nagelkerken et al. 2008; Ferreira et al. 2019). Species within these guilds have their life cycle strictly related to the estuarine ecosystem, using a variety of habitat types at different stages of their life cycle (Potter et al. 2015). For instance, the marine estuarine dependent species, represented by Mugilidae, Lutjanidae and Gerreidae taxa (Nagelkerken et al. 2008; Igulu et al. 2014), mostly use mangrove habitats as shelters and seagrass beds as feeding areas during the juvenile phase (Blaber 2007; Vasconcelos et al. 2010; Schrandt et al. 2015), whereas solely estuarine individuals use those areas to complete their whole life cycle, typically inhabiting a variety of available habitats as they grow (Potter et al. 2015). Either way, for both guilds, estuarine and coastal habitats make up an essential component of species life history, helping to support substantial species populations.

Another possible explanation for the great abundance of individuals of solely estuarine and marine estuarine dependent guilds throughout the whole study period is that species within these guilds often have physiological and morphological adaptations that allow them to support the challenging conditions of these areas (Matthews et al. 2010). For example, high plasticity in diet (Rueda 2002; Contente et al. 2010), and wide salinity tolerance (Elliott et al. 2007) are two main features that species in these guilds possess, assisting their permanence in estuarine environments even when changes in environmental conditions or productivity levels occur. In contrast, species that are not considered obligate users of estuarine environment (i.e. marine estuarine opportunist and marine stragglers), tend to lack these adaptations, making their abundance very limited (da Silva and Fabré 2019), and typically occurring in these areas for a short period of time (Ferreira et al. 2019; Macedo et al. 2021).

Habitats had a significant effect on species composition of guilds with a certain degree of dependency on estuarine systems, however, the absent of a significant effect of the interaction between habitat types and guilds on the overall density of individual shows no signs of a single habitat association pattern per guild. Although it would be expected that guilds would be linked to a specific habitat due to distinct habitat features (da Silva et al. 2021), the seasonal conditions of tropical regions may explain why this preference pattern was not observed. The great inputs of freshwater and sediments during the wet season create an estuarization process that extends the estuarine condition to the coast (Passos et al. 2016), which, causes a seasonal homogenization of habitats during the wet season that may trigger a spatial rearrangement of species in the whole coastal landscape.

The strong effects of rainfall regimes on other conditions of tropical regions, such as salinity, pH, dissolved oxygen, and turbidity, have been widely described in literature, and are typically responsible for changes not only in species composition, but also in habitats' configuration (Chollett et al. 2007; Short et al. 2007; McKenzie et al. 2016). For instance, a previous study conducted in one of the studied estuaries described how rainfall affect the physical-chemical components of the different habitats found within, where the salinity profile of habitat types is driving by the great input of freshwater, and temperature and the levels of dissolved oxygen are very similar among habitats during the wet season (da Silva et al. 2018). These changes highlight rainfall as one of the main structuring factors of estuarine and coastal fish assemblages in tropical regions, with the habitat selection mechanisms of species being strongly influenced by seasonal regimes (da Silva et al. 2018, 2021).

Moreover, coastal habitats have significant changes in their dynamics during rainy months as a response to higher rainfall rates. Wave actions in beach areas, for instance, tend to be stronger, producing a remineralization process of organic matter that makes a greater quantity of nutrients available in the water column (Lacerda et al. 2014). For tropical seagrass beds, rainfall regimes cause substantial reductions of seagrass coverage and its total biomass (Koch et al. 2007), whereas mangrove areas typically have significant changes in turbidity and dissolved oxygen levels (Barletta et al. 2005). Those fluctuations on habitat features are often responsible for the reorganization of species in the estuarine space (Elliott et al. 2007), either by forcing species to leave specific habitat types, or attracting new species to them. This whole process might explain why seasonality had an important effect on the species composition of guilds that complete their whole life cycle in estuarine areas, such as the solely estuarine species and estuarine and marine individuals.

On the other hand, there was no seasonal effects on species composition of the marine estuarine dependent guild, neither a correlation with environmental conditions was found, which may be associated to the life cycle of species in this guild. Marine species that are estuarine dependent typically use estuaries and coastal habitats as juveniles and remain in those areas until they are ready for their recruitment (Potter et al. 2015). Thus, spending a considerable period of time there, which could explain why this guild composition is not affected by seasonal changes. For instance, in the tropics, many marine dependent fishes spawn in the middle/end of the wet season, with pelagic eggs and larvae being transported into estuaries and remaining in these areas until late dry season (Rousseau et al. 2018).

The solely estuarine species was the only guild that had significant changes associated to an interaction between habitat type and seasons, with a significative correlation between this guild and rainfall and other environmental variables that vary greatly with seasonality (pH and turbidity). These results indicate that the coastal dynamics allows species in those guilds to use the whole habitat mosaic at different scales of space and time. Indeed, studies suggest that solely estuarine species perform constant migrations between different habitats as they grow either to search for shelter and/or food, or to avoid the interaction of adults with juveniles, which could affect the development process of these individuals (Jones 1968; Bonin et al. 2015). Those spatial and temporal segregations not only reduce species competition for resources, but also increase the functionality of ecosystems allowing species to perform their functions in different habitat types and seasons (Nyström 2006).

The absent of significant effects of habitat type and seasons on the marine estuarine opportunist and marine straggler guilds can be related to their non-dependency on estuarine environments. Fishes in these guilds are facultative estuarine users, with many species occasionally find their way into an estuary (Able 2005), either by being carried by tidal currents or intentionally entering the estuarine habitats for a short period of time to feed. That makes their habitat usage pattern very variable, with ontogenetic, annual, and cohort-specific scales playing a significant role in their occurrence and abundance (Able 2005). Nevertheless, in our study, the marine stranglers were associated to changes in rainfall and salinity rates, as well as to the distance between habitat types and the estuary's mouth, with species being more abundant in sandy beach habitats, which are closer to the estuaries' mouth and where salinity rates are often higher, especially during the dry season. Similar results were found in the Yucatan peninsula, in the Gulf of Mexico, where these vagrant species where also associated with areas with higher salinity profile and closer to the coast (Aguilar-Medrano et al. 2020). This result indicates that the pattern of habitat usage by these species can be related to their physiological limitation, specifically their osmoregulatory mechanisms. The understanding of this pattern of occurrence is crucial, as those species play a significant role in the functioning of tropical regions, as they increase niche differentiation among assemblages, enhancing functional redundancy (da Silva and Fabré 2019).

4.5. Conclusion

Our findings highlight that both habitat type and seasons are important structuring factors of the whole structure of coastal fish assemblages, especially for those species that depend on these areas during one part of their life cycle. Considering the vulnerability of estuarine and coastal habitats in tropical regions and their importance for many fish species, protected areas should ensure the whole habitat diversity of these areas in no-take zones, where the pressure from human activities can be avoided. Mangroves and beaches are classical targets of conservation strategies, mainly due their importance to human populations. However, the preservation of these habitat types is always focused on each environment as independent entities, not taking into consideration the mosaic complex that they are part of. The perspective of the estuarine mosaic is a novel tool that may be important to reconsider the limitations of conservation areas. For this reason, the integrated protection of beaches, mangroves and seagrass compose an imperative strategy to sustain the complexity of inshore coastal areas that are highly productive for coastal fisheries and fundamental to maintain coastal livelihoods.

4.6. Acknowledgments

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5. CAPÍTULO III: Biogeographic patterns in the biodiversity dimensions of estuarine fish assemblages from the Western Atlantic[3]

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Abstract

Understanding how different biodiversity components are related across different environmental conditions is a major goal in macroecology and conservation biogeography. We investigated correlations among different dimensions of estuarine fish diversity (species richness, phylogenetic and functional diversity) along the three biogeographic realms of the Western Atlantic. We combined data from 232 estuaries and 1216 species, which were characterized by seven functional traits and by phylogenetic affinity. Our results provide new insights into the relationship between environmental drivers and the dimensions of fish diversity along the Western Atlantic. As expected, spatial scale had a significant role in the effects of variables, with different combinations of factors having unique relationships with dimensions at the macro (the whole Western Atlantic) and meso (for each biogeographic realm) scales. Overall, estuarine fish diversity dimensions were all correlated to estuary mouth width and sea surface temperature, with wider entrances and warmer waters hosting the highest values of SR, PD and FD. However, at smaller scales, arrangements in each dimension varied according to distinct environmental features of regions.

5.1. Introduction

Current threats to biodiversity are mainly related to human activities and the way they transform and impact the planet (Schlacher et al., 2016; Ripple et al., 2017). With significant increases in human population around the globe, natural resources have undergone overexploitation and continuously habitat loss (Pinsky et al., 2011), resulting in faster habitat degradation processes and higher extinction rates that are often compared to previous mass extinction events (Stork, 2010). Unsurprisingly, this biodiversity crisis has widely encouraged the development of different strategies to mitigate species loss, with the definition of prioritization areas for conservation being one of the most implemented approaches to date (Pereira et al., 2012). However, indicators show that we are still facing unprecedent levels of decreases in biodiversity and ecosystem services (Butchart et al., 2010; Velazco et al., 2019), with many issues related to how conservation actions are designed and set. For instance, in aquatic ecosystems, cryptic diversity of many taxa makes unclear how many species are at risk, or whether these species are successfully protected by current strategies (Cox et al., 2016). This, in part, results from conservation actions being mainly proposed through species-based indicators (i.e. species richness, vulnerability and endemism) which neglects the multidimensional concept of biodiversity (Doxa et al., 2016).

Biological communities are products of complex evolutionary and ecological processes, with the biodiversity concept going beyond the identification and count of species in a particular region (Mazel et al., 2014). Indeed, many studies have discussed that measuring only species richness may result in significant loss of unique functional and evolutionary information, which could affect the integrity and stability of assemblages and ecosystems (Doxa et al., 2016; Brum et al., 2017; Xu et al., 2019). To address these limitation, measures of phylogenetic and functional features of assemblages have emerged as an important component of ecological studies, providing more detailed information on assembly mechanisms and filtering processes (Petchey & Gaston, 2006; Teresa & Casatti, 2017). While phylogenetic diversity provides an evolutionary picture of communities, by demonstrating the accumulated history of species (Faith, 1992), functional diversity reflects the diversity of morphological, physiological and ecological attributes found within (Violle et al., 2007; Cianciaruso et al., 2009). Therefore, successful strategies for ecosystems' conservation should embrace all biodiversity facets to guarantee the maintenance of ecosystems' functions and their essential services to humans (Pollock et al., 2017).

However, though current studies have begun to unravel the complex relationships between the different dimensions of diversity (Xu et al., 2019), available knowledge is still limited and mostly based on restricted ecosystems or groups (Bernard-Verdier et al., 2013; Brum et al., 2017). In estuaries and coastal lagoons, for example, only few studies have used integrative approaches to analyze what drives biodiversity dimensions in these areas (Teichert et al., 2018; Hultgren et al., 2021), with conceptual gaps remaining as one of main obstacles to fully comprehend these ecosystems dynamics. Estuaries are among the most complex and productive ecosystems on earth, with many ecological and economic services provided (Blaber & Barletta, 2016). These areas function as nurseries for many taxa, which depend on these habitats for at least one part of their life cycle (Beck et al., 2001; Nagelkerken et al., 2015). Among them, fishes standout as one of the most diverse and dynamics groups within the estuarine biota (Elliott et al., 2007), with assemblages being mainly comprised of marine, freshwater and brackish species. These species are one of the main components of estuaries' functioning and resilience (Baptista et al., 2015; da Silva & Fabré, 2019), performing a wide range of functions, such as the control and the transport of organic matter to coastal areas (Lebreton et al., 2011).

Global patterns in the richness (Vasconcelos et al., 2015), species composition (Henriques et al., 2017a) and traits (Henriques et al., 2017b) of estuarine fishes have been recently described, showing a possible divergence between diversity dimensions, with biogeographic regions having a stronger effect on traits than species richness (Henriques et al., 2017b). This observed pattern may result from a variety of factors, such as different assembly processes, unique filtering mechanisms and the evolutionary history of communities (Bernard-Verdier et al., 2013), with spatial scales also playing a significant role in the structuring of dimensions (Arnan et al., 2017). In the Western Atlantic, for example, while dispersal limitations (i.e. hard barriers) and temperature filters appear to act as structuring factors of fish assemblages (Henriques et al., 2017a), trait composition in this region is more related to variables associated to the connectivity between estuaries and the ocean (Henriques et al., 2017b). Although we could expect that distinct environmental drivers would shape each dimensions of diversity along the Western Atlantic, the great variability of environment conditions throughout its extension, along with distinct sea geology configurations makes the Western Atlantic a highly complex region, with three biogeographic realms and more than 30 ecoregions being previously identified for its coast (Spalding et al., 2007). Each region is characterized by distinct water temperature profiles, or historical and broadscale isolation patterns that affect and select species depending on their shared or unique evolutionary history (Spalding et al., 2007). Therefore, each dimension might be affected by a particular set of variables at different spatial scales.

Since the Western Atlantic represents an important hotspot of species richness, hosting great numbers of species in estuarine systems (Vasconcelos et al., 2015), it is crucial that we identify which factors drive the dimensions of biodiversity along its extension. Thus, the present study aimed to investigate biogeographic patterns in the dimensions of estuarine fish diversity throughout the Western Atlantic, exploring the relationships between diversity and drivers at different spatial scales. Two main hypothesis drove our study: (1) at the macro scale (the whole Western Atlantic), all diversity dimensions would be related to biogeographic variables (i.e. temperature profile), (2) for the meso scale (inside the biogeographic realms), diversity dimension would respond differently to analyzed variables, being more associated to environmental conditions of each region.

5.2. Materials and methods

5.2.1. Estuarine fish assemblages' dataset

We compiled information from estuarine systems and coastal lagoons distributed along the Western Atlantic. The dataset was built using available information from books, scientific papers, and research reports that presented a list of fish species sampled from a particular estuarine system. Publications were searched in Google Scholar using the search strings "estuary", "fish" and the name of each country located in the America continent, using both English and the native language of the country (Portuguese, Spanish, or French). Each publication was downloaded and analyzed following some criteria that were used to standardize the data screening process: 1) the list of all species collected during the sampling period had to be reported, thus, works presenting only the most abundant species or species that contributed the most for the total biomass were not included in the dataset; 2) sampling information (i.e., fishing gear) should be available; and 3) studies carried out throughout estuarine gradients (i.e. with sampling point in rivers or along the coast), were only accepted when separate species list were given for each sampled environment, with only species occurring in the estuarine area being included in the dataset. Species names were checked and validated according to the current taxonomy of fishes using the "rfishbase" package (Boettiger et al., 2012), and revised records were used to build a presence/absence matrix. It is important to note that it was not the aim of our study to produce an exhaustive sample, which would be practically unachievable. Rather, we aimed to create a broadly representative and geographically unbiased sample of estuarine fish species occurring across the Western Atlantic.

5.2.2. Explanatory variables

For each estuary, we gathered data on variables that could potentially reflect filtering mechanisms of species, phylogenetic lineages, and traits, such as climatic conditions, estuary morphology and sea geology. Annual mean sea surface temperature, mean salinity, dissolved oxygen levels, chlorophyll concentration outside the estuary, and nearby current velocity were recovered from the Bio-ORACLE website – https://www.bio-oracle.org – (Tyberghein et al., 2012; Assis et al., 2018). Annual mean precipitation was retrieved from the WorldClim database using the "sdmpredictors" package in the software R statistics. Estuary area and mouth width were often available in the publications used to build the species dataset, however, whenever this information was absent, we measured both variables using the Google Earth – https://earth.google.com/web/ –. At last, continental shelf width was measured using shapefiles in the QGIS software version 3.16 (QGIS.org, 2021).

5.2.3. Phylogeny and functional traits of fish species

To reconstruct a species-level phylogeny of estuarine fish present in the Western Atlantic, we assessed the most current taxonomy of fish species following Betancur-R et al. (2017). A total of 100 trees were retrieved from the "fishtree" package in the software R statistics (Chang et al., 2019), which provides access to sequences, phylogenies, fossil calibration and diversification rates for ray-finned fishes, available in the Fish Tree Life website – https://fishtreeoflife.org – (Betancur-R et al., 2017). All 100 phylogenetic topologies recovered were used to build a final Majority-Rule Consensus Tree using the "phytools" package (Revell, 2020).

Functional traits were selected based on their well-known relationship with species performance in estuarine environments, such as prey detection and capture, energy allocation in the body, swimming efficiency, and habitat use and association (Henriques et al., 2017b). Overall, seven traits were chosen (Table 1), and we compiled a species-trait database with information retrieved from online datasets and published data for all species (Beukhof et al., 2019; Froese & Pauly, 2020). As removing species with missing data could affect final results, thus, leading to misinterpretations (Nakagawa & Freckleton, 2008; Brum et al., 2017), whenever information was not available for a particular species, we used existing data for the closest species in the same genus or family.

Table 1 – Functional traits used to estimate the functional diversity of fish species along the estuarine systems of the Western Atlantic

Trait	Ecological meaning	Reference
Maximum body size	Reflects position in the food web, metabolic rates, dispersal ability, mobility and home range	Henriques *et al.,* (2017b)
Body shape	Indicates swimming performance, and patterns in habitat use	Ribeiro *et al.,* (2016)
Habitat association	Relates to the use of water-column, and adaptations to habitats	Beukhof *et al.,* (2019)
Salinity preference	Reflects the physiological ability to deal with osmotic stress in brackish estuarine waters	Henriques *et al.,* (2017b)
Trophic guild	Relates to the position in the food web, and shows the influence of a species on abundance of others	Henriques *et al.,* (2017b)
Feeding mode	Reflects feeding strategies and it is also associated to species diet	Floeter *et al.,* (2018)
Reproductive guild	Indicates dispersal ability, colonization potential, and population growth	Lefcheck & Duffy, (2015)

5.2.4. Diversity dimensions

Fish diversity dimensions were evaluated for each estuary using equivalent diversity measures, to allow comparisons between future models. The taxonomic component of diversity was expressed by species richness (SR), taking into consideration the total number of species found in each estuary. Phylogenetic diversity was assessed by Faith's PD index (Faith, 1992), which measures the extent of uniquely evolved characters among species using the final Majority-Rule Consensus Tree created for our pool of species. Functional diversity was evaluated using the dendrogram length functional diversity (FD), proposed by Petchey & Gaston (2002), a non-abundance weighted diversity that measures diversity at all hierarchical scales simultaneously, incorporating the small functional differences between species (Petchey & Gaston, 2002). Although FD and PD are expected to be correlated and have a significant relationship with SR, many studies have shown that this relationship is rather weak at broader scales (Arnan et al., 2017), with PD and FD covarying in different ways along geographic and environmental gradients (Bernard-Verdier et al., 2013; Purschke et al., 2013), thus being suitable for studies that cross biogeographic regions.

5.2.5. Data analysis

Since one of the main purposes of our study was to identify drivers of fish diversity dimensions at different scales, we used general linear models – GLMs – to assess the effect of explanatory variables on dimensions using two approaches: 1) modelling the whole fish assemblage dataset, including all sampled estuaries and species; and 2) modelling each biogeographic realm individually, considering the classification of Spalding et al. (2007). Before analyzes, the existence of spatial autocorrelation was investigated by fitting semivariogram models to the data using the "nlme" package in R statistics. Variables were also checked for collinearity ($r>0.7$), and then standardized by subtracting the variable mean to each value and dividing it by the variable standard deviation.

Because several explanatory variables may influence the diversity dimensions of fish species, a multi-model inference approach was used (Burnham et al., 2011), taking into consideration the effect of all possible combinations of variables on each dimension. We then used a model averaging approach to reduce model selection bias and account for selection uncertainties

(Burnham & Anderson, 2002). The best set of models was chosen by the corrected Akaike Information Criterion (ΔAICc<4), and the hierarchal partitioning of explanatory variables included in each model was calculated to assess individual effects of variables. Each selected model was tested for normality and homoscedasticity. All analyzes were carried out in the software R statistics at a significance level of $p<0.05$.

5.3. Results

A total of 232 estuarine systems and coastal lagoons were analyzed in our study, with 1216 species being found in these ecosystems along the Western Atlantic. The Tropical Atlantic realm hosted the highest number of species, with 49.3% of all species being found only in this region, and 25.7% being common to other realms (Fig. 1). The Temperate Northern Atlantic had 16.6% of unique species and 16.2% of shared species with other regions, whereas the Temperate South America showed lowest species richness, with only 8.2% of exclusive species and 16.2% of shared species (Fig. 1).

Several explanatory variables were correlated throughout the Western Atlantic, with the significance and power of correlations varying across biogeographic realms (see Fig S1 on supplementary information). Therefore, more than 50 models were constructed with different sets of variables to avoid collinearity. Overall variability in SR, PD and FD throughout the Western Atlantic were positively correlated to estuary mouth width and sea surface temperature (Fig. 2), indicating that systems with greater connectivity with the sea and warmer waters host a greater number of species with phylogenetic and functional divergence among them. Furthermore, continental shelf width also played a significant role in shaping functional diversity, with estuaries located in regions of narrow shelves having lower FD among fish assemblages.

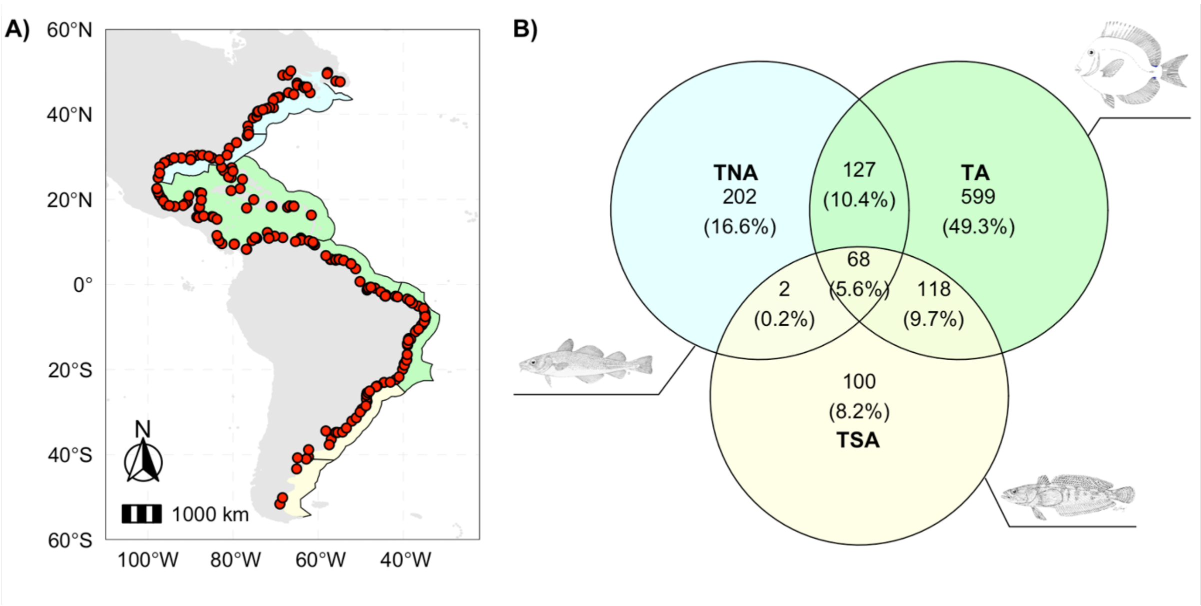

Fig. 1 – Map of the Western Atlantic showing the location of the 232 estuarine systems and coastal lagoons that were analyzed in the present study (A). The plot also shows the number and percentage of unique and shared species for all biogeographic realms with the representation of one of the most common species that was unique in each realm (B). TNA – Temperate Northern Atlanti; TA – Tropical Atlantic; and TSA – Temperate South America.

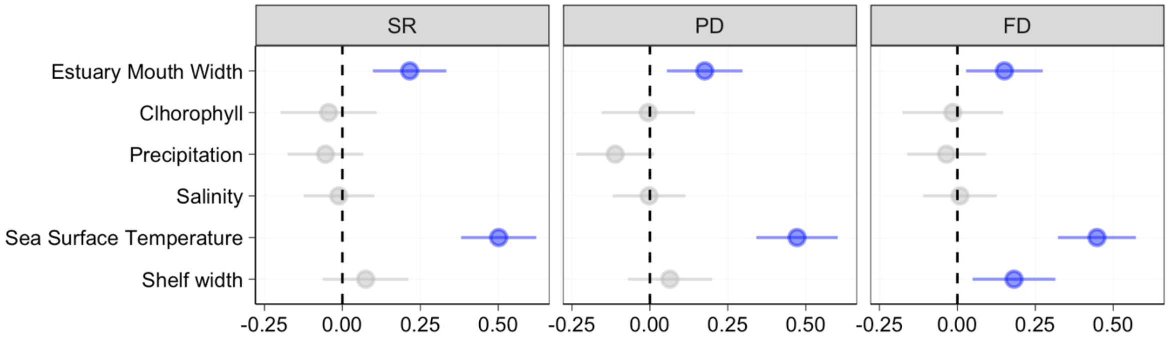

Fig. 2 – General Linear Model coefficient estimates (±95% confidence intervals) showing the magnitude and direction of effects of explanatory variables on each diversity dimension of estuarine fish species along the Western Atlantic. Blue dots and lines represent a positive effect, red dots and lines show a negative effect, and gray dots and lines indicate no significant effect found for the variable.

Across biogeographic realms, models for each diversity dimension varied greatly in explanatory power and predictive performance (Table 2), with different set of variables being selected for each realm (Fig. 3, see Table S1 for p-values of variables included in the models). For the Temperate Northern Atlantic (TNA), all three dimensions were positively correlated to mouth width, sea surface temperature and shelf width, whereas chlorophyll concentration outside the estuary had a negative effect on all dimensions (Fig. 3A). For the Tropical Atlantic (TA), variabilities in SR and PD were positively correlated to estuary area and dissolved oxygen levels, with both dimensions being negatively affected by higher precipitation rates in the region. FD in this realm was only related to the continental shelf width, with a positive relationship being found (Fig. 3B). In the Temperate South America (TSA), precipitation and estuary mouth width were related to all three dimensions, but chlorophyll concentration had only significant effects on SR and FD (Fig. 3C).

Table 2 – Generalized Linear Models fitted to the variation of diversity dimensions of estuarine fish species from the Western Atlantic, and its biogeographic realms: total explained deviance (Exp. %), linear regression of observed and predicted values (r2), total number of samples (n). Biogeographic realms: TNA – Temperate Northern Atlantic, TA – Tropical Atlantic and TSA – Temperate South America.

Model fit	Total			TNA			TA			TSA		
	SR	PD	FD	SR	PD	FD	SR	PD	FD	SR	PD	FD
Exp. (%)	25	21	20	60	58	56	16	17	15	50	46	41
r^2	0.24	0.19	0.18	0.54	0.51	0.49	0.12	0.13	0.11	0.42	0.37	0.31
n	233	233	233	55	55	55	144	144	144	34	34	34

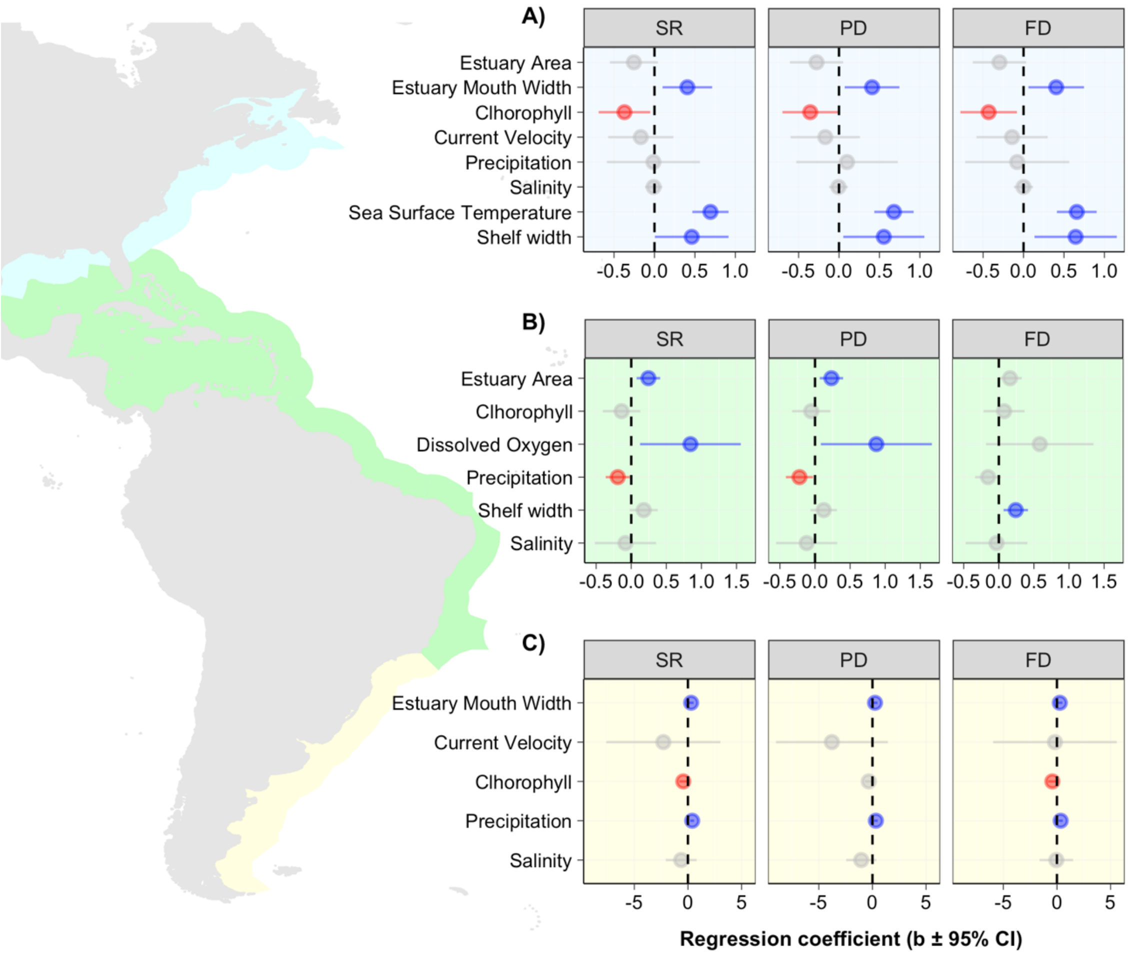

Fig. 3 – Model coefficient estimates (±95% confidence intervals) showing the magnitude and direction of effects of explanatory variables on each diversity dimension of estuarine fish species along the biogeographic realms of the Western Atlantic: A) Temperate Northern Atlantic, B) Tropical Atlantic, and C) Temperate South America. SR – species richness, PD – phylogenetic diversity and FD – functional diversity. Blue dots and lines represent a positive effect, red dots and lines show a negative effect, and gray dots and lines indicate no significant effect found for the variable.

5.4. Discussion

Our results provide new insights into the relationship between environmental drivers and the dimensions of fish diversity along the Western Atlantic. As expected, spatial scale has a significant role in the effects of variables, with different combinations of factors having unique relationships with dimensions at the macro (the whole Western Atlantic) and meso (for each biogeographic realm) scales. Overall, estuarine fish diversity dimensions were all correlated to estuary mouth width and sea surface temperature, with wider entrances and warmer waters hosting the highest values of SR, PD and FD. Both variables have been previously highlighted in the works of Henriques et al., (2017a,b) as one of the main drivers of species and traits composition of estuaries at a global scale. Temperature gradients impose suitable or unsuitable conditions for species, selecting species and traits based on their physiological tolerances, which appears to be related to the phylogenetic history of species as PD also respond positively to this variable. In the same way, greater connectivity with the sea allows the occurrence of marine species with dispersal ability and different sets of traits that enhance FD in these areas. However, the magnitude and effect size of explanatory variables varied greatly across biogeographic realms, with distinct factors affecting diversity dimensions.

In the Temperate Northern Atlantic, for example, besides temperature and mouth size, other variables had also significant effects on all three dimensions of fish diversity, such as continental shelf width (positive effect) and chlorophyll concentration (negative effect). The Temperate Northern Atlantic is characterized by a clear temperature profile, with temperatures in the southern portion having modest seasonality (Phlips et al., 2020) while varying greatly at the northern region (Gobler et al., 2012). Temperature differences between regions are responsible for filtering species composition, selecting specific settlement mechanisms (Able et al., 2006) and tolerance ranges for each estuary (Morson et al., 2019). This shapes not only the total number of species (SR) but also traits (FD) that appears to be related to the evolutionary history of species (PD). Another important structuring factors of estuarine biota in this realm were the estuary mouth width and continental shelf width, which are directed related to the connectivity between estuarine systems and the open sea, acting as regulators of freshwater runoffs and saltwater inputs (Ohrel & Register, 2006), and controlling fish migration and larval dispersion (Akin et al., 2003).

In the Tropical Atlantic, SR and PD showed the same patterns in relation to explanatory variables, with both dimensions being positively affected by estuary area and dissolved oxygen levels. Estuary size and area are typically related to geomorphology, rivers runoff and entrance regimes, often having a greater degree of marine influence, which could explain why both SR and PD increased with total area (Harrison & Whitfield, 2006). Furthermore, larger systems tend to have high structural complexity, mainly represented by the great diversity of habitat types found within, such as mangroves, seagrass beds, saltmarshes, mudflats, and coastal sandy beaches (Sheaves et al., 2014). Each one of these habitat types has its own characteristics and dynamics, creating a highly complex mosaic that shapes the estuarine biota and not only attracts a greater number of species, but also distinct phylogenetic lineages with different habitat selection mechanisms (Pihl et al., 2007; Larmuseau et al., 2011). The positive relationship between SR and PD with dissolved oxygen levels was also expected, as oxygen is required for aerobic metabolism, and is typically related to higher diversity of prey items for estuarine fish species (i.e. macrobenthic faunal) (Islam et al., 2013).

Additionally, precipitation was also a significant driver of SR and PD in the Tropical Atlantic, with greater rainfall rates being negatively correlated to both dimensions. While would be expect that regions with stronger rainfall regimes would host greater numbers of species, since rainfall is typically associated to increases in productive levels of estuaries (Krumme et al., 2012; da Silva et al., 2018), recent studies have addressed how intricate seasonality may be for tropical areas. For instance, throughout the Tropical Atlantic, rainfall frequency and volume may create a process called “estuarization”, which is characterized by the extension of estuarine conditions to the coastal ecosystem (Longhurst & Pauly, 1987; Blaber et al., 1997; Barletta et al., 2003). This process, which has been documented in many regions in the Tropical Atlantic realm, such as the Guiana shelf (McConnell, 1962), the Gulf of the Mexico (Chittenden, 1976; Yanez-Arancibia, 1985) and the Northeastern Brazil, creates a temporal corridor that allows estuarine species to leave estuaries and inhabit adjacent coastal areas, thus causing a temporal decrease in the number of species in the estuarine zone. Nonetheless, even though it appears that this dynamic is a key component of both ecosystems – enhancing the connectivity between estuarine and coastal zones – (Passos et al., 2016; da Silva & Fabré, 2019), authors have also discussed that future climatic changes may jeopardize the stability and resilience of this process by intensifying rainfall regimes and producing a permanent homogenization of both ecosystems, thus affecting their functionality. Indeed, studies carried out in this region have already shown that narrow shelves may facilitate the transit of estuarine species to coastal areas, enhancing the functional diversity of coastal assemblages, but negatively impacting the functional structure of estuaries (Passos et al., 2016). This process may also explain why FD was positively correlated to continental shelf width, as estuarization tends to be weaker at larger shelves (Lowe-McConnell, 1987).

On the order hand, precipitation was one of the main drivers of all diversity dimensions in the Temperate South America, having a positive effect along with estuary mouth width. Both variables can be linked to the connectivity between the estuarine systems and the ocean, which have direct impacts on the structuring of assemblages. Studies carried out along the Temperate South America have shown a significant prevalence of marine species in the estuarine fauna, with rare occurrence or total absence of freshwater species (Garcia et al., 2001; Vilar et al., 2011). This not only results from the higher salinity profile that estuaries have in these areas (i.e. Paranaguá estuarine complex), but also from the close relationship between precipitation and productivity (Blaber & Barletta, 2016). At normal condition, rainfall regimes in this realm are associated to greater productivity in estuarine areas by stimulating phytoplankton growth and increasing photosynthetic efficiency (Vizzo et al., 2021). The growth in productivity attracts marine species from coastal zone, rising the number of species as well as the phylogenetic and functional complexity of these ecosystems (Mouchet et al., 2013). In addition, the absence of a significant relationship between temperature and diversity dimensions in this realm might be unexpected as a great variability on the temperature profile occurs throughout the whole realm, but it is important to acknowledge that only a small number of estuarine systems in the southern portion of this region have been studied, which may have masked the effect of this variable in our analyzes. Nevertheless, it is important to highlight that latitude had also a significant effect on dimensions, which can be related to the environmental conditions from the south portion of this province which is very distinct from the north portion.

In conclusion, our study suggests that distinct environmental profiles among biogeographic regions are drivers of change for the components of estuarine fish diversity along the Western Atlantic, with dimensions responding differently to environmental gradients depend on the spatial scale. Although at broader scale diversity dimensions appear to have similar responses to variables related to historical and isolation patterns (i.e. temperature and connectivity between estuary and the sea), our results show that at smaller scales arrangements in each dimension may vary according to distinct environmental features of regions. This observed pattern is crucial to the planning and management of estuarine ecosystems, which have been undergone unprecedent levels of human-induced impacts. Our results highlight that conservation actions should take in consideration regional features when designing and implementing management strategies for species and ecosystems.

5.5. References

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6. DISCUSSÃO GERAL

Nosso estudo sugere que diferentes fatores influenciam a composição específica e funcionalidade de ambientes estuarino-costeiros, evidenciando o efeito da escala espacial na compreensão dos padrões que regem a biodiversidade destes ecossistemas. A nível local, foi possível identificar que em regiões tropicais ,a diversidade de habitats em ambientes costeiros em conjunto com a sazonalidade atuam em um processo sinérgico, permitindo um rearranjo espacial e temporal de diferentes conjunto de espécies, enriquecendo a composição funcional e filogenética desses ambientes (DA SILVA et al., 2022; DA SILVA; DOLBETH; FABRÉ, 2021). Tal padrão de ocupação temporal e espacial diferenciada já havia sido evidenciado também em outras regiões tropicais do Atlântico Ocidental (AGUILAR-MEDRANO; HERNÁNDEZ DE SANTILLANA; VEGA-CENDEJAS, 2020), indicando que a existência de mosaicos costeiros nesta região são de grande importância para o funcionamento ecossistêmico destas áreas.

Contudo, a nível regional, diferentes combinações de fatores estão relacionadas com as dimensões da diversidade de peixes nas escalas macro (todo o Atlântico Ocidental) e meso (para cada domínio biogeográfico). No geral, as dimensões da diversidade regional de peixes estuarino-costeiros foram todas correlacionadas com a largura da boca do estuário e a temperatura da superfície do mar, com entradas mais amplas e águas mais quentes apresentando os maiores valores de diversidade taxonômica (DT), filogenética (DP) e funcional (DF). Ambas as variáveis foram anteriormente destacadas nos trabalhos de Henriques et al., (2017a,b) como um dos principais fatores estruturantes da composição de espécies e traços na escala global. Os gradientes de temperatura parecem atuar como um determinante da composição especifica regional destas áreas, impondo condições adequadas ou inadequadas para um conjunto distinto de espécies, selecionando as populações e suas características com base em suas tolerâncias fisiológicas, o que parece estar relacionado à história filogenética das espécies, pois DP também responde positivamente a essa variável (HENRIQUES et al., 2017a, 2017b). Da mesma forma, a maior conectividade com o mar permite a ocorrência de espécies marinhas com diferentes conjuntos de características que potencializam a DF nessas áreas, desempenhando um papel crucial na escala regional atuando como conectoras entre a escala local e global pela sua capacidade de dispersão.

De fato, a nível local, nosso estudo evidenciou que esta conectividade entre estuários e outros habitats costeiros é de extrema importância para a manutenção da funcionalidade ecossistêmica, atuando principalmente no incremento de redundância das funções chaves. Estudos prévios já haviam identificado que a ocorrência de espécies marinhas de forma ocasional em estuários e outros habitats costeiros aumentam a diferenciação de nichos (DA SILVA; FABRÉ, 2019). Todavia, os resultados apresentados aqui complementam tal informação indicando que tal ocorrência é resultado de um efeito sinérgico entre a diversidade de habitats e os regimes sazonais que permitem que diferentes conjuntos de espécies habitem os distintos habitats que compõem os mosaicos costeiros ao longo da dinâmica natural desses ecossistemas.

Contudo, é importante evidenciar que os padrões identificados podem sofrer alterações diante do atual cenário que vivemos (MAHONEY; BISHOP, 2017). As mudanças climáticas, por exemplo, têm grande potencial para afetar as variáveis que influenciam as diferentes dimensões da diversidade de peixes nestas áreas, tais como temperatura da superfície do mar, níveis de clorofila e o regime de chuvas. Nas provinciais temperadas, as mudanças na temperatura dos oceanos podem atuar não apenas na criação de barreiras que limitem a persistência de espécies locais, apresentando também grande potencial para o surgimento de corredores térmicos que permitam a ocorrência de espécies de outras regiões (DE QUEIROZ et al., 2018; PEÑA RIVAS; AZZURRO; LLORIS, 2013), alterando o pool de espécies regional e podendo modificar toda a dinâmica ecossistêmica destas áreas.

Em regiões tropicais, um aumento das chuvas, especialmente durante a estação seca, impactaria o escoamento de água doce e o abastecimento de sedimentos, eventualmente causando uma homogeneização de habitats estuarino-costeiros e interferindo na dinâmica identificada no nosso estudo (BERNARDINO et al., 2015; MARENGO et al., 2010). Embora uma homogeneização temporária pareça ser um componente-chave do funcionamento do ecossistema estuarino, aumentando a conectividade do habitat e facilitando os movimentos das espécies, a homogeneização permanente impactaria a integridade individual dos habitats, alterando suas características e condições, afetando as espécies que habitam essas áreas (GARTNER et al., 2013). Por exemplo, nosso estudo demonstrou que peixes dependentes de estuários tendem a usar diferentes habitats à medida que crescem para completar seu ciclo de vida (DA SILVA et al., 2022). Assim, uma homogeneização permanente afetaria a dinâmica dessas espécies e interferiria em seu processo de desenvolvimento (NAGELKERKEN et al., 2008, 2015).

Sendo assim, considerando a vulnerabilidade dos habitats estuarinos e costeiros ao longo do Atlântico, e sua importância para muitas espécies de peixes, estratégias de conservação devem levar em consideração um conjunto de variáveis de natureza local e regional. A perspectiva do mosaico de habitats, por exemplo, é uma ferramenta que pode ser importante para reconsiderar as limitações das áreas de conservação. Por esta razão, a proteção integrada de diferentes habitats representa uma estratégia imperativa para sustentar a complexidade das áreas costeiras, altamente produtivas para a pesca e fundamentais para manter os meios de subsistência.

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8. ANEXOS

Supplementary information for

Biogeographic patterns in the diversity dimensions of estuarine fish assemblages from the Western Atlantic

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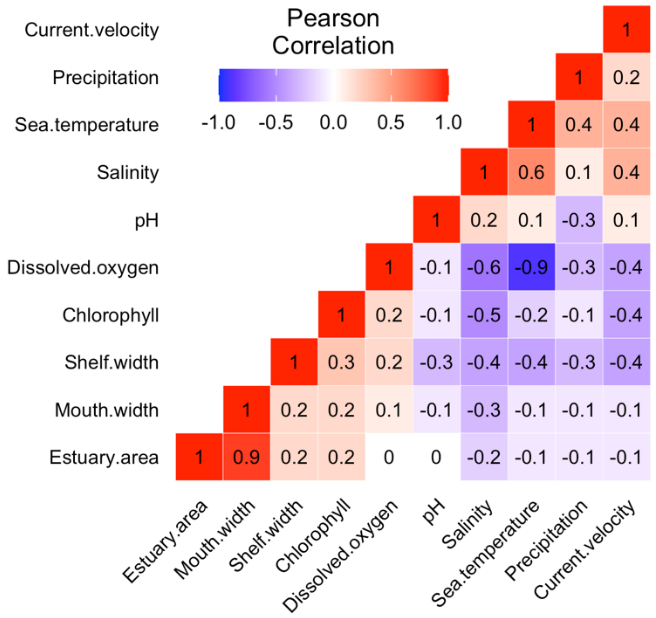
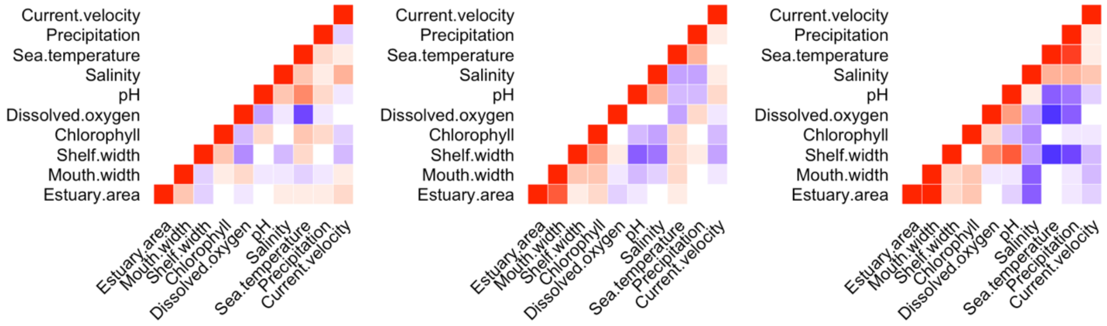
Supporting Information Content

- Figure S1
- Table S1


A) Western Atlantic


B) Temperate Northern Atlantic

C) Tropical Atlantic

D) Temperate South America

Fig. S1 – Pearson's correlation for explanatory variables in the Western Atlantic (A), and its respective biogeographic realms (B–D).

Table S1. Effect and significance of explanatory variables in each dimension of fish diversity for biogeographic realms of the Western Atlantic.

Variable	TNA						TA						TSA					
	SR		PD		FD		SR		PD		FD		SR		PD		FD	
	Ef.	p	Ef.	p	Ef.	p	Ef.	p	Ef.	p	Ef.	p	Ef.	p	Ef.	p	Ef.	p
Estuary area		0.092		0.098		0.076	+	0.004	+	0.006		0.063						
Mouth width	+	0.009	+	0.017	+	0.021							+	0.012	+	0.038	+	0.311
Shelf width	+	0.046	+	0.353	+	0.013		0.078		0.198	+	0.006						
Chlorophyll	-	0.022	-	0.041	-	0.015		0.312		0.697		0.615	-	0.018		0.052	-	0.035
Current velocity		0.409		0.438		0.526								0.397		0.155		0.949
Dissolved oxygen							+	0.021	+	0.031		0.134						
Precipitation		0.965		0.756		0.811	-	0.291	-	0.024		0.103	+	0.000	+	0.000	+	0.000
Salinity		0.851		0.903		0.991		0.714		0.593		0.883		0.391		0.146		0.947
Sea surface temperature	+	0.000	+	0.000	+	0.000		0.237		0.081		0.066						