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PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS (ZOOLOGIA)

ALINE PAIVA MORAIS DE MEDEIROS

DIVERSIDADE TAXONÔMICA, FUNCIONAL E FILOGENÉTICA DE PEIXES RECIFAIS DA PARAÍBA

JOÃO PESSOA

2021

ALINE PAIVA MORAIS DE MEDEIROS

DIVERSIDADE TAXONÔMICA, FUNCIONAL E FILOGENÉTICA DE PEIXES RECIFAIS DA PARAÍBA

Tese de Doutorado apresentada ao Programa de Pós-Graduação em Ciências Biológicas, área de concentração Zoologia, da Universidade Federal da Paraíba, como parte dos requisitos para obtenção do título de doutora em Ciências Biológicas.

Orientador: Prof. Dr. Bráulio Almeida Santos

Co-orientadora: Profa. Dra. Beatrice Padovani Ferreira - UFPE

JOÃO PESSOA

2021

Ata da 140ª Apresentação e Banca de Defesa de Doutorado de Aline Paiva Morais de Medeiros

Ao(s) trinta dias do mês de abril de dois mil e vinte e um, às 13:00 horas, no(a) Ambiente Virtual, da Universidade Federal da Paraíba, reuniram-se, em caráter de solenidade pública, membros da banca examinadora para avaliar a tese de doutorado de **Aline Paiva Morais de Medeiros**, candidato(a) ao grau de Doutor(a) em Ciências Biológicas. A banca examinadora foi composta pelos seguintes membros: **Dr. Bráulio Almeida Santos (Orientador - UFPB/PB); Dr.Ronaldo Bastos Francini-Filho (USP/SP); Dr. João Lucas Leão Feitosa (UFPE/PE); Dr. Ricardo de Souza Rosa (UFPB/PB); Dr. Alexandre Vasconcellos (UFPB/PB).** Compareceram à solenidade, além do(a) candidato(a) e membros da banca examinadora, alunos e professores do PPGCB. Dando início à sessão, a coordenação fez a abertura dos trabalhos, apresentando o(a) discente e os membros da banca. Foi passada a palavra ao(à) orientador(a), para que assumisse a posição de presidente da sessão. A partir de então, o(a) presidente, após declarar o objeto da solenidade, concedeu a palavra a **Aline Paiva Morais de Medeiros**, para que dissertasse, oral e sucintamente, a respeito de seu trabalho intitulado **"Diversidade taxonômica, funcional e filogenética de peixes recifais da Paraíba".** Passando então a discorrer sobre o aludido tema, dentro do prazo legal, o(a) candidato(a) foi a seguir arguido(a) pelos examinadores na forma regimental. Em seguida, passou a Comissão, em caráter secreto, a proceder à avaliação e julgamento do trabalho, concluindo por atribuir-lhe o conceito APROVADA. Perante o resultado proclamado, os documentos da banca foram preparados para trâmites seguintes. Encerrados os trabalhos, nada mais havendo a tratar, eu, orientador(a), como presidente, lavrei a presente ata que, lida e aprovada, assino juntamente com os demais membros da banca examinadora.

João Pessoa, 30/04/2021.

Bráulio Almeida Santos
Orientador(a)

Ronaldo B. Francini Filho
Examinador(a)

João Lucas Leão Feitosa
Examinador(a)

Ricardo S Rosa
Examinador(a)

Examinador(a)

Aline Paiva Morais de Medeiros
(discente ciente do resultado)

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ALINE PAIVA MORAIS DE MEDEIROS

DIVERSIDADE TAXONÔMICA, FUNCIONAL E FILOGENÉTICA DE PEIXES RECIFAIS DA PARAÍBA

Esta tese foi julgada e aprovada para a obtenção do Grau de Doutora em Ciências Biológicas, área de concentração Zoologia no Programa de Pós-Graduação em Ciências Biológicas na Universidade Federal da Paraíba.

João Pessoa, 30 de abril de 2021.

BANCA EXAMINADORA

Prof. Bráulio Almeida Santos – Doutor – UFPB – Orientador

Prof. Alexandre Vasconcellos – Doutor – UFPB

Prof. Ricardo de Souza Rosa – Doutor – UFPB

Prof. João Lucas Leão Feitosa – Doutor – UFPE

Prof. Ronaldo Bastos Francini Filho – Doutor – USP

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RESUMO

Nesta tese avaliei como a diversidade de peixes recifais se distribui ao longo de recifes naturais, incluindo recifes rasos e profundos, e naufrágios centenários localizados ao longo da plataforma continental da Paraíba, Brasil. Especificamente, os objetivos foram realizar uma revisão bibliográfica sobre o uso das métricas de ‘diversidade’ em estudos de comunidades de peixes recifais, e calcular, em múltiplas escalas espaciais (alfa, beta e gama), a diversidade taxonômica, funcional e filogenética das comunidades de peixes recifais. Estruturei a tese em três capítulos. O primeiro capítulo corresponde a uma revisão abrangente da literatura na qual sintetizo, junto com outros colegas, as principais métricas utilizadas no estudo da diversidade de peixes recifais desde 1970. Detectamos que a grande maioria dos estudos tem utilizado métricas de ‘entropia’ que possuem sérias limitações matemáticas enquanto estimadores de ‘diversidade’. A maioria tem ignorado o componente espacial da diversidade (i.e. diversidade beta) e, quando o considerou, utilizou estimadores de ‘entropia’ que são dependentes da diversidade alfa. Uma minoria tem estimado adequadamente a diversidade funcional e filogenética das comunidades, a despeito da relevância dessas dimensões da diversidade biológica para o manejo e conservação. O segundo capítulo foi dedicado aos recifes naturais rasos e profundos e teve como objetivo testar a hipótese de refúgio dos recifes profundos (HRRP). Coletamos informações de 22 recifes, distribuídos ao longo de um gradiente de profundidade (2-62 m), e calculamos métricas de diversidade capazes de particionar a diversidade gama (regional) em seus componentes independentes alfa (local) e beta (entre locais), para as dimensões taxonômica, funcional e filogenética. Embora alguns resultados deem suporte à HRRP, a maioria indica que a diversidade de peixes recifais encontradas nos recifes rasos não está completamente encapsulada nos recifes profundos. Cada recife contribui significativamente para a diversidade regional e deve ser manejado e protegido de acordo. No terceiro capítulo, comparamos as comunidades de peixes entre 4 recifes artificiais (i.e. embarcações naufragadas acidentalmente entre 1873 e 1926) e 8 recifes naturais utilizando o mesmo arcabouço metodológico aplicado no segundo capítulo. O objetivo foi avaliar se os recifes artificiais beneficiam ou prejudicam a diversidade de peixes e em qual escala espacial isto ocorre. Os recifes artificiais apresentaram uma maior diversidade alfa e gama do que os recifes naturais vizinhos, muito provavelmente porque ‘roubaram’ espécies dos ambientes naturais circundantes. Em contraste, apresentaram menor diversidade beta do que os recifes naturais, indicando que são habitats biologicamente mais homogêneos que os ambientes naturais. Juntos, esses resultados indicam que os recifes artificiais, mesmo após um século de colonização, são incapazes de proteger integralmente a diversidade regional de peixes. Iniciativas de manejo e a conservação de peixes recifais devem priorizar a proteção e a restauração dos recifes naturais existentes. O afundamento de estruturas artificiais deve ser tratado secundariamente, e caso seja efetivado, deve ser implementado e monitorado criteriosamente para evitar a degradação dos recifes naturais circundantes.

Palavras-chave: Números de Hill, partição, alfa, beta, ictiofauna, refúgio, gradiente de profundidade, recifes naturais, recifes artificiais.

ABSTRACT

In this thesis I evaluated how the reef fish diversity is distributed along natural reefs, including shallow and deep reefs, and centenary shipwrecks located along the continental shelf of Paraíba, Brazil. Specifically, the goals were to carry out a literature review on the use and misuse of 'diversity' metrics in studies of reef fish communities, and to estimate, in multiple spatial scales (alpha, beta and gamma), the taxonomic, functional and phylogenetic diversity of reef fish communities. I organized the thesis into three chapters. The first chapter corresponds to an extensive literature survey in which my colleagues and I synthesize the metrics most used on reef fish diversity studies since 1970. We highlight that the majority of studies have been applying 'entropy' metrics, which have serious mathematical limitations, rather than properly 'diversity' estimators. Most studies lack information on the spatial component of diversity (i.e. beta) and when this component is used, they are actually 'entropy' estimators, which are dependent on alpha diversity. Only few studies have been adequately estimating the functional and phylogenetic components of diversity of reef fish communities, despite of their relevance to management and conservation strategies. The second chapter was dedicated to compare shallow and deep natural reefs, which the main goal was to test the deep reef refuge hypothesis (DRRH). We surveyed 22 reefs, located along a depth gradient (2-62 m), and partitioned the gamma (regional) diversity into its alpha (local) and beta (the difference between two areas) independent components to estimate the taxonomic, functional and phylogenetic diversity. Although some data support the DRRH, most results indicate that the reef fish diversity of shallow reefs are not fully encapsulated in the deep reefs. Each reef contributes significantly to the regional diversity and should be managed and protected accordingly. In the third chapter, we compared the fish community between 4 artificial reefs (i.e. accidentally shipwrecked vessels dating from 1873 to 1926) and 8 natural reefs under the same methodological approach applied in second chapter. The goal was to evaluate whether artificial reefs increase or diminish the fish diversity, and the role they play on structuring the diversity on a spatial scale. Artificial reefs showed higher alpha and gamma diversity than their natural counterparts, most likely because they 'steal' species from adjacent natural reefs. Conversely, artificial reefs showed lower beta diversity rates than natural reefs, indicating that these reefs are biologically more heterogeneous than those. Altogether, these results indicate that artificial reefs, even after one century of colonization, are unlikely to fully protect the regional fish diversity. Management and conservation initiatives to protect and restore reef fish diversity should prioritize the existing natural reefs. The sinking of artificial structures should be discussed secondarily, and if decided in favor, must be implemented and monitored with caution to avoid further degradation of adjacent natural reefs.

Keywords: Hill numbers, partition, alpha, beta, ichthyofauna, refuge, depth gradient, natural reefs, artificial reefs.

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SUMÁRIO

1 INTRODUÇÃO GERAL

Os ecossistemas recifais encontram-se distribuídos ao longo das zonas tropical e subtropical, tipicamente entre as latitudes 30° N e 30° S (Tittensor *et al.*, 2010). Embora com ampla distribuição, esses ecossistemas ocupam apenas 0,1% do assoalho marinho e abrigam mais de 6000 espécies de peixes (Cowman *et al.*, 2017; Parravicini *et al.*, 2013). Em uma escala global, as áreas que hospedam a maior diversidade de organismos associados aos recifes estão na região do Indo-Pacífico (Mora *et al.*, 2003), seguidas pela região do Caribe (Bellwood e Wainwright, 2002). Essas áreas de maior diversidade são consideradas como centros de origem de espécies, geralmente apresentando alto grau de endemismo (Cowman, 2014).

O Atlântico Ocidental, que engloba a região do Caribe e os recifes localizados nas Américas, está separado do Pacífico por barreiras geográficas históricas (i.e. fechamento do Istmo do Panamá e do Mar de *Tethys*; Albert e Reis, 2011; Bellwood e Wainwright, 2002; Cowman e Bellwood, 2013) e por correntes marítimas frias (Maida e Ferreira, 1997). No Atlântico Ocidental há também barreiras físicas e filtros ambientais entre os ecossistemas recifais. Por exemplo, os ecossistemas recifais do sudoeste do Atlântico estão separados do Caribe pela pluma do Rio Amazonas ao Norte (Floeter *et al.*, 2008); estão separados de ilhas oceânicas no meio do Atlântico e dos recifes da África pela barreira no meio do Atlântico ao leste (Luiz *et al.*, 2012); e, ao sul, pela corrente fria das Malvinas (Anderson *et al.*, 2015; Laborel-Deguen *et al.*, 2019; Maida e Ferreira, 1997). Dessa forma, o Atlântico Ocidental engloba três províncias biogeográficas diferentes: Caribe, Brasil e Argentina (Pinheiro *et al.*, 2018). O isolamento geográfico por barreiras físicas da Província Brasileira contribuiu para o surgimento de novas espécies (Rocha, 2003), com cerca de 20% das espécies recifais residentes sendo endêmicas do Brasil (Pinheiro *et al.*, 2018).

Pinheiro *et al.* (2018), baseado na similaridade da ictiofauna, propôs a divisão da Província Brasileira, que vai desde o norte do Estado do Amapá até o sul do Estado de Santa Catarina (Floeter *et al.*, 2008). São cinco subprovíncias: 1. Arquipélago de São Pedro e São Paulo; 2. Arquipélago Fernando de Noronha e Atol das Rocas; 3. O complexo Vitória-Trindade; 4. leste e sudeste do Brasil (do norte da Bahia ao sul de Santa Catarina);

5. norte e nordeste do Brasil (norte do Amapá ao sul de Sergipe). A subprovíncia norte-nordeste do Brasil é considerada a segunda em maior riqueza de espécies de peixes recifais, com 259 espécies. Essa região encontra-se sob influência da corrente marítima Brasileira, apresenta alta turbidez da água, possui formações recifais associadas a bancos de arenito formados por algas calcárias e baixa diversidade de corais (Laborel-Deguen *et al.*, 2019; Leão e Dominguez, 2000; Maida e Ferreira, 1997).

Inserida na subprovíncia norte-nordeste do Brasil, está a Paraíba. O Estado conta com uma plataforma continental relativamente estreita e com a quebra do talude a cerca de 70 m de profundidade (Feitoza, Rosa e Rocha, 2005; Leão e Dominguez, 2000). As formações recifais, geralmente paralelas à linha da costa, são de vários formatos e dimensões e são características da Formação Barreiras (Barbosa, 1987; Laborel-Deguen *et al.*, 2019). Cerca de 225 espécies de peixes recifais já foram documentadas para a região, incluindo 39 espécies endêmicas do Brasil (Pinheiro *et al.*, 2018; base de dados disponível em https://swatlanticreeffishes.wordpress.com/database/). Recentemente, foi instituída uma Área de Proteção Ambiental (APA) estadual, que abarca cerca de 10% da plataforma continental paraibana e engloba tanto recifes naturais (rasos e profundos) quanto artificiais (Paraíba, 2018).

Independente da escala geográfica trabalhada, os ecossistemas recifais têm sofrido diversos impactos, como sobrepesca (Downing *et al.*, 2005), poluição (Zaneveld *et al.*, 2016), branqueamento massivo e consequente morte de corais (Cheal *et al.*, 2010), turismo descontrolado (Medeiros *et al.*, 2007), dentre outros. Esses impactos podem acarretar em perdas de habitat e da estrutura tridimensional dos recifes, com uma consequente perda de diversidade (Cheal *et al.*, 2010; Tittensor *et al.*, 2007). Assim, é importante destacar o papel das áreas marinhas protegidas na manutenção da diversidade e dos serviços ecológicos desempenhados pelos ecossistemas recifais (Anderson *et al.*, 2014; Appolloni *et al.*, 2017; Bonaldo *et al.*, 2017). Esses serviços incluem proteção costeira, produção pesqueira, desenvolvimento de fármacos e áreas de contemplação (Elliff e Kikuchi, 2017; Spalding *et al.*, 2017).

Estudos de ecologia que mensurem diferentes escalas da diversidade, por exemplo, ainda são escassos em diferentes ecossistemas recifais (Brandl *et al.*, 2018; Manel *et al.*, 2020; Mora, Tittensor e Myers, 2008). Esses estudos permitem traçar estratégias de manejo apropriadas para cada região, estabelecer áreas marinhas protegidas que abarquem diferentes aspectos da diversidade, manter estoques pesqueiros para evitar a sobre-exploração, e salvaguardar a diversidade dos ecossistemas recifais no Antropoceno (Bellwood *et al.*, 2019; Randin *et al.*, 2020). Assim, entende-se por diversidade uma estimativa quantitativa que fornece informações sobre o número efetivo de entidades biológicas que compõem uma comunidade, sendo uma medida bastante intuitiva e que permite comparações (Jost, 2006). A riqueza de espécies, por exemplo, é uma medida de diversidade, mas que ignora a abundância das espécies e consequentemente tem limitações do ponto de vista ecológico.

A diversidade pode ser decomposta em diferentes componentes espaciais: gama (γ), alfa (α) e beta (β) (Marcon e Hérault, 2015). Gama representa a diversidade regional; alfa representa a diversidade de uma área dentro de uma região; e beta representa a diversidade entre duas ou mais áreas. Assim, alfa e beta compõem a diversidade gama de uma região (Jost *et al.*, 2010). Há duas formas de calcular gama: 1. Propriedade multiplicativa ($\gamma = \alpha*\beta$), que assume que alfa e beta são componentes independentes (Jost, 2007; Whittaker, 1972); 2. Propriedade aditiva ($\gamma = \alpha+\beta$), que produz valores de beta que são dependentes dos de alfa e, portanto, não permitem comparações confiáveis entre áreas que diferem em termos de alfa (Baselga, 2010a; Jost *et al.*, 2010). A propriedade multiplicativa tem sido utilizada tanto para estimar a diversidade beta regional, que fornece um valor único de comunidades completamente distintas para toda a região, como para calcular a diversidade beta entre pares de comunidades da região e a contribuição relativa dos componentes de aninhamento e substituição (Baselga, 2010b; Lande, 1996). O conceito de diversidade, bem como o cálculo, pode ser aplicado para espécies, funções, linhagens filogenéticas ou até mesmo genes (Chao, Chiu e Jost, 2010; Chiu e Chao, 2014; Gaggiotti *et al.*, 2018). Cada um desses componentes é independente e fornece informações complementares sobre a diversidade real das comunidades (Chao, Chiu e Jost, 2014).

O conjunto de equações de Hill (1973) e suas derivações (Jost, 2006, 2007) expressam o número efetivo de espécies de uma comunidade, conhecido como diversidade verdadeira de espécies por cumprir o princípio matemático da replicação, propriedade que os índices tradicionais de diversidade (e.g. Shannon-Wiener, Simpson) não cumprem (Chao, Chiu e Jost, 2014). Dessa forma é atribuído a cada espécie um valor consensual distinto (Gotelli e Chao, 2013), e se o número de espécies de uma comunidade dobrar, mantendo-se a equitabilidade entre as espécies, a métrica de diversidade também dobrará, fato que não ocorre com as medidas tradicionais, transformando-as em medidas de entropia, não de diversidade (Jost, 2006). O mesmo princípio pode ser empregado para diversidade filogenética (Chao, Chiu e Jost, 2010), se assumirmos que cada comprimento de um ramo filogenético pode ser tratado como uma entidade distinta e, assim, todos os comprimentos de cada ramo de uma árvore filogenética serão igualmente distintos filogeneticamente. Da mesma forma, o valor atribuído para a distância funcional em cada par de espécies também pode ser tratado como uma unidade funcional distinta (Chiu e Chao, 2014). A vantagem de usar essas métricas é que, além de integrar os diversos sistemas de medida para diversidade taxonômica, funcional e filogenética, as equações também são ordenadas pelo fator q que pondera a métrica pela abundância das espécies (Chao, Chiu e Jost, 2014). Quando q=0, o valor da abundância de todas as espécies retorna a 1 e o índice considera apenas a riqueza de espécies. Quando q=1, o índice retorna à abundância das espécies, sem favorecer raras ou abundantes. Quando q=2, a abundância das espécies é elevada ao quadrado, favorecendo as espécies mais abundantes. Dessa forma, a diversidade (^{q}D) é dada para espécies raras (^{0}D), típicas (^{1}D) e dominantes (^{2}D).

O desenvolvimento de ferramentas computacionais de livre acesso e código aberto (R Core Team, 2018; Stamatakis, 2006), atrelado à disponibilidade de base de dados de distribuição e atributos de espécies (Froese e Pauly, 2019; NCBI, 2010; Pinheiro *et al.*, 2018), bem como a facilidade ao acesso de filogenias robustas (Betancur-R *et al.*, 2017; Rabosky *et al.*, 2018) permitem que hoje possamos mensurar mais facilmente diferentes aspectos da diversidade de ecossistemas. Com a popularização do mergulho de Scuba e o avanço de tecnologias de sensoriamento remoto, também se tornou mais acessível o estudo em ecossistemas recifais mais profundos (> 30m de profundidade) (Hixon, 2011).

O crescente interesse no estudo de áreas recifais mais profundas (também chamadas de mesofóticas; entre 30m e 150 m de profundidade) e afastadas da costa (ou seja, menos impactados pelos distúrbios humanos costeiros), fez com que pesquisadores propusessem a ideia de que recifes naturais mais profundos funcionariam como refúgio para espécies recifais em face à degradação e perda de habitat em áreas rasas (Glynn, 1996; Hoegh-Guldberg *et al.*, 2007). Dessa maneira, os recifes profundos manteriam populações viáveis de espécies e as exportariam para recifes rasos impactados. Essa ideia de refúgio, embora antiga (Glynn, 1996), só ganhou visibilidade na última década (Kahng *et al.*, 2010), sendo formalmente descrita como Hipótese de Refúgio dos Recifes Profundos (HRRP - Bongaerts *et al.*, 2010) em um estudo com corais no Caribe. Desde então, diversos estudos vêm sendo realizados com o intuito de testar a hipótese de refúgio em diferentes regiões do mundo: Grande Barreira de Corais (Jankowski, Graham e Jones, 2015), Micronésia (Coleman *et al.*, 2018), Ilhas Marianas (Lindfield *et al.*, 2016), Brasil (Morais e Santos, 2018; Pereira *et al.*, 2018), Golfo do México (Semmler, Hoot e Reaka, 2017) e também focando em escalas geográficas maiores (Rocha *et al.*, 2018). Há consenso de que algumas espécies podem se refugiar nas áreas mais profundas, porém não há um consenso até que ponto os recifes profundos são capazes de resguardar comunidades inteiras (Laverick *et al.*, 2018), i.e. múltiplas espécies e linhagens evolutivas que despenham diferentes funções em diferentes escalas espaciais.

Um bom modelo para testar a HRRP a partir da diversidade são os peixes. Esse grupo biológico, além de bastante diverso, desempenha inúmeras funções nos ecossistemas recifais, é bastante impactado pelas ações antrópicas e é um dos principais recursos econômicos marinhos (Chaves, Nunes e Sampaio, 2010; Stuart-Smith *et al.*, 2013). Estudos de diversidade em peixes podem avaliar a eficácia de uma área marinha protegida e identificar áreas prioritárias para conservação (Franco *et al.*, 2012; Olavo *et al.*, 2011; Soares *et al.*, 2020; Tyler *et al.*, 2011), uma vez que esse grupo apresenta uma resposta rápida e direta pelo aumento da abundância e do tamanho do corpo (Claudet, García-Charton e Lenfant, 2011). Para o presente estudo, peixes recifais foram definidos como espécies associadas ou adjacentes (~ 1m de distância) aos recifes (Rocha, 2003). Essa definição não implica fidelidade das espécies ao recife, mas simplesmente que as espécies utilizam esses ambientes em algum estágio do desenvolvimento, como abrigo ou área de forrageio (Hixon e Beets, 1993; Pinheiro *et al.*, 2018). Dessa forma, todas as espécies registradas foram incorporadas ao estudo.

Em face à degradação e perda da complexidade estrutural dos recifes naturais, estruturas artificiais tais como os naufrágios poderiam aumentar a disponibilidade de habitats e garantir a manutenção da diversidade regional (Brown-Peterson, Leaf e Leontiou, 2021; Rilov e Benayahu, 2000). Essa associação entre a complexidade, a limitação do habitat e a distribuição das espécies é um dos pilares importantes da ecologia de comunidades (Hortal *et al.*, 2009; MacArthur e Wilson, 1967; Simpson, 1949; Tews *et al.*, 2004). Quanto maior a complexidade e a heterogeneidade, maior a diversidade que poderia estar associada à uma região (Bejarano, Mumby e Sotheran, 2011; Galzin *et al.*, 1994; Luckhurst e Luckhurst, 1978). Riqueza, abundância, biomassa e estrutura trófica de comunidades de peixes têm sido associadas à complexidade estrutural de recifes naturais, que promovem abrigo, proteção e áreas de forrageio para diferentes espécies ao longo do desenvolvimento (Beukers e Jones, 1998; Böhm e Hoeksema, 2017; Brandl *et al.*, 2018; Rilov e Benayahu, 2000). Nesse contexto, estruturas artificiais como naufrágios poderiam então contribuir para o aumento da heterogeneidade ambiental e consequente manutenção da diversidade em áreas recifais.

No entanto, há duas hipóteses contrastantes relacionadas ao papel ecológico de estruturas artificiais. Por um lado, as estruturas artificiais poderiam reduzir a pressão turística e pesqueira sobre os recifes naturais porque aumentariam a diversidade local e regional (Bohnsack, 1989; Hall, Herbert e Stafford, 2021; Santos, Oliveira e Cúrdia, 2013) (hipótese de produção; sensu Wilson *et al.*, 2001). Por outro lado, as estruturas artificiais poderiam "roubar" espécies dos recifes naturais a partir de mecanismos de seleção de habitat e recrutamento de larvas (Leibold *et al.*, 2004; Mercader *et al.*, 2019; Nicholls e Racey, 2006), o que empobreceria os recifes naturais vizinhos e favoreceria a sobre-exploração dos recursos pesqueiros (hipótese de atração; Wilson *et al.*, 2001). Usando a partição da diversidade de peixes nos componentes independentes alfa e beta, seria então possível entender qual o papel dos recifes artificiais para na manutenção da diversidade regional de peixes.

Embora a composição da ictiofauna de recifes rasos da Paraíba seja bem estudada (Feitoza *et al.*, 2002; Honório, Ramos e Feitoza, 2010; Osório, Rosa e Cabral, 2006; Ramos, 1994; Rocha, Rosa e Feitoza, 2000; Rocha, Rosa e Rosa, 1998; Rosa, Rosa e Rocha, 1997; Silva *et al.*, 2014; Souza *et al.*, 2007), ainda há pouca informação sobre a ictiofauna associada aos recifes profundos (Feitoza, Rosa e Rocha, 2005; Silva, 2018) e também associada aos naufrágios (Cardoso *et al.*, 2020). Seguindo essa mesma tendência, estudos de diversidade funcional e filogenética ainda são escassos ou inexistentes para a região (mas veja Araújo *et al.*, 2020; Pereira *et al.*, 2018). Também falta conhecimento acerca da contribuição dos componentes alfa e beta da diversidade regional de peixes recifais. Os resultados de estudos com abordagens que integrem diferentes aspectos e componentes da diversidade possuem implicações tanto do ponto de vista teórico, no entendimento sobre os mecanismos de manutenção da diversidade e regras de montagem das comunidades (Leibold *et al.*, 2004; Mazel *et al.*, 2018), quanto do ponto de vista mais aplicado, para a conservação de espécies, no desenho e gestão de áreas naturais protegidas (Andrade *et al.*, 2015; Loiseau *et al.*, 2017; Mouillot *et al.*, 2013; Winter, Devictor e Schweiger, 2013).

Nesse contexto, nesta tese avaliei como a diversidade de peixes recifais se distribui ao longo de recifes naturais, incluindo recifes rasos e profundos, e naufrágios centenários localizados ao longo da plataforma continental da Paraíba. Estimei a diversidade taxonômica, funcional e filogenética das comunidades e as particionei em seus componentes espaciais alfa e beta a fim de mensurar a contribuição de cada um deles para a diversidade regional (gama). Também quantifiquei a contribuição relativa dos componentes de aninhamento e substituição que compõem a diversidade beta par-a-par. Três perguntas centrais nortearam o estudo: i) Como a profundidade afeta as dimensões da diversidade?; ii) Qual a contribuição relativa dos componentes alfa e beta para a diversidade gama dos peixes recifais?; iii) Qual o papel dos recifes artificiais (i.e. naufrágios) na manutenção da diversidade regional dos peixes recifais? Assim, dividi a tese em seis seções: 1. Introdução geral; 2. Objetivos; 3. Capítulo I; 4. Capítulo II; 5. Capítulo III; 6. Considerações finais e conclusão.

O capítulo I trata de uma revisão da literatura sobre como a diversidade vêm sendo medida em estudos de peixes recifais. Nele, estão incluídos estudos de diversidade taxonômica, funcional e filogenética, e seus componentes espaciais alfa e beta, bem como uma descrição dos índices mais comumente utilizados para mensurar diferentes aspectos da diversidade. O capítulo II tem como objetivo entender qual o papel dos recifes profundos como refúgio para a comunidade de peixes recifais da Paraíba. Para isso, a diversidade gama taxonômica, funcional e filogenética foi particionada em seus componentes alfa e beta, e comparada entre recifes naturais rasos (<30m de profundidade) e profundos (>30m de profundidade). O capítulo III compara a diversidade de peixes entre recifes artificiais (i.e. naufrágios centenários) e recifes naturais na costa da Paraíba a fim de entender o papel de estruturas artificiais para a manutenção da diversidade regional. Para isso, foram calculadas as diversidades alfa e beta taxonômica, funcional e filogenética. Por último, faço considerações sobre os três capítulos e destaco as principais conclusões para cada capítulo.

2 OBJETIVOS

2.1 GERAL

O trabalho tem como objetivo principal quantificar, em múltiplas escalas espaciais (gama, alfa e beta) as diversidades taxonômica, funcional e filogenética das comunidades de peixes recifais da Paraíba, considerando recifes naturais (rasos e profundos) e artificiais.

2.2 ESPECÍFICOS

- Revisar as métricas utilizadas para medir a diversidade de peixes recifais, identificando as principais lacunas do conhecimento e apontando a direção para pesquisas futuras;
- Avaliar o papel da profundidade e de embarcações naufragadas sobre as diversidades taxonômica, funcional e filogenética das comunidades de peixes recifais;
- Particionar a diversidade gama taxonômica, funcional e filogenética em seus componentes espaciais alfa e beta;
- Contextualizar os padrões de diversidade observados com estratégias de manejo e conservação em escala regional.

3 CAPÍTULO I – THE USE AND MISUSE OF DIVERSITY METRICS IN STUDIES OF REEF FISH COMMUNITIES

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Tipo de trabalho: Artigo de revisão

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Marine Environmental Research – Review Articles

The use and misuse of diversity metrics in studies of reef fish communities

Aline P. M. Medeiros[a], Aiara P. L. R. Cardoso[a], Juliano Morais[a,b], Beatrice P. Ferreira[c], Ricardo Betancur-R[d,e], Marcelo O. Soares[f,g,h], Bráulio A. Santos[i]*

[a] Programa de Pós-Graduação em Ciências Biológicas, Universidade Federal da Paraíba, Cidade Universitária, Castelo Branco, 58051-900. João Pessoa, PB, Brazil.

[b] ARC Centre of Excellence for Coral Reef Studies and College of Science and Engineering, James Cook University, Townsville, QLD 4811, Australia.

[c] Universidade Federal de Pernambuco, Centro de Tecnologia, Departamento de Oceanografia, Cidade Universitária, 50670-901. Recife, PE, Brazil.

[d] Department of Biology, The University of Oklahoma, 730 Van Vleet Oval, Room 314, Norman, OK 73019, USA
[e] Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington DC 20560, USA
[f] Instituto de Ciências do Mar-LABOMAR, Universidade Federal do Ceará, Av. da Abolição, 3207, Meireles, 60165-081, Fortaleza, CE, Brazil
[g] Institut de Ciència i Tecnologia Ambientals (ICTA), Universitat Autònoma de Barcelona (UAB), Carrer de les Columnes, Edifici Z, Barcelona, Spain
[h] Dipartimento di Scienze e Tecnologie Biologiche e Ambientali (DISTEBA), Università del Salento, Lecce, Italy
[i] Universidade Federal da Paraíba, Centro de Ciências Exatas e da Natureza, Departamento de Sistemática e Ecologia, Cidade Universitária, Castelo Branco, 58051-900. João Pessoa, PB, Brazil.

*Corresponding author: braulio@dse.ufpb.br

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Highlights

- The concept of diversity has been applied in different contexts on reef fish studies
- Most studies applied richness and/or abundance as surrogate of community diversity
- The huge majority of studies use metrics of entropy and do not measure diversity
- Beta diversity has been less estimated than alpha diversity
- Functional and phylogenetic dimensions of fish diversity deserve more attention

Abstract

Species richness and abundance have long been used, combined or not, to describe the diversity of local fish communities (alpha diversity) and the differences among communities (beta diversity). A fair number of indices have been employed to account for different aspects of diversity, including the most-known Shannon, Simpson, and Jaccard indices. However, as we show here, most of them estimate entropy rather than diversity, do not comply with the replication principle, and do not express diversity in effective number of biological entities, impairing comparisons between fish communities. Moreover, many metrics assume that all individuals and species in the community belong to the same genus and play the same functional role, ignoring the phylogenetic and functional dimensions of diversity. To properly measure the diversity of fish communities and improve the effectiveness of management and conservation actions worldwide, we suggest the adoption of the unifying framework based on Hill numbers.

Keywords: Alpha diversity; Beta diversity; Biodiversity; Conservation; Coral reef; Functional diversity; Hill numbers; Management; phylogenetic diversity

1 Introduction

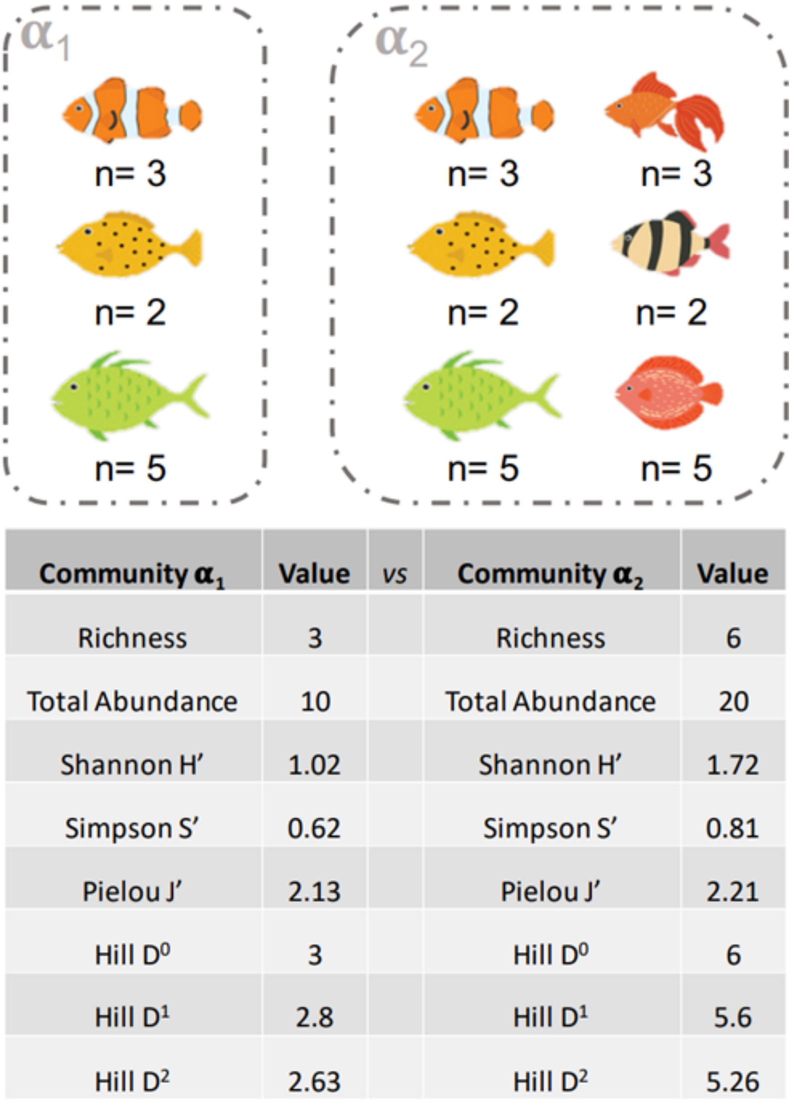
The reef ecosystems cover approximately 0.1% of the ocean floor, but harbor more than 2500 fish species (Cowman et al., 2017) and provide dozens of goods and services such as coastal protection, fishing, tourism and recreational spots (Costanza et al., 2014; Elliff and Kikuchi, 2017; Hafezi et al., 2021). Measuring diversity of reef fish communities is therefore critical not only to identify the major patterns and processes that originate and underpin marine fish diversity, but also to support environmental planning to the socioeconomic activities we have been developing in reef ecosystems around the world (Bender et al., 2013; Francisco-Ramos and Arias-González, 2013; García-Hernández et al., 2014; Loiseau et al., 2017; Ramírez-Ortiz et al., 2017). For instance, diversity studies have addressed questions concerning the effectiveness of marine protected areas (Appolloni et al., 2017; Bonaldo et al., 2017; Tyler et al., 2011), the impact of human stressors (Andrade et al., 2015; Mouillot et al., 2013), and regional diversity patterns (Hubert et al., 2012; Jankowski et al., 2015). A large body of literature has been developed so far, but the ‘diversity’ metrics have not been updated and deserves an in-depth evaluation. Most are prior to 1950, such as Shannon, Simpson, and Jaccard indices, which may no longer be appropriate to describe reef fish communities and to allow comparisons between communities (Jost, 2010, 2006).

Here we review the literature to identify how diversity has been measured and interpreted in studies of reef fish communities (see Supplementary material for details). Our goal was not to invalidate the studies that eventually failed in this task, but to call attention that results from previous studies may need to be updated in terms of the diversity indices employed. To support our line of argument, we briefly summarized the mathematical and biological limitations of traditional metrics, described the three dimensions of diversity (taxonomic, functional, and phylogenetic diversities), presented the metrics used more often to estimate them, and indicated what they represent at the alpha and beta scales. Then, we used the outcomes of our review to point out the most common metrics, identify theoretical and geographic gaps and suggest future directions the study of reef fish diversity.

2 Mathematical and biological limitations of traditional metrics

The goal of any diversity index is to estimate the biological variability of different community components in space and/or time (Hill, 1973). Historically, the most frequent measures applied to compare two different communities have been richness and abundance (Magurran, 2004). However, richness, abundance and diversity itself are different terms and, consequently, have different interpretations (Gotelli and Chao, 2013; Hurlbert, 1971; Loiseau et al., 2017; Naeem et al., 2012). While richness and abundance are related to simply counts of entities, the term ‘diversity’ offers a measure of both species number (i.e. richness) and evenness (i.e. equitability – how evenly the individuals in a community are distributed among the different species; Jost, 2006).

However, the way studies have measured ‘diversity’ by simply combining abundance and richness has several mathematical and biological limitations. Most indices of ‘diversity’ are indeed measures of ‘entropy’ (Jost, 2006). In his seminal work on this topic, Jost (2006, p.363) states “The radius of a sphere is an index of its volume but is not itself the volume, and using the radius in place of the volume in engineering equations will give dangerously misleading results”. With a few exceptions, what most researchers have done so far is to measure the radius, the diameter, the surface, but not the volume of the sphere that represents the diversity of biological communities. To do so, we should measure the effective number of its elements rather than the heterogeneity between them. If a community with eight equally-common species has a diversity of eight species and a community with sixteen equally-common species has a diversity of sixteen species, then the diversity of the second community should be twice that of the first (Jost, 2006). However, because the entropy gives the uncertainty in the species identity of a sample, not the effective number of species in the community, such metrics of ‘entropy’ do not comply with the replication principle and make comparisons between communities unfeasible (Fig. 1).



Community α_1	Value	vs	Community α_2	Value
Richness	3		Richness	6
Total Abundance	10		Total Abundance	20
Shannon H’	1.02		Shannon H’	1.72
Simpson S’	0.62		Simpson S’	0.81
Pielou J’	2.13		Pielou J’	2.21
Hill D^0	3		Hill D^0	6
Hill D^1	2.8		Hill D^1	5.6
Hill D^2	2.63		Hill D^2	5.26

Figure 1. The replication principle. Community 1 (α1) is represented by 10 individuals of three species, whereas community 2 (α2) is represented by six species and 20 individuals. Note that Shannon (in natural logarithm) and Simpson values do not double from community 1 to 2, but the metrics based on Hill numbers do. Hill’s equation and its derivations (Chao et al. 2014; Hill 1973; Jost 2006), often called true diversity, are expressed by the effective number of species. The advantage of using this index is that the equations are ordered by a q factor that weights the community by species abundances; ^0D, ^1D, and ^2D may be interpreted as the diversity of rare, typical and dominant species. This set of equations can be also partitioned into independent alpha and beta components (Jost et al., 2010).

The traditional metrics of ‘entropy’ also ignore the functional and phylogenetic dimensions of fish diversity. Because only abundance and richness are taken into account, they assume that all individuals and species in a community are phylogenetically equivalent and play the same functional role, which clearly is an unrealistic assumption. Some metrics of taxonomic ‘diversity’ do consider the hierarchical taxonomic classification of the species (e.g. class, order, family, genus), which is essential to incorporate the knowledge of systematics on ecological indices (Clarke and Warwick, 2001, 1999), but they still do not comply with the replication principle, assume that evolution is constant and ignore phylogenetics. Such limitations, if not recognized, may lead to misinterpretations, overstatements, and poor guidelines for reef ecosystem management and conservation.

Regardless the dimension studied (species, functional, or phylogenetic), the diversity may be partitioned into spatial components: (i) local, within-community component [alpha (α) diversity], also known as the mean of the diversities of local reef communities; (ii) between-community component [beta (β) diversity], which measures the extent of change in community composition; (iii) total or regional component [so-called gamma (γ) diversity] (Chiu and Chao, 2014; Lande, 1996; Loreau, 2000; Whittaker, 1972). This partitioning of fish diversity into different spatial components is widely accepted to elucidate the processes underlying species distributions and diversity turnover (De Bello et al., 2010; Marcon and Hérault, 2015). The portioning may be multiplicative or additive. The multiplicative property assumes that gamma diversity is a product of beta and alpha diversities (Whittaker, 1972), which makes their components independent (Jost, 2007). The additive property predicts that gamma diversity is a sum of alpha and beta dependent components (Lande, 1996) and warrants caution in interpretation. While decomposing the gamma diversity into alpha and beta components using this additive approach, the metrics of ‘entropy’ (e.g. Gini-Simpson index) fail to produce beta values that are independent from the alpha ones. The larger the size of alpha, the smaller the size of beta. This can make the plant beta diversity between two Antartica tundras, which have only two species that cooccur everywhere in the continent at different abundances, be 33% larger than the beta between two tropical rainforests of different continents (Panama and Malaysia), which otherwise host hundreds of plant species but share none of them (see Jost, 2007, p. 2427, for more details on this example). Unfortunately, this mathematical limitation also applies to classical Sorensen, Jaccard, and Morisita-Horn indices and rises concerns about their application in the reef fish research (Jost, 2007). Similar caveats are observed in traditional metrics of functional and phylogenetic beta diversity.

The beta diversity can also be divided into nestedness and turnover components to account for species replacement and loss (Fig. 2) (Baselga, 2010), but their application in studies of reef fish diversity are still scarce (but see Araújo et al., 2020). The interest for this decomposition is quite old (Simpson, 1943) and precedes the term ‘beta diversity’ (Whittaker, 1960). In addition, Baselga (2010) has summarized the pairwise and multiple-site metrics developed since Simpson’s seminal work, highlighted their limitations and proposed new indices. Nestedness occurs when the species composition of local communities with smaller numbers of species are subsets of the composition at richer local reef communities (Ulrich and Gotelli, 2007), while spatial turnover implies the replacement of some species by others with no significant change in species richness (Baselga, 2010).

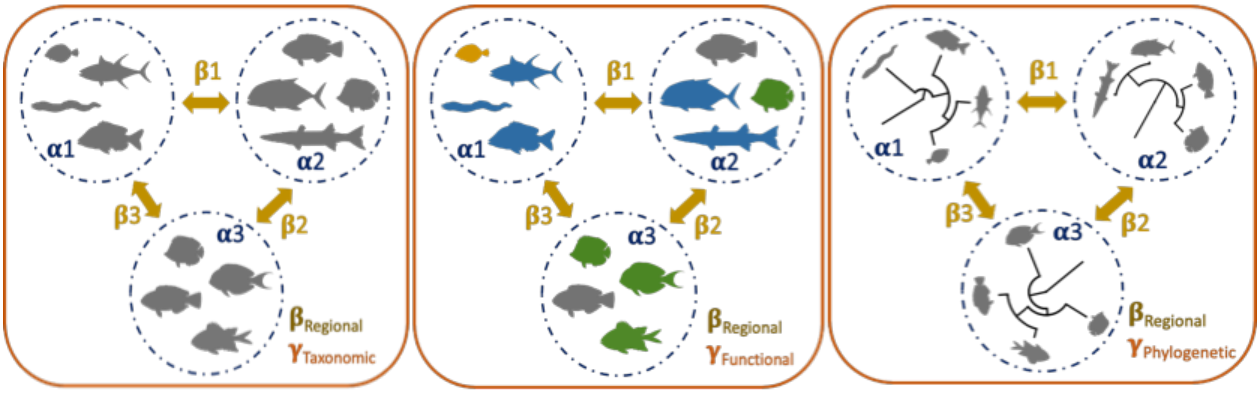


Figure 2. Scheme depicting the dimensions and spatial components of reef fish diversity. Gamma (γ) diversity is decomposed into alpha (α) and beta (β) components for the taxonomic, functional and phylogenetic dimensions. Each dashed circle represents a local community (α) with different species, functions (differentiated by colors) and phylogenies encompassed into a region (γ). The region has a single value of regional beta diversity, which estimates the number of completely different communities in the region (Jost, 2007). In our example, this value might vary from 1, if all communities were equal, to 3, if all communities were different. Arrows indicate pairwise beta diversity from which nestedness and turnover can be estimated (Baselga, 2010). In the taxonomic panel, for instance, β2 is more

influenced by nestedness as community α3 share 2 species with community α2, while β1 is driven by turnover as communities α1 and α2 are completely different from each other. Fish shapes were reproduced from Schiettekatte et al. (2019).

Nestedness reflects a process of species loss as a consequence of any factor that promotes the orderly disaggregation of local communities (Gaston and Blackburn, 2000), while turnover indicates species sorting across different environmental conditions or spatial and historical constraints (Qian et al., 2005). Therefore, disentangling the spatial components of diversity may shed light into the underlying mechanisms of community assembly, dynamics, and historical biogeography (Araújo et al., 2020; Cardoso et al., 2020; Floeter et al., 2006; Lamy et al., 2015; Medeiros et al., 2021; Pinheiro et al., 2018). Moreover, it can provide effective guidelines for conservation planning, sustainable fishing, recreation and tourism in reef ecosystems (e.g. Andrade et al., 2015; Appolloni et al., 2017).

3 Dimensions of fish diversity

3.1 Taxonomic dimension

The number of species in a given reef community is the most pivotal and intuitive measure of community heterogeneity, once it can be easily compared (Magurran, 2004). The greater the number of fish species and the more equally their relative abundances are distributed in the community (evenness), the greater the diversity (Pielou, 1966). Several indices have been proposed since the early 1940’s and adapted to calculate some aspects of diversity, such as Simpson index (Simpson, 1949), Hill numbers (Hill, 1973), Pielou’s evenness (Pielou, 1966), Fisher index (Fisher et al., 1943), and Shannon’s index (Shannon, 1948; adopted from information theory).

These traditional metrics use different parametric or nonparametric statistical approaches. While parametric measures assume a species abundance distribution (i.e. log-normal), as in Fisher index, nonparametric methods disregard any statistical distribution of the underlying species abundance. Such indices are widely applied not only in reef ecology, but also in information science and economics (Jost, 2007, 2006), with Shannon entropy (Shannon, 1948) and Simpson index being the most disseminated ones (Leps et al., 2006;

Magurran, 2004). Shannon's quantifies the uncertainty in fish species identity of a randomly chosen individual in the reef community, considering both richness and evenness. Whereas the Simpson index measures the probability that two randomly chosen individuals belong to different species (Chao et al., 2014; Gotelli and Chao, 2013; Jost et al., 2010). Pielou (1966) determined different scales of community sampling to calculate evenness, using Shannon entropy as theoretical background, with its highest values when the individuals are distributed as equally as possible between species.

Regardless of the index applied, the diversity of a given reef community should incorporate three major aspects: richness (number of species), relative importance of a species (i.e. a weight is attributed to each species) and evenness (the degree of distribution of individuals in a community). As shown above, different indices describe different aspects of community diversity and a few do measure the effective number of fish species. Also, the majority of these indices do not comply with the mathematical replication principle (Jost, 2006, 2010; Jost et al., 2010; Fig. 1). Noteworthy, the taxonomic dimension is often described and compared with species composition analyses that may or may not be weighted by abundance and summarized by multivariate ordinations. Such analyses are familiar to ecologists, including, for instance, Principal Component Analysis, Non-metric Multidimensional Scalings, and dendrograms based on Bray-Curtis, Euclidian distance, Jaccard and similar indices. However, they do not give the effective number of completely different communities in the region and thus cannot be decomposed into independent alpha and beta components, as Jost's true diversity indices do.

3.2 Functional dimension

Functional diversity generally involves understanding communities and ecosystems based on the functions performed by reef organisms. On the one hand, if a single trait level is strongly linked to an ecosystem function, abundance of this trait may best predict the functioning. On the other hand, the complementarity of different traits may be the most important driver of ecosystem functioning, thus their abundance and evenness in the reef community will be more relevant (Hillebrand and Matthiessen, 2009; Mouillot et al., 2013; Vile et al., 2006). Such multidimensional space can be defined as the variation in the expression degree of multiple functional traits that influence ecosystem level processes (Naeem et al., 2012; Petchey and Gaston, 2006; Tilman, 2001). In a recent work, Bellwood et al. (2018) defined the term function as ‘the movement or storage of energy or material’, in which all functional traits should be related to a process-based unifier of material fluxes. Noteworthy, reef species are not equal in their effects on ecosystem functioning since their functional traits do not contribute equally to ecosystems processes (Villéger et al., 2017). That said, fish species abundance can also influence the degree of which every ecosystem process is performed (Stuart-Smith et al., 2013). For instance, it is well known the role of herbivore/grazer fishes in coral reefs ecosystems for controlling macroalgae outbursts (Thibaut et al., 2012). Abundance acts as a key factor in measuring functional diversity once it gives a weight for each functional entity, which captures the role that each reef species plays in ecosystem functioning (Gagic et al., 2015). Besides having a great explanatory power when compared to functional indices that do not account for abundance, functional metrics that incorporate abundance are important for studies of the response of diversity to environmental gradients (Mouillot et al., 2013) and its effects on reef ecosystem functioning (Leps et al., 2006).

The functional difference between fish species can be measured by the dissimilarity or distances between their trait profile in distance matrices (Chao et al., 2010; Leps et al., 2006; Mouchet et al., 2010; Pavoine et al., 2009). The first point is that the selected traits reflect ecosystem functions, otherwise the metrics calculated onwards will be irrelevant and based on unstable foundations (Bellwood et al., 2018). Assuming that the traits do describe the functions, many indices have been proposed to account for the functional variability within and among communities. Examples are the Functional Attribute Diversity (FAD; Walker et al., 1999), which quantifies the sum of all functional pairwise distances between species belonging to the same community; Rao’s quadratic entropy (Q; Rao, 1982), which estimates the mean functional distance between two randomly chosen individuals; and community weighted mean (CWM), which calculates the mean of trait values present in the community weighted by the relative abundance of taxa bearing each value (Lavorel et al., 2008).

Similar to the indices that describe the taxonomic dimension of diversity, some functional indices consider abundance in their equations (i.e. Rao’s Q and CWM), while others do not (i.e. FAD; Mouchet et al., 2010). Villéger et al. (2008) proposed a different set of components for measuring the functional space, namely functional richness, functional evenness and functional divergence. While functional richness represents the amount of functional space filled by a given reef community, functional evenness corresponds to the regularity in which the species abundances are distributed, and functional divergence indicates how far high species abundances are from the center of the functional space (Mouchet et al., 2010; Schleuter et al., 2010). Mouillot et al. (2013) offers a very thorough explanation on how to assess and interpret diverse functional indices under a trait-space framework.

Unfortunately, many of these indices are dependent on fish species richness and require standardized effect sizes (SES) to become comparable. However, when SES is calculated the metrics are expressed in units of standard deviation, which neither represent the effective number of elements that compose the functional dimension of the community nor comply with the replication principle. More recently, the indices of true diversity based on Hill equations and their derivations provide a promising alternative to properly measure the functional diversity of reef fish communities and decomposing it into independent alpha and beta components (Chiu and Chao, 2014).

3.3 Phylogenetic dimension

Imagine two distinct fish communities with the same species richness, abundance, evenness, and functional diversity, but different species composition. Although indistinguishable from many parameters, both communities could conceal very particular evolutionary and biogeographic histories (Pinheiro et al., 2017). One reef community might be composed of closely related species (i.e., young lineages), while the other might comprise a set of more distantly related taxa (i.e., a combination of both ancient and young lineages). With the diversity of species and functions being equal, the community of closely related species is less phylogenetically diverse than a community with distantly related species (Gotelli and Chao, 2013; Naeem et al., 2012; Warwick and Clarke, 1995; Winter et al., 2013). Thus, phylogenetic diversity is an aspect that considers the degree of relatedness (or the evolutionary relationships) among a set of species in a given community. It is usually based on elapsed time since divergence (Chao et al., 2010; Tucker et al., 2017), but pioneer metrics do not require time-calibrated phylogenies (Faith, 1992).

To calculate the phylogenetic diversity, it is first necessary to hypothesize the evolutionary relationships among fish species or other entities (Winter et al., 2013). The growing availability of multi-locus datasets (prompted by improvements in sequencing technologies), coupled with advances in phylogenetic inference approaches (Brower, 2018; Felsenstein, 1985; O'Meara, 2012; Rannala and Yang, 2008), have contributed to the increasing availability of taxonomically-dense time-calibrated phylogenies for fishes (Betancur-R et al., 2017; Rabosky et al., 2018), thus allowing the implementation of phylogenetic diversity estimations in studies of reef fish communities. As seen in the other dimensions of fish diversity, different indices have been developed to account for different aspects of phylogenetic diversity.

The phylogenetic or cladistic diversity (Faith, 1992) is a measure calculated as the sum of branch lengths between root and tips for a community, it is related to richness and does not consider fish species abundance (Chao et al., 2014). Other indices that do not depend mathematically on species richness have been developed as methods on phylogenetic inference have improved in recent years. Tucker et al. (2017) offer a very thorough review on alpha and beta phylogenetic measures, which includes more than 50 indices. They subdivide the phylogenetic dimension into phylogenetic richness, divergence and regularity at both alpha and beta scales. Examples of the metrics are the average taxonomic distinctness, which calculates the sum of all branch lengths connecting two species averaged across all species and represents the mean distance between two randomly chosen species (AvTD; Warwick and Clarke, 1998); Rao's quadratic entropy (Rao, 1982), based on Simpson's index considering abundance; and phylogenetic entropy (Hp), based on Shannon's entropy and abundance-sensitive (Allen et al., 2009). Like most metrics of taxonomic and functional diversity, the majority of phylogenetic metrics do not comply with the replication principle and cannot be decomposed into independent alpha and beta components. However, Chao et al. (2014) modified the Hill equations and generated an index that solve these problems and properly calculate the effective number of phylogenetic elements.

4 The most common metrics

In this section we present the outcomes of our review to point out the most common metrics applied in the study of reef fish diversity. Our survey resulted in 77 papers published between 1970 and 2018 with the word ‘diversity’ in its title (see Supplementary material for methodological procedures). The vast majority of the 77 studies (n=75, 97%) estimated alpha diversity (see Fig. S1), revealing a concerning gap in the study of beta diversity, which was considered in only 8 papers (Fig. 3). More than 95% (n=73) evaluated only the taxonomic dimension, frequently measuring abundance, richness and species composition (Fig. 3). About 10% (n=8) somehow assessed the phylogenetic dimension, but only one did use a time-calibrated phylogenetic tree; the others worked with taxonomic hierarchies as proxy of phylogenetic trees (Fig. 3). About 5% (n=4) estimated functional diversity (Fig. 3), though 29 studies described some aspect of one or more functional traits (e.g. trophic guilds and body size).

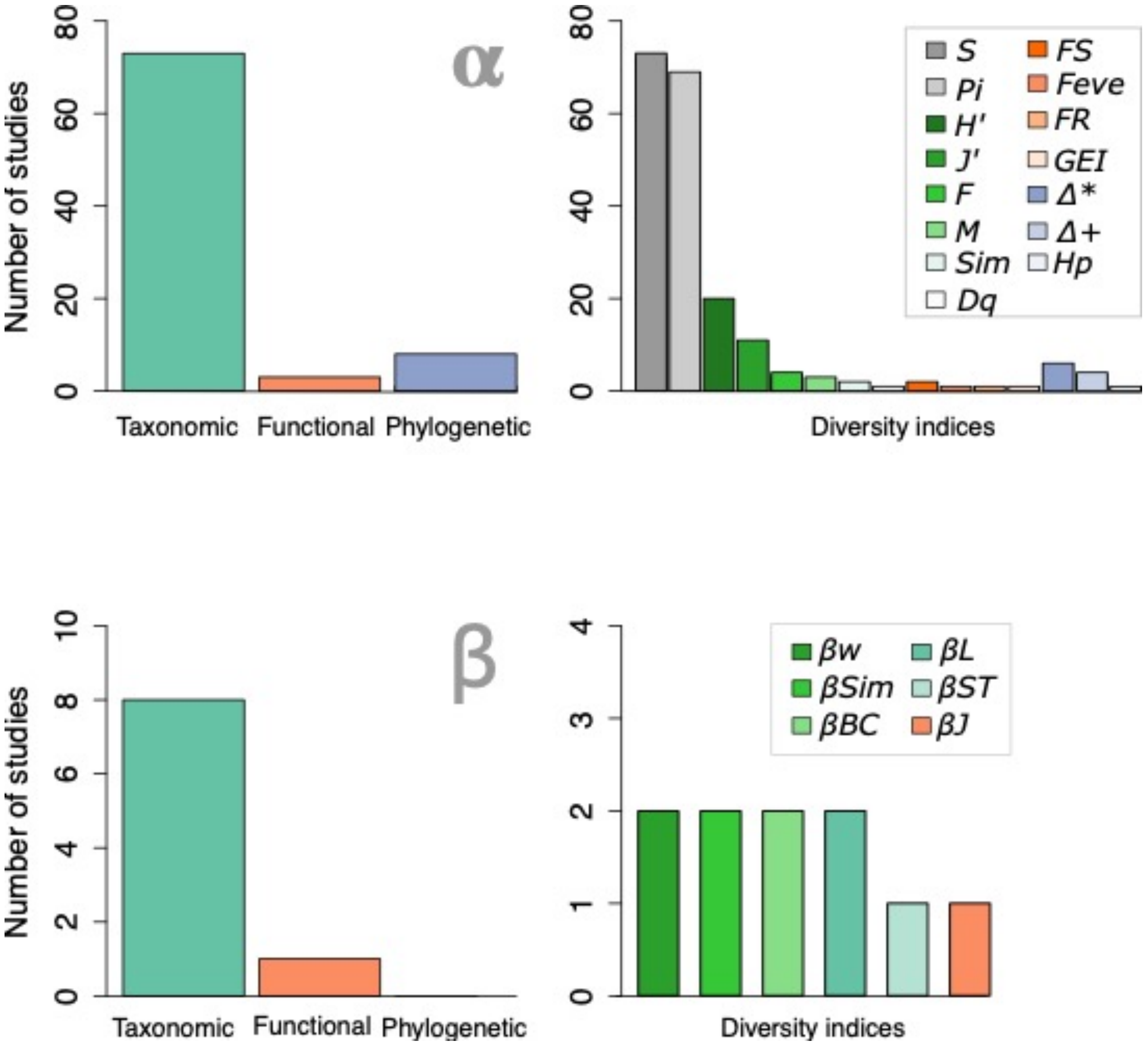


Figure 3. Information gathered from 77 articles regarding the metrics used to measure taxonomic, functional and phylogenetic reef fish diversity. Top right: number of studies that measured taxonomic, functional and phylogenetic alpha (α) diversity. Top left: indices used to describe and calculate alpha diversity, where S = richness, Pi = abundance, H’ = Shannon entropy (Shannon, 1948); J’ = Pielou`s evenness (Pielou, 1966); Sim = Simpson index (Simpson, 1949); F = Fisher index (Fisher et al., 1943); M = Margalef index; Dq = Hill numbers (Hill, 1973); FS = Functional richness; FE = Functional evenness (Villéger et al., 2008); FR = Functional redundancy; GEI = Generalized Entropy Index (D’Agata et al., 2014); Δ* = Taxonomic distinctness (Clarke and Warwick, 1999); Δ+ = Average taxonomic distinctness

(Clarke and Warwick, 2001); Hp = Phylogenetic Entropy (Allen et al., 2009). Bottom right: number of studies that measured taxonomic, functional and phylogenetic beta (β) diversity. Bottom left: indices used to describe and calculate beta diversity, where βw = Whittaker turnover (Whittaker, 1972); βSim = Simpson dissimilarity (Simpson, 1949); βL = Lande's beta diversity (Lande, 1996); βST = Smith's turnover (Talbot et al., 1978); βJ = Jaccard's pairwise dissimilarity (Villéger et al., 2013); βBC = Bray-Curtis dissimilarity (Bray and Curtis, 1957).

Among the 75 alpha diversity studies, about 43% (n=32) used metrics of entropy (i.e. Shannon entropy, Simpson's, evenness; functional evenness), while 57% (n=43) measured only species richness and/or fish abundance. For beta diversity, the most common metrics were Whittaker's, Simpson's dissimilarity, Lande's, Bray-Curtis dissimilarity, Jaccard's pairwise dissimilarity and Smith's turnover. In terms of diversity indices, 42% of the studies (n=31) applied one or more indices. Shannon entropy (H') was the most commonly used index (n=20), followed by Pielou's evenness (n=11), Fisher's (n=4) and Margalef's (n=3) indices. Other indices appeared only a few times, such as Hill numbers and Simpson's. In terms of functional diversity, the metrics applied were functional richness (n=2), functional evenness (n=1), functional redundancy (n=1) and generalized entropy index (n=1) (one study applied more than one metric). Regarding the phylogenetic dimension, the most common metric was taxonomic distinctness (n=6) and average taxonomic distinctness (n=4); only one study accounted for phylogenetic entropy. In Table 1 we offer a brief description of the 21 metrics retrieved from our survey.

378 **Table 1.** The high and heterogenous number (21) of metrics on taxonomic, functional and phylogenetic diversity to assess reef fish diversity. We provide the formula and a brief explanation on what each index represents. This survey comprised 77 articles currently published on this topic.

Measure	**Formula**	**What Measures**
Richness	S	Number of species, functional traits, lineages or alleles in a given area
Abundance	p_i	Number of individuals of each species
Shannon-Winner index (Shannon, 1948)	$H' = -\sum_{i=1}^{S} p_i \ln p_i$	Entropy – The uncertainty in the species identity of a randomly chosen individual in the community
Pielou's evenness (Pielou, 1966)	$J' = \frac{H'}{\log S}$	Evenness – Equivalent distributions of species. The ratio of the observed entropy to the maximum possible in a collection having the same number of species
Simpson index (Simpson, 1949)	$Sim = \sum_{i=1}^{S} {p_i}^2$	Evenness – The probability that two randomly chosen individuals – selected with replacement – belong to different species
Hill numbers (Hill, 1973)	$D^q = \left(\sum_{i=1}^{S} {p_i}^q\right)^{1/(1-q)}$ Where *q* is the is a factor that weights the metric by species abundance p_i	Diversity metric that considers richness and evenness
Margalef's index	$M = \frac{(S-1)}{\ln N}$ *N* corresponds to the total number of individuals in the sample and *S* is the number of species recorded	Species richness index

Measure	Formula	What Measures
Fisher index – Parametric family (Fisher et al., 1943)	$S = \alpha \, ln \, e(1 + p_i \alpha)$ Where α represents the coefficient of diversity and *ln e* corresponds to the logarithmic base e	Describes the relationship between the number of species and the number of individuals in those species
Whittaker species turnover (Whittaker, 1972)	$\beta w = \gamma/\alpha - 1$ where β represents beta diversity, γ represents gamma diversity and α represents alpha diversity	Quantifies how many times the species composition changes completely among the subunits of the dataset
Simpson dissimilarity (Simpson, 1949)	$\beta\mathrm{Sim} = \frac{min(b,c)}{a + min(b,c)}$ Where *a* is the number of species common to both sites, *b* is the number of species that only occur in the first site and *c* is the number of species that only occur in the second site	Measure of spatial turnover between two sites (Mellin et al., 2014)
Bray-Curtis dissimilarity (Bray and Curtis, 1957)	$\beta\mathrm{BC} = 1 - \frac{2Pbc}{P_b + P_c}$ Where P_{bc} is the sum of all individuals found in both *b* and *c* sites, P_b is the number of individuals counted in *b* site and P_c is the number of individuals counted in *c* site	Measure of turnover between two sites that takes into consideration abundance (Mellin et al., 2014)
Jaccard's pairwise dissimilarity (Villéger et al., 2013)	$\beta\mathrm{J} = \frac{V(C_1) + V(C_2) - 2 \cdot V(C_1 \cap C_2)}{V(C_1) + V(C_2) - V(C_1 \cap C_2)}$ Where $V(C_1)$ and $V(C_2)$ are the functional richness (based on the convex hull volume) for communities *1* and *2* respectively, and $V(C_1 \cap C_2)$ is its intersection	Functional dissimilarity between two communities

Measure	Formula	What Measures
Lande’s β-diversity (Lande, 1996)	$\beta = (b + c)/2$ Where b is the total number of species that occur in the region (gamma) but not in the focal area and c is the number of species that occur in the area (alpha) but not in the region	Quantifies how much more species diversity the entire dataset contains than the average subunit within that dataset
Smith’s turnover (Talbot et al., 1978)	$\beta_{SM} = \frac{1}{2}\left(\frac{l}{n_j} + \frac{g}{n_k}\right) \cdot 100\%$ Where *l* is the number of species lost between areas *j* and *k*, *g* is the number of species gained between areas *j* and *k*, n_j and n_k are the number of species in areas *j* and *k*, respectively	Calculates species resemblance between two areas
Functional richness	FS = minimal spanning tree (MTS) method (Moulton and Pimm, 1987; Yeager et al., 2017) FS = number of functional groups (Halpern and Floeter, 2008)	The term “functional richness” was used for different approaches, with each having a different interpretation
Functional evenness (Villéger et al., 2008)	$\mathrm{FEve} = \frac{\sum_{i=1}^{S-1} min\left(PEW_l, \frac{1}{S-1}\right) - \frac{1}{S-1}}{1 - \frac{1}{S-1}}$ Where PEW_l is the partial weighted evenness for the branch *l*	Quantifies the regularity with which the functional space is filled by species, weighted by abundance
Functional redundancy (Ricotta et al., 2016)	$FR = \frac{Sim - Q}{Sim}$	Metric based on functional dissimilarities that quantifies how many species within a community perform similar functions

Measure	Formula	What Measures
	Where Sim is the Simpson index and Q is the Rao's quadratic entropy (Rao, 1982)	
Taxonomic distinctness (Clarke and Warwick, 1999)	$$\Delta^{*} = 2\frac{\left[\sum \sum_{i<j} \omega_{ij}\right]}{S(S-1)}$$ The sum over all species where w_{ij} corresponds to the taxonomic path between species *i* and *j*.	The average distance between two randomly chosen but taxonomically different organisms, where this distance is defined as the path length through a standard Linnean or phylogenetic tree connecting these species
Average taxonomic distinctness (Clarke and Warwick, 2001)	$$\Delta^{+} = \frac{\left[\sum \sum_{i<j} \omega_{ij}\right]}{S(S-1)}$$	Measurement of evolutionary relatedness or distinctness between two taxonomic entities
Generalized entropy index (based on Shannon)	$$H_k = -\sum_{t=1}^{T} l(b_t) \times p_k(b_t) \times ln[p_k(b_t)]$$ Where *T* is the phylogenetic tree for the species pool, $l(b_t)$ is the length of branch b_t and $pk(bt)$ is the local proportion of abundance	Reflects the phylogenetic and functional composition structure of a community and could be based on phylogenetic trees or functional dendrograms (D'Agata et al., 2014)
Phylogenetic entropy (Based on Shannon)	$$Hp = -\sum_{b\, \in BT} L_b P_b \ln(P_b)$$ Where T is the rooted tree for the community, Lb represents the length of branch b of T, and Pb is the proportion of individuals of present-day species (Allen et al., 2009)	Phylogenetic entropy

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5 Summary and future directions

With the advent of more sophisticated analytical and computational tools in the past few decades, a bulk of fish diversity indices have emerged (Chao et al., 2014; Gaggiotti et al., 2018; Villéger et al., 2008). Besides offering new interpretations, these recent indices have helped disentangling the underlying mechanisms shaping fish diversity patterns (Mouillot et al., 2013). Tucker et al. (2017), Véron et al. (2019) and Villéger et al. (2017), along with Jost (2007) and Baselga (2010) provide very thorough reviews on taxonomic, functional, and phylogenetic diversity metrics that could be implemented in further studies. R packages and codes are currently available to anyone, which might increase scientific reproducibility and favor consensus between researchers worldwide. Nonetheless, our results show that a minority of the studies on reef fish community published in the last decades has implemented those metrics, even when the title of the manuscript suggests otherwise.

What emerges from our review is that studies are still using richness and abundance to describe reef fish diversity instead of calculating indices that take both richness and abundance into consideration. In those studies where this procedure was applied, reef community entropy rather than diversity was estimated with the classical metrics such as Shannon’s and Pielou’s. The fish diversity itself has rarely appeared in the literature, despite Hill numbers are available since 1973 and Jost’s modifications since 2006. In fact, we observe that the concept of diversity and entropy has been often used interchangeably to describe variability within a reef fish community or between communities, regardless the effective number of their biological entities (i.e. species, functions, lineages; Chao et al., 2014). Such misuse is likely to produce doubtful conclusions. We acknowledge that there may be more studies that did apply true diversity metrics and properly measured diversity in effective number of its elements, but they did not mention the word ‘diversity’ in its title and fell out of our criteria. However, that should not reduce our concern about urgently improving the diversity metrics used in reef fish community ecology.

For functional and phylogenetic diversities, our results are even more concerning, as these dimensions have been largely ignored. We must mention that globally our reefs home more than 2,500 fish species that perform a variety of functions and safeguard irreplaceable evolutionary histories (Leprieur et al., 2016; Mouillot et al., 2013; Mazel et al., 2018; Winter et al., 2013). Discussing diversity of reef fishes without taking these dimensions into account is misleading and potentially risky. Given the increasing threats faced by marine ecosystems and the associated biodiversity erosion (Morais et al., 2018), it is urgent that we properly estimate diversity of our reefs. This requires adopting metrics that (i) express 'diversity' (not entropy) in effective number of elements, (ii) comply with the replication principle, (iii) can be partitioned into independent alpha and beta components, and (iv) unify the estimation of diversity in its taxonomic, functional and phylogenetic dimensions (Jost 2006, 2007, 2010; Chao et al., 2014; Chiu and Chao, 2014).

We recommend the framework proposed by Chao et al. (2014), which is based on Hill numbers of taxonomic entities (species), phylogenetic entities (branches of unit-length), or functional entities (species-pairs with unit-distance between species). We have employed this framework recently (Medeiros et al., 2021) to compare fish diversity between shallow (< 30m depth) and deep (> 30m depth) reefs of the southwestern Atlantic. To support our recommendation, we revisited part of our data, calculated the traditional Shannon entropy and Simpson dissimilarity and compared them to the Hill numbers of species at alpha and beta scales (Table 2). Because Hill numbers satisfy the replication principle, we can assert that compared with shallow reefs the deep reef communities encapsulate 25%, 65%, and 150% more diversity of rare (Hill ${}^{0}D$), typical (Hill ${}^{1}D$) and dominant species (Hill ${}^{2}D$), respectively (Table 2). The Shannon index H', even taking abundance into consideration, underestimated this difference by indicating that 'diversity' of deep reefs is only 20% greater than that of shallow reefs (Table 2). For beta diversity, the interpretation was even more blurry when comparing the values based on Hill numbers with the Simpson dissimilarity (Table 2).

Table 2. Diversity measured of fish communities from shallow (< 30m depth) and deep (> 30m depth) reefs of the southwestern Atlantic. H' = Shannon entropy (Shannon, 1948); Sim = Simpson index (Simpson, 1949); Hill Dq = Hill numbers (Hill, 1973). Data gathered from Medeiros et al. (2021).

Metric	**Scale**	**Shallow Reefs**	**Deep reefs**	**Magnitude of difference in deep reefs with respect to shallow reefs**
Hill ^{0}D	alpha	56	70	+25%
Hill ^{1}D	alpha	12.2	20	+64%
Hill ^{2}D	alpha	4	10	+150%
H'	alpha	2.5	3	+20%
Hill ^{0}D	beta	3.5	2.7	-23%
Hill ^{1}D	beta	3.1	3.2	+3%
Hill ^{2}D	beta	3.2	4.2	+31%
Sim	beta	0.8	0.9	+12%

Before calculating the metrics, it is very important to standardize samples (i.e. local communities) by coverage rather than by size (i.e. total number of individuals in the community) (Chao and Jost, 2012) to avoid biased comparisons of alpha and beta components (see Morais and Santos, 2018; Cardoso et al., 2020; Medeiros et al., 2021). If possible, we recommend going beyond the taxonomic dimension and analyzing the three dimensions together in the same study (Bender et al. 2013; Medeiros et al., 2021). Although taxonomic inventories are still lacking in many regions (Mora et al., 2008), there are extensive, useful databases with trait information that may support functional analyses (e.g. Pinheiro et al., 2018). They have been compiled with effort of dozens of researchers and deserve being better explored. Finally, because diversity is not evenly distributed across space, the beta component of fish diversity should be used more often to guide conservation and management actions on reef fishes.

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7 Author's Contributions

A. P. M. M. and B. A. S. led the writing and conceived the idea of the manuscript. All authors participated in the development of ideas and contributed critically to improve the writing, giving approval for publication.

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Author-supplied supplementary PDF

The use and misuse of diversity metrics in studies of reef fish communities

Aline P. M. Medeiros[a], Aiara P. L. R. Cardoso[a], Juliano Morais[a,b], Beatrice P. Ferreira[c], Ricardo Betancur-R[d,e], Marcelo O. Soares[f,g,h], Bráulio A. Santos[i]*

[a] Programa de Pós-Graduação em Ciências Biológicas, Universidade Federal da Paraíba, Cidade Universitária, Castelo Branco, 58051-900. João Pessoa, PB, Brazil.

[b] ARC Centre of Excellence for Coral Reef Studies and College of Science and Engineering, James Cook University, Townsville, QLD 4811, Australia.

[c] Universidade Federal de Pernambuco, Centro de Tecnologia, Departamento de Oceanografia, Cidade Universitária, 50670-901. Recife, PE, Brazil.

[d] Department of Biology, The University of Oklahoma, 730 Van Vleet Oval, Room 314, Norman, OK 73019, USA
[e] Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington DC 20560, USA
[f] Instituto de Ciências do Mar-LABOMAR, Universidade Federal do Ceará, Av. da Abolição, 3207, Meireles, 60165-081, Fortaleza, CE, Brazil
[g] Institut de Ciència i Tecnologia Ambientals (ICTA), Universitat Autònoma de Barcelona (UAB), Carrer de les Columnes, Edifici Z, Barcelona, Spain
[h] Dipartimento di Scienze e Tecnologie Biologiche e Ambientali (DISTEBA), Università del Salento, Lecce, Italy
[i] Universidade Federal da Paraíba, Centro de Ciências Exatas e da Natureza, Departamento de Sistemática e Ecologia, Cidade Universitária, Castelo Branco, 58051-900. João Pessoa, PB, Brazil.

*****Corresponding author: braulio@dse.ufpb.br

Appendix S1 – Extended methods with results and brief discussion on geographic and theoretical gaps

We conducted our survey using the Web of Science and Scopus databases by searching for the words ‘reef’, ‘fish*’, and ‘diversity’ in the title of papers published since 1970 and 2018. We focused on the title to enhance the probability that the study explicitly dealt with metrics of community diversity. We carefully filtered the studies to exclude those that did not fit into the scope of our research, such as acoustic diversity, parasite diversity, reviews, and papers not written in English. This resulted in 90 papers (see Table S1 for the parameters analyzed). Among them, 13 studies matched the genetic diversity category, measuring allelic richness, nucleotypic diversity and average diversity, among others. Because those studies and their metrics focused on populations rather than communities, we also excluded them from downstream analysis. However, we offer a brief overview for genetic diversity, as well as the metrics used to account for this dimension of population diversity (Appendix S2). After winnowing the studies that fitted our criteria (n=77, available at Dryad), we perused them for the metrics used to quantify fish diversity at alpha and beta scales. Besides metrics, we took note on the dimension of fish diversity, survey methods, depth, ecoregion, and study location (within or out protected areas) to highlight possible geographic and theoretical gaps.

Most studies (n=66; 86%) were concentrated in the tropical zone, specifically in the Indo-Pacific and Caribbean regions (Fig. S1). This pattern was expected as the tropical zone encompasses most of the diversity of reef fishes (Mora et al., 2008, 2003). Only 35 out of 232 marine ecoregions (sensu Spalding et al., 2007) were represented in the 77 studies evaluated (see Fig. S1), which implies that about 90% of the global ecoregions remain understudied in terms of reef fish diversity. The region with the highest number of studies was the Indo-Pacific (n=57; 74%), recognized as the center of diversity of reef fishes (Bellwood and Wainwright, 2002). Regarding depth range, only 12 studies (16%) were carried out in mesophotic zones (30-150 m depth). This lack of information could be due to environmental and budget constraints (Hinderstein et al., 2010). Moreover, only a few studies were carried out in marine protected areas (n=12) or in both protected and non-protected areas (n=12), with most studies (68%) performed in regions without protection. By and large, these numbers demonstrate a concerning knowledge gap, because marine protected areas are known to be effective at fostering both ecological resilience, fishery and tourism sustainability on coral reefs (Appolloni et al., 2017; Edgar et al., 2014; Hixon, 2011; Tkachenko and Soong, 2010). About 80% of the studies (n=62) relied on non-destructive sampling, which follows the popularization of SCUBA diving and the possibility to collect underwater data without fish extraction from the ocean (Hixon, 2011).

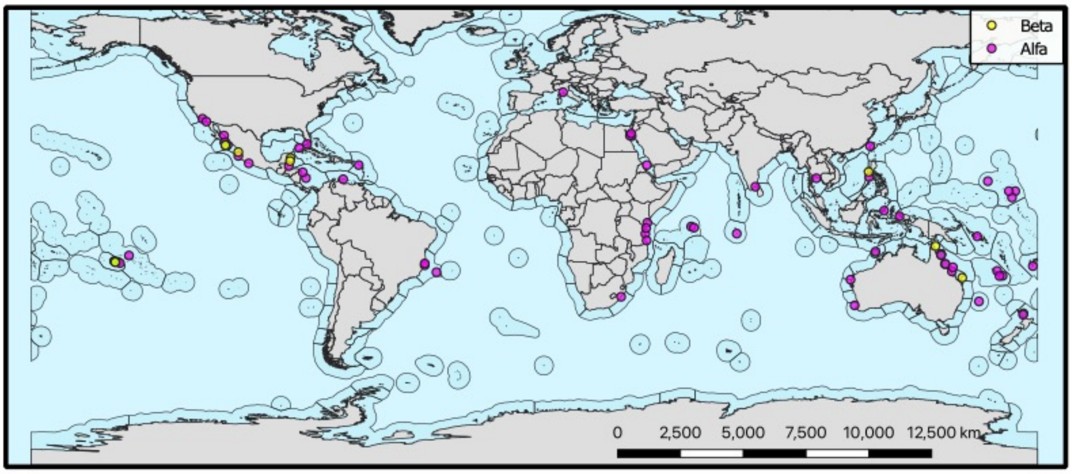

Figure S1. Distribution of the 77 studies evaluated in our survey. Delimited areas indicate marine ecoregions (sensu Spalding et al., 2007).

Regarding geographic gaps, our analyses revealed that the majority of the global ocean has been poorly sampled for reef fishes. We suggest paying more attention to regions with few studies, such as the Brazilian Province that features a high level of endemism (Araújo et al., 2020; Pinheiro et al., 2018), the Red Sea, and the Persian/Arabian Gulf (Bouwmeester et al., 2020), with only a few studies. Considering the ecoregions proposed by Spalding et al. (2007), many of them also lack studies on reef fish diversity and should be included in the future. More studies should focus on mesophotic reefs (> 30 m depth) to understand patterns of connectivity in a cross-shelf gradient and how diversity is spatially structured along a depth gradient (García-Hernández, Sanchez, Hammerman, & Schizas, 2018; Rocha et al., 2018).

Mesophotic reefs have been recently brought into light as a potential limited refuge for coral and fish species in face of shallow reefs degradation (Bongaerts et al., 2010; Pereira et al., 2018). A recent study demonstrated that, when analyzed the refuge hypothesis under different aspects of diversity (i.e. taxonomic, functional and phylogenetic), each metric yield information on the community, thus complementing each other (Medeiros et al., 2021). Besides potentially acting as refuge, mesophotic reefs could host different species, important sets of functions and different lineages (Soares et al., 2021). Thus, studies focusing on species, functional and phylogenetic diversity patterns could help disentangling the mechanisms that shape diversity along the depth gradient (Amado-Filho et al., 2016; Medeiros et al., 2021; Rosa et al., 2016) and can also help to develop appropriate conservation strategies for reef fish in the context of ongoing global environmental changes (Lazzari et al., 2020; Loiseau et al., 2017).

Table S1. Information gathered from studies (*N* = 90) retrieved from the survey.

Data	Abbreviation	Notes
Authors	-	Name of authors in the manuscript
Title	-	Title of the manuscript
Year of publication	Year	-
Journal	-	-
Impact factor	IF	Impact factors based on year 2016
Marine protected area	MPA	If the research was performed in an MPA or not (Y – performed in an MPA; N – Not performed in an MPA; B – studied comparing MPA and no MPA)
Location	-	Country or region where the research was performed

Ocean	-	Ocean where the research was performed (A – Atlantic; I – Indic; M – Mediterranean; R – Red Sea; P – Pacific; W – worldwide)
Zone	-	Ocean where the research was performed (ST – Subtropical; T – Tropical)
Minimum depth	MD	Minimum depth of surveys (m)
Maximum depth	MxD	Maximum depth of surveys (m)
Survey method	-	DB – Data Base; D – Destructive; UVC – Underwater visual census; SC – Stationary census; TC – Transect census; RUVC – Remote underwater video census
Diversity Type	Type	Species or Taxonomic diversity; Functional diversity; Phylogenetic diversity; Genetic diversity
Diversity component	Alpha, Beta	Which diversity component each study was referring to
Diversity Metrics	Diversity metrics found in the papers retrieved from our survey	S = richness, Pi = abundance, H’ = Shannon entropy (Shannon, 1948); J’ = Pielou`s evenness (Pielou, 1966); Sim = Simpson index (Simpson, 1949); F = Fisher index (Fisher et al., 1943); M = Margalef index; Dq = Hill numbers (Hill, 1973); FS = Functional richness; FE = Functional evenness (Villéger et al., 2008); FR = Functional redundancy; GEI = Generalized Entropy Index (D’Agata et al., 2014); Δ* = Taxonomic distinctness (Clarke and Warwick, 1999); Δ+ = Average taxonomic distinctness (Clarke and Warwick, 2001); Hp = Phylogenetic Entropy (Allen et al., 2009). Bottom right: number of beta (β) diversity studies that measured taxonomic, functional and phylogenetic types of diversity. Bottom left: indices used to describe and calculate beta diversity, where βw = Whittaker turnover (Whittaker, 1972); βSim = Simpson dissimilarity (Simpson, 1949); βL = Lande’s beta diversity (Lande, 1996); βST = Smith’s turnover (Talbot et al., 1978); βJ = Jaccard’s

	pairwise dissimilarity (Villéger et al., 2013); βBC = Bray-Curtis dissimilarity (Bray and Curtis, 1957); Allelic richness (AllS), Karyotypic diversity (KD), Nei's genetic diversity (Nei) and K2P model of species divergence (K2P)

Appendix S2 – Extended results of genetic diversity

Genetic diversity is related to the variety of genes found at the population level (Nei, 1978). As the other types of diversity mentioned, there are many distinct approaches to measure the gene range in a set of individuals or species (Fauvelot et al., 2003; Nei, 1978; Nei and Tajima, 1981), calculated based on different genetic components, such as nucleotides, haplotypes or both (Castellanos-Gell et al., 2016; Delrieu-Trottin et al., 2014; Messmer et al., 2012).

Different aspects of genetic diversity could be measured although, as in species diversity, they usually are an account of entropy. As an example, Nei has proposed at least five metrics of genetic diversity that considers distinct aspects: haplotype and nucleotide diversities, heterozygosity and genetic distance and genetic identity (Nei, 1978). All these indices are used to describe different aspects of genetic variability within populations (Affonso and Galetti Junior, 2007; Pini et al., 2011).

All studies (100% of the 13 papers) estimated alpha genetic diversity, mainly (n=11) using Nei's diversity index, followed by allelic richness (n=2), karyotypic diversity (n=1), and kimura-2-parameter (n=1). More details regarding the genetic metrics retrieved from those studies can be found in Table S2.

Table S2. Genetic diversity metrics retrieved from thirteen papers in our survey. Here we provide the formula, and a brief explanation of which each index represents.

Measure	Formula	What Measures
Allelic richness (Van Loon et al., 2007)	$AllS = s_0 + S_{obs}$ Where s_0 is the number of alleles present in the population but not in the observed sample and S_{obs} is the number of alleles observed in the sample	Based on *Chao2* richness estimator, it is possible to estimate allelic richness lager populations
Karyotypic diversity (Martinez et al., 2015; Rabosky et al., 2014)	KD = estimated from phylogenetic trees	Measures the diversity of chromosome arms or fundamental number

Nucleotide diversity (Nei and Li, 1979)	$\text{NucD}\pi = 2 \cdot \sum_{i=2}^{n}\sum_{j=1}^{n-1} x_i \cdot x_j \cdot \pi_{ij}$ where x_i and x_j are the respective frequencies of the *i*th and *j*th sequences, π_{ij} is the number of nucleotide differences per nucleotide site between the *i*th and the *j*th sequences and *n* is the number of sequences in the sample	Genetic variation
Haplotype diversity (Nei and Tajima, 1981)	$\text{HapD}H = \frac{n}{n-1}\left(1 - \sum_{i} x_i^2\right)$ Where x_i is the relative haplotype frequency of each haplotype in the sample and *n* is the sample size	Is a measure of uniqueness of a haplotype in a given population
Average heterozygosity (Nei, 1978)	$H = \sum_{j}^{L} \frac{h_j}{L}$ Where h_j is the heterozygosity *per* locus and *L* is the total number of loci. $h_j = 1 - p^2 - q^2$, where *p* and *q* are the allele frequencies	At a single locus, is the probability that any two alleles chosen at random from the population to be different to each other. To all loci, is an estimate of the extent of genetic variability in the population
Genetic distance (Nei, 1978)	$D = -ln \frac{\sum_l \sum_u X_u Y_u}{\sqrt{(\sum_u X_u^2)(\sum_u Y_u^2)}}$ Where *X* and *Y* represent two different populations with the u^{th} allele at the l^{th} locus	Genetic divergence between species or populations within a specie
Genetic identity (Nei, 1978)	$D' = -\,ln \frac{J_{XY}}{\sqrt{J_X J_Y}}$ Where J_{XY} is the probability for a member of the *X* population and a member of *Y* population having the same allele, J_X is the probability for the two members of population *X* having the same allele at a particular locus and J_Y is the corresponding probability in population *Y*. The measure is performed with the sum of all loci.	Estimates the proportion of genes that are identical in two populations
Kimura-2-parameter (Kimura, 1980)	$K2P = -\frac{1}{2} ln\{(1 - 2\text{P} - \text{Q})\sqrt{1 - 2\text{Q}}\}$ Where P and Q are respectively the fractions of nucleotides sites showing type I (transition) and type II	Measure of nucleotide substitution *per* site to estimate evolutionary distances

(transversion) differences two sequences compared

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4 CAPÍTULO II – DEEP REEFS ARE NOT REFUGIUM FOR SHALLOW-WATER FISH COMMUNITIES IN THE SOUTHWESTERN ATLANTIC

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Deep reefs are not refugium for shallow-water fish communities in the southwestern Atlantic

Aline P. M. Medeiros[1] | **Beatrice P. Ferreira**[2] | **Fredy Alvarado**[3] |
Ricardo Betancur-R[4,5] | **Marcelo O. Soares**[6,7,8] | **Bráulio A. Santos**[9]

[1]Programa de Pós-Graduação em Ciências Biológicas, Universidade Federal da Paraíba, João Pessoa, PB, Brazil

[2]Departamento de Oceanografia, Centro de Tecnologia, Universidade Federal de Pernambuco, Recife, Brazil

[3]Departamento de Agricultura, Centro de Ciências Humanas, Sociais e Agrárias, Universidade Federal da Paraíba, Bananeiras, PB, Brazil

[4]Department of Biology, The University of Oklahoma, Norman, OK, USA

[5]Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA

[6]Instituto de Ciências do Mar-LABOMAR, Universidade Federal do Ceará, Meireles, Brazil

[7]Institut de Ciència i Tecnologia Ambientals (ICTA), Universitat Autònoma de Barcelona (UAB), Barcelona, Spain

[8]Dipartimento di Scienze e Tecnologie Biologiche e Ambientali (DISTEBA), Università del Salento, Lecce, Italy

[9]Departamento de Sistemática e Ecologia, Centro de Ciências Exatas e da Natureza, Universidade Federal da Paraíba, João Pessoa, PB, Brazil

Correspondence
Bráulio A. Santos, Departamento de Sistemática e Ecologia, Centro de Ciências Exatas e da Natureza, Universidade Federal da Paraíba, Cidade Universitária, Castelo Branco, 58051-900, João Pessoa, PB, Brazil.
Email: braulio@dse.ufpb.br

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Abstract

1. The deep reef refugia hypothesis (DRRH) predicts that deep reef ecosystems may act as refugium for the biota of disturbed shallow waters. Because deep reefs are among the most understudied habitats on Earth, formal tests of the DRRH remain scarce. If the DRRH is valid at the community level, the diversity of species, functions, and lineages of fish communities of shallow reefs should be encapsulated in deep reefs.
2. We tested the DRRH by assessing the taxonomic, functional, and phylogenetic diversity of 22 Brazilian fish communities between 2 and 62 m depth. We partitioned the gamma diversity of shallow (<30 m) and deep reefs (>30 m) into independent alpha and beta components, accounted for species' abundance, and assessed whether beta patterns were mostly driven by spatial turnover or nestedness.
3. We recorded 3,821 fishes belonging to 85 species and 36 families. Contrary to DRRH expectations, only 48% of the species occurred in both shallow and deep reefs. Alpha diversity of rare species was higher in deep reefs as expected, but alpha diversity of typical and dominant species did not vary with depth. Alpha functional diversity was higher in deep reefs only for rare and typical species, but not for dominant species. Alpha phylogenetic diversity was consistently higher in deep reefs, supporting DRRH expectations.
4. Profiles of taxonomic, functional, and phylogenetic beta diversity indicated that deep reefs were not more heterogeneous than shallow reefs, contradicting

expectations of biotic homogenization near sea surface. Furthermore, pairwise beta-diversity analyses revealed that the patterns were mostly driven by spatial turnover rather than nestedness at any depth.

5. *Conclusions*. Although some results support the DRRH, most indicate that the shallow-water reef fish diversity is not fully encapsulated in deep reefs. Every reef contributes significantly to the regional diversity and must be managed and protected accordingly.

KEYWORDS

coral reefs, depth, fish, mesophotic coral ecosystems

1 | INTRODUCTION

As shallow-water coral reef ecosystems are gradually degraded by human activities, identifying areas where biodiversity can be maintained has become a conservation priority worldwide (Morais et al., 2018; Soares et al., 2020). These areas comprise marginal reefs such as turbid-zone and high-temperature areas, macrotidal reefs, tide pools, volcanic CO_2 vents, *ojos* (low pH springs), areas with submarine groundwater discharge, mangrove systems, upwelling areas, temperate mesophotic ecosystems, mesophotic coral ecosystems, and cold-water coral ecosystems (Camp et al., 2018; Enochs et al., 2020; Soares et al., 2021). Growing attention has been paid to the mesophotic coral ecosystems (deep reefs hereafter), which are usually characterized by the presence of light-dependent corals and other habitat-forming benthic organisms (i.e., octocorals, antipatharians, macroalgae, and sponges) that are typically found at depths ranging from 30 to 150 m in tropical and subtropical regions (Asher et al., 2017; Hinderstein et al., 2010; Pinheiro et al., 2019; Pyle & Copus, 2019; Rosa et al., 2016).

The deep reefs are closely linked to shallow reef areas, usually forming a contiguous or semi-contiguous belt of habitats along a depth gradient (Lindfield et al., 2016). However, unlike the shallow reefs (<30 m depth), the deep reefs are presumably less exposed to ocean warming and other human pressures such as coastal pollution, overfishing, and nonregulated tourism (Hoegh-Guldberg & Bruno, 2010; Mies et al., 2020; Mora et al., 2011; Soares et al., 2020), leading researchers to postulate that deep reefs could act as depth refuge, refugium, or resilience area for reef biota in face of a massive loss of shallow reefs ("deep reef refugia hypothesis" sensu Bongaerts et al., 2010; see also Glynn, 1996; Kahng et al., 2010; Loya et al., 2016). By *depth refuge*, we mean a depth range that provides short-term buffering or shelter for one or multiple species or a biological community against a particular disturbance episode; *depth refugium*, a depth range that provides a long-term buffering or shelter for one or multiple species or a biological community against a particular or multiple disturbance types; and *resilience area*, a depth range that harbors one or multiple species or a biological community that is/are resilient over the long term to a particular or multiple disturbance types (sensu Bongaerts & Smith, 2019).

The potential of deep reefs as depth refuges, refugia, and resilience areas has been assessed at different regions around the world (Rocha et al., 2018), such as the Great Barrier Reef (Jankowski et al., 2015), Micronesia (Coleman et al., 2018), Mariana Islands (Lindfield et al., 2016), and the Coral Triangle (Andradi-Brown et al., 2019). Nonetheless, to date there is no consensus on the role of deep reefs to fully encapsulate the diversity of shallow-water communities (Bongaerts et al., 2017; Morais & Santos, 2018; Pereira et al., 2018; Semmler et al., 2017). The biological level of the studies (e.g., population or community), the ecological group (e.g., invertebrate or vertebrate, mobile or sessile), the level of structural connectivity (contiguous or separated) between shallow and deep reefs, the different diversity metrics selected by researchers (e.g., species richness per se, presence/absence indices), and weak theoretical foundations are among the major reasons that have impaired the consensus.

The metacommunity theory combined with reliable metrics of community diversity provides a useful framework to test the DRRH. If the hypothesis is valid at the community level, the metacommunity—the entire gradient of deep and shallow local communities—must be mainly structured by mass effects (sensu Leibold et al., 2004). Under this scenario, local environmental conditions are less important than dispersal capacity and species may colonize any site along the depth gradient, becoming more abundant in sites where conditions are more suitable. High reproduction rates in suitable sites allow populations to export individuals to unsuitable sites and protect smaller populations from local extinction (Leibold et al., 2004). When these rescue effects are scaled up to communities, compositional similarity between suitable and unsuitable sites tends to increase, with local communities of unsuitable sites being nested within suitable sites. From the DRRH perspective, the unsuitable sites are represented by the shallow disturbed reefs, which home only a small number of stress-tolerant species that tend to homogenize the reefs and impoverish the shallow region, resulting in low alpha, beta, and gamma diversity. Conversely, the deep conserved reefs represent the suitable sites, where a greater number of species coexist locally, replace each other from one reef to another, and comprise a species-rich region, resulting in high alpha, beta, and gamma diversity. This rationale may be applied not only for the diversity of species as commonly observed in the literature, but also for functions and lineages.

Here, we tested the DRRH for reef fishes using a community-level approach able to partition the taxonomic, functional, and phylogenetic gamma diversity into independent alpha and beta components (Jost, 2007). We classified the species into six complementary functional traits to examine the role of depth in safeguarding functions of fish communities. We also estimated a phylogenetic tree using maximum-likelihood and backbone constraint analyses to calculate the phylogenetic diversity. We sampled 22 reef fish communities in Northeast Brazil to assess six predictions derived from the DRRH (see Morais & Santos, 2018, for a similar study with corals): (a) Depth-generalist fish species should dominate the metacommunity because if species are exclusive to shallow or deep areas they could not be rescued from eventual local extinction; (b) deep reefs should contain greater gamma diversity than shallow reefs to be able to export species to and replenish shallow reefs, provided that species composition of the shallow areas is nested within the deep areas; (c) alpha diversity should be greater in deep reefs due to reduced anthropogenic pressure in deeper areas; (d) regional beta diversity should be smaller among shallow reefs than among deep reefs owing to increased disturbance and biotic homogenization driven by the proliferation of stress-tolerant species near sea surface; (e) pairwise beta patterns of shallow reefs should be mostly driven by nestedness than spatial turnover, while nested effects should become weaker between deep reefs; and (f) functional diversity of shallow communities should be a subset of the functional diversity of deep communities, with exclusive functional traits observed only in deep reefs.

2 | MATERIALS AND METHODS

2.1 | Study area

We carried out the study in southwestern Atlantic reef ecosystems located along the Northeastern Brazilian subprovince (Pinheiro et al., 2018; between 7°0′023S 34°50′0″W and 7°15′0″S 34°30′0″W; Figure 1). The region is under influence of the South Equatorial Current and has the water temperature ranging from 23 to 30°C, with a thermocline found at about 50 m depth where water temperature declines to 23°C and visibility increases from 20 to 50 m (Feitoza et al., 2005; Maida & Ferreira, 1997; Rocha, 2003). This area is known for having rock-based reefs of various shapes and dimensions forming lines parallel to the coastline, with a sharp decline of the seafloor at near 70 m depth (Feitoza et al., 2005; Leão & Dominguez, 2000). The reefs are covered by extensive growths of benthic organisms, especially calcareous algae, macroalgae, and macrobenthos (i.e., Zoanthidae and sponges) (Honório et al., 2010); coral cover varies from 0.3% to 20% (Morais & Santos, 2018). Reef fish composition of shallow areas is well-studied (Feitoza et al., 2002; Honório et al., 2010; Osório et al., 2006; Ramos, 1994; Rocha et al., 2000; Rocha et al., 1998; Rosa et al., 1997; Silva et al., 2014; Souza et al., 2007), while fishes of deep reefs are poorly known (but see Feitoza et al., 2005). Common disturbances of shallow reefs include mass tourism, pollution, and overfishing (Leão et al., 2016). For instance, Medeiros et al. (2007) documented the effects of tourism in the study region, including community homogenization, changes in the trophic structure, and the dominance of stress-tolerant species. Disturbance of deep reefs is scantly documented, but fishermen report overfishing.

2.2 | Data survey

We surveyed 22 coral reefs ranging from 2 to 62 m maximum depth. Reefs were categorized into shallow (<30 m depth; *n* = 8 reefs) and deep (>30 m depth; *n* = 14 reefs). To sample fish communities at each reef, we performed SCUBA dives using high-resolution video records (GoPro Hero 4) and following the browsing trajectory technique (Mallet & Pelletier, 2014; Mallet et al., 2016). Video recording was performed with slow movement at approximately 1 m above the

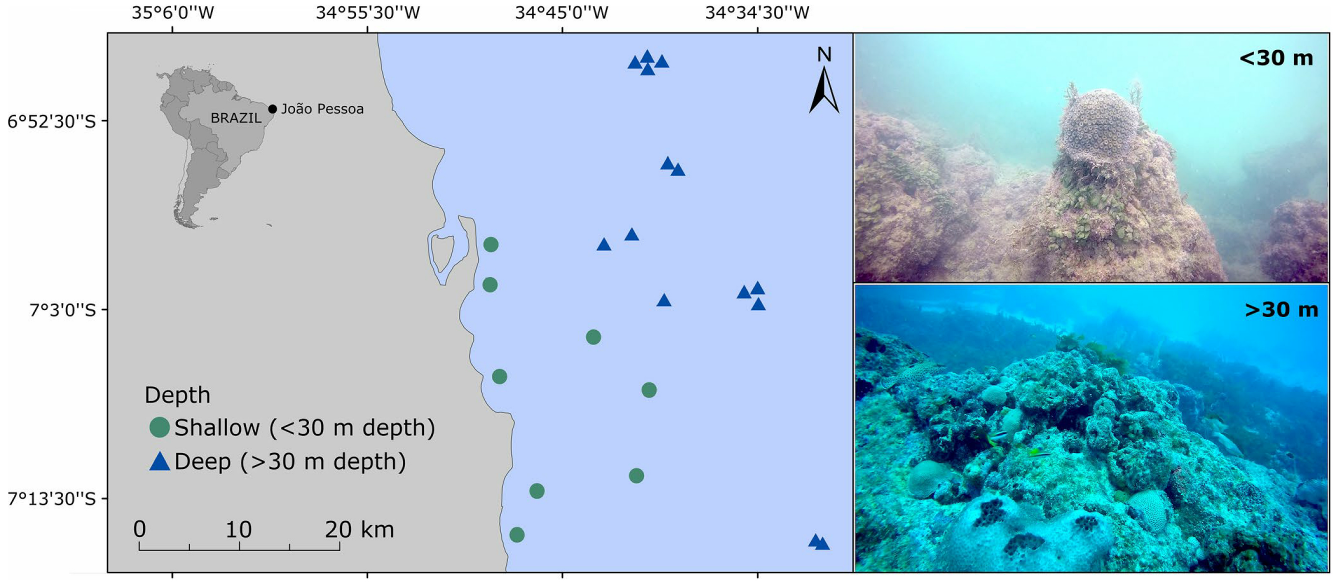

FIGURE 1 Study region in the coast of Paraiba, southwestern Atlantic, showing an example of shallow (<30 m depth; green circles) and deep reefs (>30 m depth; blue triangles)

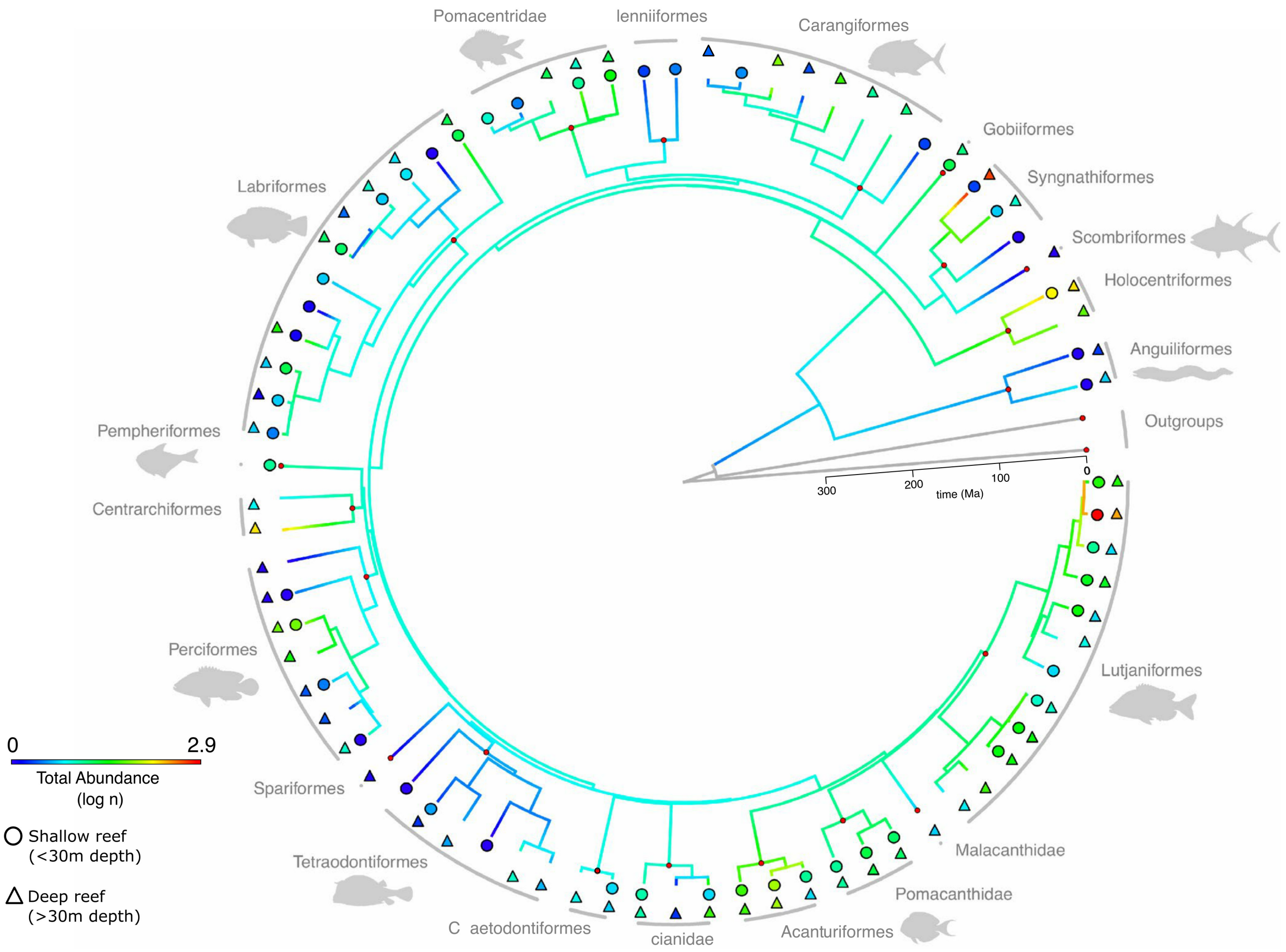

FIGURE 2 Time-calibrated phylogeny containing 77 of the 85 species recorded in the present study. Internal red circles represent taxonomic annotation (e.g., order) clades of Teleostei and the two outgroups. For visualization purposes, branch colors indicate ancestral abundance reconstruction for the Teleostei species (see Methods for details). Circles and triangles represent the abundance of species in shallow and deep areas, respectively; symbol color indicates species abundance

bottom. The goal was to comprise all the reef extent. Assuming that each reef has different shapes and features (e.g., number of crevices), we aimed to record all the extent of each reef. This approach allowed to focus in different available habitats (i.e., bottom reef, interface, and water column) to record the entire coral reef fish community (Mallet & Pelletier, 2014; Meirelles et al., 2015; Pelletier et al., 2011). This way, each reef had different recording times and trajectories, but because samples were standardized by completeness rather than size as recommend by Chao and Jost (2012) (see Section 2.3), our statistical analyses were reliable and reproducible (Cardoso et al., 2020). Videos were later analyzed to identify fish species and estimate their abundance. Identification was conducted based on our own field experience and local field guides. Species abundance was measured as the maximum number conspecifics seen simultaneously in the same frame (Barley et al., 2017; Lindfield et al., 2016).

We classified the species into six functional traits that defined the functional profile of fish communities in terms of species' behavior, habitat use, body size, and trophic niche: (a) water column position (benthic; pelagic; benthopelagic); (b) habitat use (generalist; intermediate generalist; specialist); (c) body size categories based on the total length recorded in literature (0–7 cm; 7.1–15 cm; 15.1–30 cm; 30.1–50 cm; 50.1–80 cm; >80 cm); (d) mobility (high mobility; roving; sedentary); (e) trophic categories (herbivore; macrocarnivore; macroinvertivore; small invertivore; omnivore; planktivore); and (f) spawning mode (Balistidae type; brooding; demersal eggs; pelagic eggs; ovoviviparous). We chose these functional traits based on the literature available and on the complementary functions they represent, including habitat use, food acquisition, mobility, nutrient budget, and reproduction strategies (Villéger et al., 2017). Most functional trait data were obtained from Pinheiro et al. (2018, available at https://swatlanticreeffishes.wordpress.com) and complemented with our own field records (e.g., water column).

To calculate the phylogenetic diversity, we estimated a phylogenetic tree for 77 Teleostei fish species of the 85 recorded (Figure 2). We retrieved 704 *cytochrome oxidase subunit I* (COI) and 214 *cytochrome b* (Cytb) sequences from NCBI for the species and aligned the sequences using MUSCLE v3.8.425 (Edgar, 2004) as implemented in Geneious Prime 2019.1.1 (https://www.geneious.

com). The next step was to assemble gene trees at family or order level, depending on the number of sequences available, which allowed us to identify misplaced sequences. This quality control step was conducted to avoid misidentifications or any discrepancies in the sequence selection. The phylogenetic tree was then estimated using maximum-likelihood (ML) and backbone constraint analyses. The backbone tree used was based on a multilocus phylogenetic analysis of ray-finned fishes dated with multiple fossil calibration points containing 1,661 species (Betancur-R et al., 2017). Of the 77 species with COI and/or Cytb data, 31 were previously placed in the backbone tree (accession numbers are given in Table S1). Our aim was to obtain phylogenetic placement for the remaining, previously unexamined 46 species. We conducted constraint ML searches in RAxML v8.1.20 using by-codon partitions and 10 independent iterations (Stamatakis, 2006; Stamatakis et al., 2008), and time-calibrated the resulting ML tree in TreePL v1.0 (Smith & O'Meara, 2012). The TreePL analysis was based on secondary calibrations extracted from the reference backbone tree via "congruification" (Eastman et al., 2013), a function ("congruify") implemented in the R package *geiger* (Harmon et al., 2008). We then pruned the resulting tree to retain the 77 target species using the R package *phytools* (Revell, 2012). Eight species recorded in the study, which accounted for 0.8% of the total abundance registered, were not represented in the tree, including three elasmobranchs and five Teleostei. Although the recent debates regarding the status of Epinephelinae as a separated family from Serranidae, we maintained the nomenclature following the suggestions indicated in Betancur-R et al. (2017), which recognizes the monophyly of Serranidae. The final time-calibrated tree was used to measure the phylogenetic diversity with the R package *hillR* (Chao et al., 2014).

2.3 | Data analysis

To compare fish species diversity across the depth gradient, we standardized the 22 sampled reefs by completeness rather than size, as recommended by Chao and Jost (2012). Accordingly, we estimated the sample coverage in each reef and for each depth category (shallow and deep) as follows:

$$\hat{C}_n = 1 - \frac{f_1}{n}\left[\frac{(n-1)\,f_1}{(n-1)\,f_1 + 2f_2}\right].$$

where f_1 and f_2 correspond to singletons and doubletons in the sample, respectively, and n is the original sample size (fish abundance in each reef). Sample coverage varied from 69% to 99% (mean 87%) when each reef was analyzed separately and was nearly complete when reefs were collapsed in shallow and deep regions (98% and 99%, respectively) (Table 1). Calculations were performed with the R package *iNext* (Hsieh et al., 2016). We also performed complementary species composition analyses to estimate potential spatial autocorrelation between the reefs. Mantel test indicated that species composition was not correlated with geographic distance (Appendix S1).

Gamma and alpha diversity of species, functions, and lineages was estimated based on the effective number of species, the total functional distance between species of the community, and the effective number of phylogenetic entities, respectively (so-called Hill numbers ${}^{q}D$; see also Araújo et al., 2020, and Cardoso et al., 2020). Hill numbers are a family of diversity measures developed by Hill (1973) that quantify diversity in units of equivalent numbers of equally abundant species (Gotelli & Chao, 2013). The index allows to exponentially weight species abundance by a q factor, and unlike traditional diversity metrics, it satisfies the mathematical replication principle (Chao et al., 2014; Jost, 2010). For S species, gamma and alpha diversity of order q is defined as follows:

$$D^q = \left(\sum_{i=1}^{S} p_i^q\right)^{1/(1-q)}$$

where S is the number of fish species in a reef, p_i is the abundance of the ith species, and q is the order that controls the sensitivity to species abundance. When $q = 0$ (${}^{0}D$), all abundances return to 1 and the index is equivalent to species richness (also known as the diversity of rare species); when $q = 1$ (${}^{1}D$), the index maintains the relative abundance of each species and describes the diversity of typical species; and when $q = 2$ (${}^{2}D$), the abundances are squared, giving more weight to the more abundant species and indicating the diversity of dominant species (Chao et al., 2014).

When species are examined by a set of traits that describe ecological functions, species differences can be measured by the dissimilarity or distances between their trait profile (Chao et al., 2014). To construct such functional profiles from qualitative traits and estimate functional diversity, we used Gower distance matrix (Chao et al., 2014; Chiu & Chao, 2014). To calculate alpha and gamma functional diversity, we used the total functional distance between species of the community as follows:

$$\mathrm{FD}\,(Q)^q = \left[\sum_{i=1}^{S}\sum_{j=1}^{S} d_{ij}\left(\frac{pi\,pj}{Q}\right)^q\right]^{1/(1-q)}$$

where d_{ij} denotes the functional distance between the ith and jth species, $p_i p_j/Q$ denotes Rao's quadratic entropy, and q is the order that controls the sensitivity to species abundance. Besides estimating functional diversity based on Hill numbers, we also measured the community-weighted trait means (CWMs hereafter) to identify which traits were responsible for the functional differences between shallow and deep reefs. CWM is defined as the mean of values present in the community weighted by the abundance of a taxa bearing each attribute value (Lavorel et al., 2008).

Alpha and gamma phylogenetic diversity was also measured under a species-neutral approach that satisfies the replication principle using the Hill number framework (Chao et al., 2014). Phylogenetic diversity was estimated as follows:

$$\mathrm{PD}\,(T)^q = \left\{\sum_{i \in B_T} L_i\left(\frac{a_i}{T}\right)^q\right\}^{1/(1-q)}$$

TABLE 1 Information on depth, sampling effort, and sampling coverage of each reef studied in Northeast Brazil

Reef code	Depth (m)	Depth category	Sampling effort (min)	Sample coverage (%)	Sample coverage by depth category
1	2.4	Shallow	31'26''	85	Shallow 98%
2	2.6	Shallow	23'48''	83	
3	7.7	Shallow	40'04''	89	
4	9.1	Shallow	44'30''	89	
5	9.3	Shallow	33'53''	98	
14	18	Shallow	19'41''	72	
6	20.1	Shallow	28'09''	86	
7	24.5	Shallow	24'19''	80	
8	30	Deep	23'03''	75	Deep 99.7%
9	30	Deep	26'16''	96	
10	30	Deep	31'50''	99	
11	33	Deep	37'43''	96	
12	33	Deep	34'28''	98	
13	33	Deep	28'24''	93	
15	34	Deep	70'19''	89	
16	35	Deep	23'30''	69	
17	35	Deep	20'30''	93	
18	40	Deep	26'02''	95	
19	44.7	Deep	105'01''	96	
20	48	Deep	35'26''	95	
21	54.4	Deep	66'05	89	
22	62.3	Deep	53'09''	97	

where L_i is the length (or duration) of branch i in the set B_T, a_i corresponds to the total abundance descended from branch i, and q is the order that controls the sensitivity to species abundance. The metric expresses the effective number of maximally distinct lineages over a time interval (Chao et al., 2010).

We applied two approaches to examine beta-diversity patterns: multiplicative and additive. The multiplicative approach, where beta = gamma/alpha (Jost et al., 2010), assumes that alpha and beta are independent components and could be calculated considering rare (^0D), typical (^1D), and dominant (^2D) species (Jost, 2007; Jost et al., 2010). This approach can be interpreted as the regional beta diversity, as only one value of beta diversity is given for N sites. Regional beta diversity of species corresponds to the effective number of completely distinct communities in the region (e.g., the shallow region). For functional diversity, this metric describes the functional differentiation among communities, and for phylogenetic diversity, it expresses the effective number of equally large and completely distinct assemblages, meaning no shared branches between communities (Chao et al., 2014).

For the beta additive approach, we considered the presence/absence of species corresponding to Hill numbers species diversity of order ^0D. The additive approach produces pairwise beta-diversity values and was used to partition beta into nestedness and turnover components (Baselga, 2010). In this sense, the multiplicative approach estimated the number of completely distinct communities in the shallow and deep areas, while the additive approach shed light into the mechanisms underlying such patterns. The multiplicative approach was applied to construct the taxonomic, functional, and phylogenetic beta profiles of shallow and deep reefs for rare (^0D), typical (^1D), and dominant (^2D) species, while the additive partitioning of beta species diversity was employed to measure species nestedness and turnover between shallow and deep reefs, as well as within shallow areas and within deep areas. Alpha, gamma, and beta were measured in R using *entropart* (Marcon & Hérault, 2015) for species diversity, the functional diversity R function available in Chiu and Chao (2014), and the package *hillR* (Chao et al., 2014) for phylogenetic diversity estimation.

Finally, we performed a one-way Wilcoxon test to test whether diversity metrics were higher in deep reefs when compared to their shallow counterparts for rare (^0D), typical (^1D), and dominant (^2D) species, functions, and lineages. Treating depth as a continuous variable in generalized least-squares regressions produced similar outcomes (Appendix S2). CWM values of shallow and deep reefs were also compared using the one-way Wilcoxon test. The diversity estimations and Wilcox test were performed in R software (R Core Team, 2018), using the packages *entropart* (Marcon & Hérault, 2015), *cluster* (Becker et al., 1988), *FD* (Becker et al., 1988), and *hillR* (Chao et al., 2014).

3 | RESULTS

We recorded 3,821 individuals distributed in 85 fish species, 36 families, and 10 orders (Table 2). The 10 most representative families were Labridae (eight species), Haemulidae (7), Labridae: Scarinae (6), Serranidae (6), Carangidae (6), Lutjanidae (5), Pomacentridae (5), Acanthuridae (3), Pomacanthidae (3), and Sciaenidae (3). Ten species represented 70% of individuals: *Haemulon squamipinna* (23%), *Mulloidichthys martinicus* (18%), *Holocentrus adscencionis* (6%), *Kyphosus incisor* (6%), *Acanthurus chirurgus* (4%), *Carangoides bartolomaei* (3%), *Haemulon aurolineatum* (3%), *Lutjanus alexandrei* (3%), *Cephalopholis fulva* (2%), and *Pareques acuminatus* (2%). In terms of vertical distribution, 41 species occurred in both shallow and deep areas, while 15 species occurred only in shallow reefs and 29 only in deep reefs (Table 2), indicating that depth-generalist species do not dominate the metacommunity. Seven species were listed in the IUCN Red List (Table 2), including *Scarus trispinosus* (endangered) and other three Scarinae species (vulnerable), *Ginglymostoma cirratum* (vulnerable), *Elacatinus figaro* (vulnerable), and *Mycteroperca bonaci* (vulnerable). No nonindigenous or invasive species were recorded.

3.1 | Gamma diversity

Gamma diversity of rare, typical, and dominant species was smaller in shallow than deep reefs (^{0}D Gamma$_{\text{Shallow}} = 56$ vs. Gamma$_{\text{Deep}} = 70$; ^{1}D Gamma$_{\text{Shallow}} = 20.5$ vs. Gamma$_{\text{Deep}} = 29$; ^{2}D Gamma$_{\text{Shallow}} = 12.5$ vs. Gamma$_{\text{Deep}} = 17.7$). Gamma functional diversity, expressed as the effective total functional diversity, was higher in deep reefs for ^{0}D (Gamma$_{\text{Shallow}} = 1612$; Gamma$_{\text{Deep}} = 2{,}610$), ^{1}D (Gamma$_{\text{Shallow}} = 142$; Gamma$_{\text{Deep}} = 240$), and ^{2}D (Gamma$_{\text{Shallow}} = 43$; Gamma$_{\text{Deep}} = 66$). Following the same trend, gamma phylogenetic diversity was also higher for deep reefs in all scenarios (^{0}D Gamma$_{\text{Shallow}} = 3{,}338$ vs. Gamma$_{\text{Deep}} = 3{,}503$; ^{1}D Gamma$_{\text{Shallow}} = 615$ vs. Gamma$_{\text{Deep}} = 804$; ^{2}D Gamma$_{\text{Shallow}} = 398$ vs. Gamma$_{\text{Deep}} = 452$). In the three types of diversity measured, gamma was consistently higher in deep reefs compared with their shallow counterparts, which might support the DRRH if species composition of shallow reefs was nested within deep reefs, but that was not case (see Section 3.3).

3.2 | Alpha diversity

The mean effective number of rare species was greater in deep than shallow reefs ($U = 25$, $p = 0.012$), supporting the DRRH for rare species, but did not significantly differ between shallow and deep reefs for typical and dominant species (Figure 3). Alpha functional diversity was also significantly greater for rare ($U = 26$, $p = 0.022$) and typical species in deep reefs ($U = 30$, $p = 0.041$), and tended to be greater for dominant species (Figure 3). When we analyzed the data separately by functional trait, differences between shallow and deep reefs were raised for seven trait states (Table S2). Compared with shallow reefs, deep reefs showed significantly more benthic and pelagic species ($U = 27.5$, $p = 0.023$; $U = 32.5$, $p = 0.049$, respectively), larger species (attribute 80 cm <total length >50 cm, $U = 27.5$, $p = 0.025$; attribute total length >80 cm, $U = 17$, $p = 0.004$), and ovoviviparous species ($U = 28$, $p = 0.012$). None of the functional traits were exclusive to the shallow, whereas ovoviviparous was exclusive to deep reefs. Information on all traits is available at supplementary information (Table S2).

Following expectations, alpha phylogenetic diversity was consistently greater in deep reefs than in shallow reefs, considering rare ($U = 26$, $p = 0.022$), typical ($U = 29$, $p = 0.035$), and dominant species ($U = 31$, $p = 0.047$) (Figure 3).

3.3 | Beta diversity

Regional beta diversity of species and functions showed consistent responses to depth (Figure 4). In the shallow reefs, rare, typical, and dominant species showed similar levels of beta diversity, oscillating around 3.0–3.5 completely distinct communities out of 8 possible (Figure 4). On the other hand, in the deep reefs, regional beta diversity increased dramatically from rare (^{0}D) to dominant species (^{2}D), reaching 4 completely distinct communities out of 14 possible (Figure 4). These same trends were observed for regional functional beta diversity, indicating that large aggregations—the dominant species—change more at higher depths not only taxonomically but also functionally. Conversely, rare, solitary species tended to be the same at deep waters and perform similar functions when compared to their counterparts in shallow waters.

Regarding the validity of DRRH, the curves of deep reefs in diversity profiles (Figure 4) should be above the curves of shallow reefs to indicate that deep reefs are more heterogeneous than shallow ones, but this was observed only for taxonomic and functional ^{2}D. The phylogenetic beta profile also revealed corresponding levels of regional beta diversity for rare and typical species regardless depth. However, beta diversity of dominant species did not increase in deep reefs, contradicting the expectation of phylogenetic homogenization at shallow waters for all orders of diversity.

When the pairwise beta diversity of species was decomposed into nestedness and turnover components, the spatial variation in species composition was more explained by turnover than nestedness and irrespective to depth (Figure 5). In shallow reefs, turnover accounted on average for 0.42, while nestedness for 0.24 of total beta diversity (Figure 5). Similarly, turnover between deep reefs reached 0.32 on average, while nestedness only 0.15 (Figure 5). Both results were contrary to the DRRH expectation of smaller turnover at shallow waters and indicate that each reef gives its contribution to the gamma diversity.

Taking the beta-diversity patterns together, it is possible to infer that the larger fish agglomerations at higher depths diverge taxonomically

TABLE 2 Fish species recorded in the 22 shallow and deep reefs of Northeast Brazil. Numbers in shallow and deep categories represent species abundance. The last column identifies threatened species according to IUCN's (the International Union for Conservation of Nature) red list (available at https://www.iucnredlist.org)

Family	Species	Shallow	Deep	IUCN
Ginglymostomatidae	*Ginglymostoma cirratum* (Bonnaterre 1788)		5	VU
Dasyatidae	*Hypanus berthalutzae* (Petean, Naylor & Lima 2020)		2	
	Hypanus sp		1	
Muraenidae	*Gymnothorax funebris* (Ranzani 1839)	1	5	
	Muraena pavonina (Richardson 1845)	2	1	
Ophichthidae	*Myrichthys ocellatus* (Lesueur 1825)	1	1	
Fistulariidae	*Fistularia tabacaria* (Linnaeus 1758)	1		
Scorpaenidae	*Scorpaena plumieri* (Bloch 1789)		1	
Holocentridae	*Holocentrus adscensionis* (Osbeck 1765)	22	211	
	Myripristis jacobus (Cuvier 1829)		64	
Serranidae	*Alphestes afer* (Bloch 1793)	3	2	
	Cephalopholis fulva (Linnaeus 1758)	14	68	
	Epinephelus adscensionis (Osbeck 1765)	1	11	
	Mycteroperca bonaci (Poey 1860)		2	VU
	Paranthias furcifer (Valenciennes 1828)		38	
	Rypticus saponaceus (Bloch & Schneider 1801)	1	2	
Malacanthidae	*Malacanthus plumieri* (Bloch 1786)		5	
Echeneidae	*Echeneis naucrates* (Linnaeus 1758)	2		
Carangidae	*Caranx bartholomaei* (Cuvier 1833)		129	
	Caranx latus (Agassiz 1831)	3		
	Caranx lugubris (Poey 1860)		2	
	Elagatis bipinnulata (Quoy & Gaimard 1825)		13	
	Pseudocaranx dentex (Bloch & Schneider 1801)		2	
	Selar crumenophthalmus (Bloch 1793)		57	
Lutjanidae	*Lutjanus alexandrei* (Moura & Lindeman 2007)	20	90	
	Lutjanus cf. *apodus* (Walbaum 1792)	1	3	
	Lutjanus jocu (Bloch & Schneider 1801)	4	37	
	Lutjanus synagris (Linnaeus 1758)		5	
	Ocyurus chrysurus (Bloch 1791)		63	
Haemulidae	*Anisotremus moricandi* (Ranzani 1842)	5		
	Anisotremus surinamensis (Bloch 1791)		7	
	Anisotremus virginicus (Linnaeus 1758)	15	26	
	Haemulon aurolineatum (Cuvier 1830)	46	73	
	Haemulon parra (Desmarest 1823)	3	14	
	Haemulon plumierii (Lacepède 1801)	6	21	
	Haemulon squamipinna (Rocha & Rosa 1999)	337	560	
Sparidae	*Calamus pennatula* (Guichenot 1868)		1	
Sciaenidae	*Equetus lanceolatus* (Linnaeus 1758)		1	
	Odontoscion dentex (Cuvier 1830)	3	9	
	Pareques acuminatus (Bloch & Schneider 1801)	4	68	
Mullidae	*Mulloidichthys martinicus* (Cuvier 1829)	2	682	
	Pseudupeneus maculatus (Bloch 1793)	5	43	
Pempheridae	*Pempheris schomburgkii* (Müller & Troschel 1848)	14		
Chaetodontidae	*Chaetodon ocellatus* (Bloch 1787)		7	
	Chaetodon striatus (Linnaeus 1758)	5	5	

(Continues)

TABLE 2 (Continued)

Family	Species	Shallow	Deep	IUCN
Pomacanthidae	*Holacanthus ciliaris* (Linnaeus 1758)	5	13	
	Holacanthus tricolor (Bloch 1795)	1	23	
	Pomacanthus paru (Bloch 1787)	3	10	
Kyphosidae	*Kyphosus incisor* (Cuvier 1831)		229	
Cirrhitidae	*Amblycirrhitus pinos* (Mowbray 1927)	1	6	
Pomacentridae	*Abudefduf saxatilis* (Linnaeus 1758)	15	47	
	Chromis multilineata (Guichenot 1853)	8	27	
	Stegastes fuscus (Cuvier 1830)	12		
	Stegastes pictus (Castelnau 1855)		25	
	Stegastes variabilis (Castelnau 1855)	2		
Sphyraenidae	*Sphyraena barracuda* (Edwards 1771)		16	
Labridae	*Bodianus rufus* (Linnaeus 1758)	7	38	
	Clepticus brasiliensis (Heiser, Moura & Robertson 2000)		6	
	Halichoeres brasiliensis (Bloch 1791)	5	4	
	Halichoeres dimidiatus (Agassiz 1831)	3	21	
	Halichoeres penrosei (Starks 1913)	1		
	Halichoeres poeyi (Steindachner 1867)	9	14	
	Thalassoma noronhanum (Boulenger 1890)	1	47	
	Xyrichtys martinicensis (Valenciennes 1840)	5		
Labridae: Scarinae	*Cryptotomus roseus* (Cope 1871)	1		
	Scarus trispinosus (Valenciennes 1840)	1	5	EN
	Scarus zelindae (Moura, Figueiredo & Sazima 2001)	1	7	VU
	Sparisoma amplum (Ranzani 1841)		1	
	Sparisoma axillare (Steindachner 1878)	24	20	VU
	Sparisoma frondosum (Agassiz 1831)	5	10	VU
Opistognathidae	*Opistognathus* sp		2	
Labrisomidae	*Labrisomus nuchipinnis* (Quoy & Gaimard 1824)	3		
Blenniidae	*Ophioblennius trinitatis* (Miranda Ribeiro 1919)	2		
Gobiidae	*Elacatinus figaro* (Sazima, Moura & Rosa 1997)	6	16	VU
Microdesmidae	*Ptereleotris randalli* (Gasparini, Rocha & Floeter 2001)	2		
Acanthuridae	*Acanthurus bahianus* (Castelnau 1855)	27	16	
	Acanthurus chirurgus (Bloch 1787)	42	93	
	Acanthurus coeruleus (Bloch & Schneider 1801)	11	40	
Scombridae	*Scomberomorus regalis* (Bloch 1793)		1	
Balistidae	*Balistes vetula* (Linnaeus 1758)	1		
Monacanthidae	*Cantherhines macrocerus* (Hollard 1853)		11	
	Cantherhines pullus (Ranzani 1842)		4	
Ostraciidae	*Acanthostracion polygonius* (Poey 1876)	1		
Tetraodontidae	*Canthigaster figueiredoi* (Moura & Castro 2002)		4	
	Sphoeroides spengleri (Bloch 1785)	1	1	

Abbreviation: EN, endangered; VU, vulnerable.

and functionally from a deep reef to another, although they converge phylogenetically toward particular basal clades. Carangidae, for instance, which was almost exclusive from the deep reefs, might be one of those ecologically dominant clades with many species and functions that phylogenetically homogenized the deep reefs.

4 | DISCUSSION

Our findings indicate that deep reefs may serve as refuge or refugium for some depth-generalist taxa, functions, and lineages, including some species that use the depth gradient during the ontogenetic

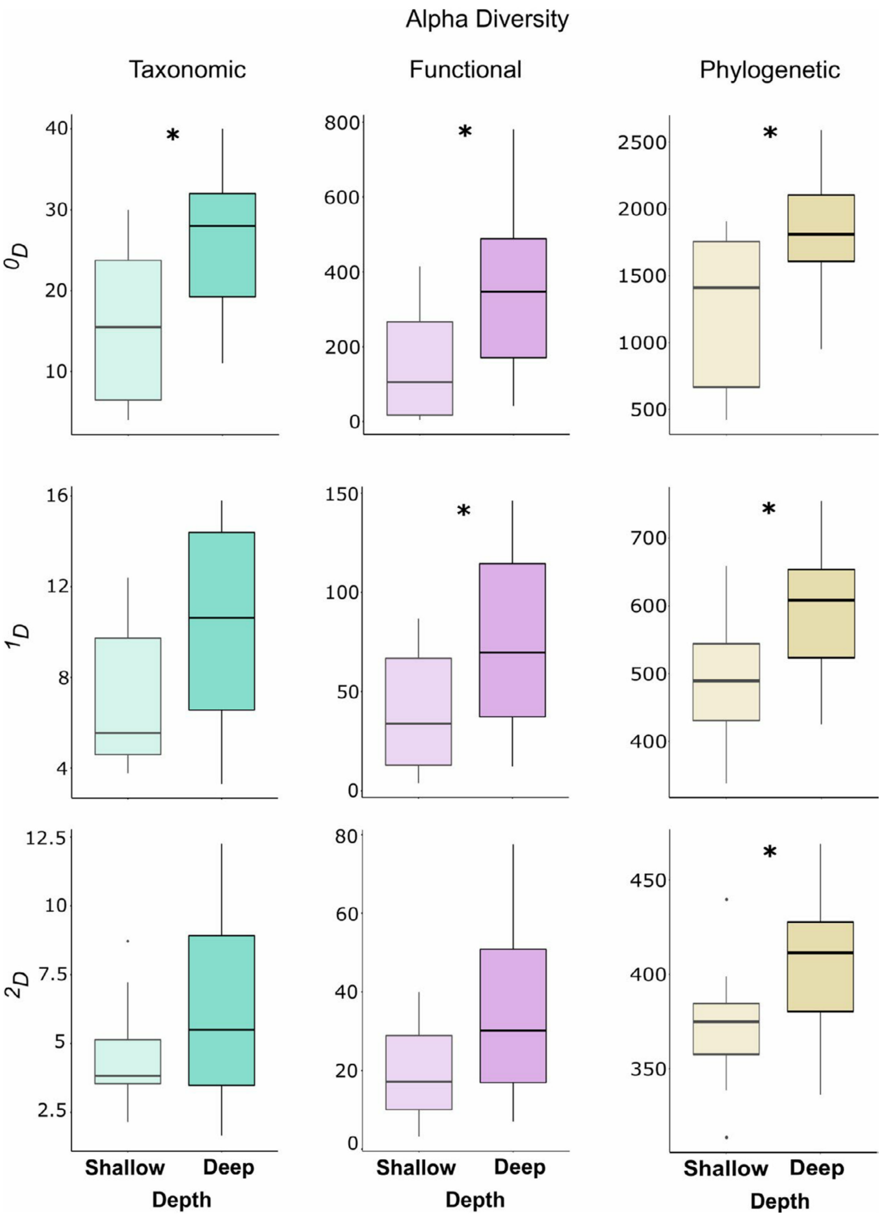

FIGURE 3 Alpha diversity of rare (^0D), typical (^1D), and dominant (^2D) fish species in shallow (<30 m depth) and deep (>30 m depth) reefs of Northeast Brazil. Asterisk represents significant difference with $p < 0.05$

migration (Aschenbrenner et al., 2016; Fredou & Ferreira, 2005). However, a representative portion of the fish diversity is exclusive to the shallow reefs or is not evenly distributed across ecologically rare, typical, and dominant groups along the depth gradient, providing limited support to the DRRH. Five findings merit special attention. First, 15 species were exclusive to the shallow reefs, indicating that their local extinction is unlikely to be reverted by immigrants from deep reefs. Second, deep reefs had more rare species than shallow reefs but not more typical and dominant species, suggesting that there are stressors in deeper areas limiting dominance locally. Third, the great contribution of the turnover component to pairwise beta-diversity patterns and the taxonomic segregation of shallow and deep reefs indicate that the shallow reefs are not a subset from the deep reefs, thus cannot be replenished by deep reefs. Fourth, the functional responses of fish communities to depth resembled the taxonomic responses, revealing similar limitations of shallow and deep reefs to protect regional fish diversity. Fifth, phylogenetic beta diversity suggested that typical and dominant species belong to a few clades irrespective to depth. Jointly, these results highlight that the deep reefs of southwestern Atlantic, as other marginal reefs around the world, have their own dynamics and deserve the same attention that shallow reefs do (Soares et al., 2021).

The number of studies documenting deviations from DRRH expectations and demonstrating the complementary nature of shallow and deep reefs to the shallow-deep diversity has gradually increased (e.g., Bongaerts & Smith, 2019; Semmler et al., 2017). For instance, Rocha et al. (2018) employed a species composition approach to test the hypothesis with reef fishes of western Atlantic and Pacific and found strong depth specificity for species in the mesophotic zone, indicating that shallow and deep communities were composed by different species rather than a subset of one another. Similar results were found in terms of fish

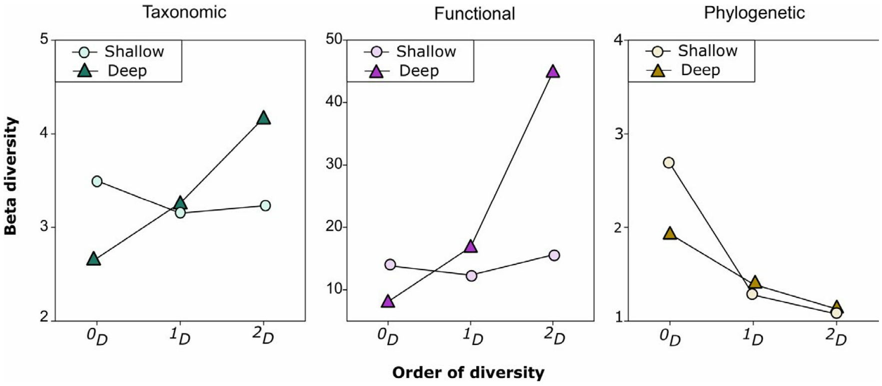

FIGURE 4 Profiles of taxonomic, functional, and phylogenetic beta diversity of rare (^{0}D), typical (^{1}D), and dominant (^{2}D) fish species in shallow (circle) and deep (triangle) reefs of Northeast Brazil

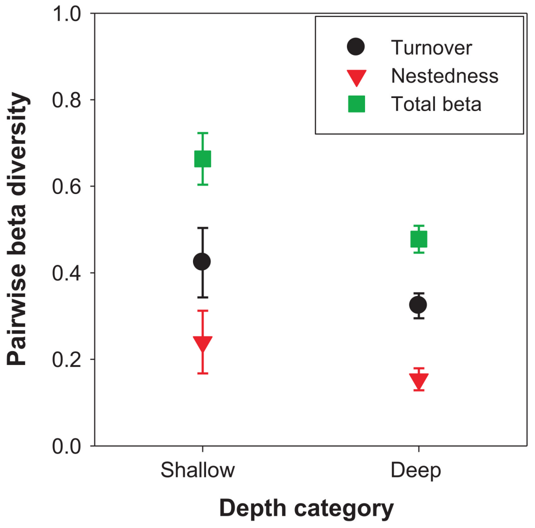

FIGURE 5 Pairwise beta diversity of shallow and deep reefs decomposed into turnover and nestedness components. Symbols represent mean values between pairs of reefs; the upper and lower error bars indicate 95% confidence interval. Total beta refers to the sum of turnover and nestedness components

abundance, species richness, trophic groups, and size classes by Pereira et al. (2018) in southwestern Atlantic. In our study region, the DRRH was tested for coral communities with the same analytical approach used here and little support for the hypothesis was observed as well (Morais & Santos, 2018). Nonetheless, we stress that particular species, functions, and lineages may do found refuge or refugium in deep reefs, but not entire fish communities (Soares et al., 2021).

In fact, our findings support the general notion that the shallow reefs diverge taxonomically and functionally from the upper limits of the mesophotic region (30–60 m) (Rocha et al., 2018), which has been also documented in tropical Atlantic (Bejarano et al., 2014; Pinheiro et al., 2016) and Pacific reefs (Coleman et al., 2018; Lindfield et al., 2016). In Gulf of Mexico, for instance, the peak of species turnover takes place at 60 m, which shares only 48% of species with adjacent mesophotic bands at 40–60 and 60–80 m and even less with the shallow area (0–20 m) (Semmler et al., 2017). The authors suggest that this compositional pattern is mostly driven by benthic community composition. This is likely to explain our results as well, but because shallow and deep reefs are several kilometers apart from each other in our study region, it is possible that the structural disconnection between shallow and deep reefs underlies the taxonomic segregation (see also Morais & Santos, 2018).

The phylogenetic dimension of fish diversity may shed light on the evolutionary potential of shallow and deep reefs to adapt to global warming and ocean sprawl (Véron et al., 2019; Winter et al., 2013). Because human stressors are more intense in shallow reefs, and only a small number of disturbance-tolerant lineages may take advantage of the new conditions in the Anthropocene (Jia et al., 2020; Ribeiro et al., 2016), we expected more phylogenetic homogenization among shallow reefs than among deep reefs. However, this did not happen, suggesting that deep reefs do not count with more evolutionary diversity to couple with ongoing and future changes. Locally, at the alpha scale, the deep reefs do accumulate more lineages than shallow reefs, but this is not enough to face multiple large-scale disturbances (Albouy et al., 2015). We stress that conservation and management actions of reef environments should incorporate the phylogenetic dimension of fish communities to protect their diversity at any depth. According to our findings, shallow and deep reefs are quite similar in terms of phylogenetic beta-diversity patterns, with a few ecologically dominant clades homogenizing them throughout the study region.

The increased gamma diversity observed in the deep reefs possibly reflects more suitable conditions for reef fish diversity or represents an important faunal corridor for species associated with deep reef formations across the Atlantic region (Olavo et al., 2011; Soares et al., 2019). Different factors can be related to the increasing gamma diversity from deep to shallow reefs. Most of them are associated with less human pressure in deep areas (Downing et al., 2005; Pereira et al., 2018; Quimbayo et al., 2018; Villéger et al., 2017), but the idea that deep reefs are undisturbed, pristine habitats has been challenged. While the shallow reefs mostly concentrate impacts such as nonregulated tourism, overfishing, and pollution associated with the proximity to the mainland (Downing et al., 2005; Pereira et al., 2018; Quimbayo et al., 2018; Villéger et al., 2017), the deep reefs are usually threatened by invasive species, marine debris, overfishing, and oil/gas exploitation (Soares et al., 2019). Although our study region did not face biological invasion and oil/gas exploitation, fishing gears were observed abandoned in some deep reefs (B.A.S., personal observation). These human stressors in presumably undisturbed deep reefs should have reduced the differences we observe today with the shallow reefs. However, because the shallow reefs of our study region have been facing mass tourism, pollution, and overfishing in the past decades, we attribute their reduced gamma diversity to increased human impacts.

Finally, from the theoretical perspective, the deviation from DRRH expectations suggests that the reef fish metacommunity is not structured by mass effects, although source–sink dynamics and rescue effects should occur for some species. In fact, the unexpected greater contribution of turnover in explaining beta-diversity patterns at any depth suggests that the metacommunity is mainly structured by species sorting (Leibold et al., 2004). In this model of metacommunity structuring, local environmental conditions are more important than dispersal capacity, allowing species to persist only under suitable conditions. The depth gradient is split into spatial (depth) niches as documented for corals (Morais & Santos, 2018), and the beta diversity becomes high because each local community (i.e., each reef) differs from one another and adds new species to the regional species pool. Because fish distribution along environmental gradients is driven by a product of biogeographic (Floeter et al., 2008; Rocha et al., 2008), historical (Slattery et al., 2011), ecological (Beukers & Jones, 1998), and abiotic factors (Darling et al., 2017), further studies are needed to understand the real role of species sorting across the southwestern Atlantic reefs. However, whatever the driver of diversity patterns, our study highlights that shallow and deep reefs complement each other and must be managed and protected accordingly.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

AUTHOR CONTRIBUTION

Aline P. M. Medeiros: Conceptualization (lead); Formal analysis (lead); Funding acquisition (lead); Investigation (lead); Methodology (lead); Writing-original draft (lead); Writing-review & editing (lead). **Beatrice Ferreira:** Data curation (supporting); Methodology (supporting); Supervision (supporting); Writing-review & editing (supporting). **Ricardo Betancur:** Formal analysis (supporting); Methodology (supporting); Software (supporting); Supervision (supporting); Writing-review & editing (supporting). **Fredy Alvarado:** Formal analysis (equal); Methodology (equal); Writing-review & editing (equal). **Marcelo Soares:** Investigation (equal); Writing-review & editing (equal). **Braulio A. Santos:** Conceptualization (lead); Formal analysis (lead); Funding acquisition (lead); Investigation (lead); Methodology (lead); Supervision (lead); Writing-original draft (lead); Writing-review & editing (lead).

ETHICAL STATEMENT

Research authorization was obtained via protocols SISBIO # 71158 and SUDEMA # 5192/19.

DATA AVAILABILITY STATEMENT

Data are available in the Dryad Digital repository at https://datadryad.org/stash/share/plf6k7Mz8oApKifT67o6nUTNwJFZ6mVJLfjw96BpvxE.

ORCID

Fredy Alvarado https://orcid.org/0000-0002-6724-4064
Ricardo Betancur-R https://orcid.org/0000-0002-9512-5011
Bráulio A. Santos https://orcid.org/0000-0001-6046-4024

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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Ecology and Evolution – Supplementary material

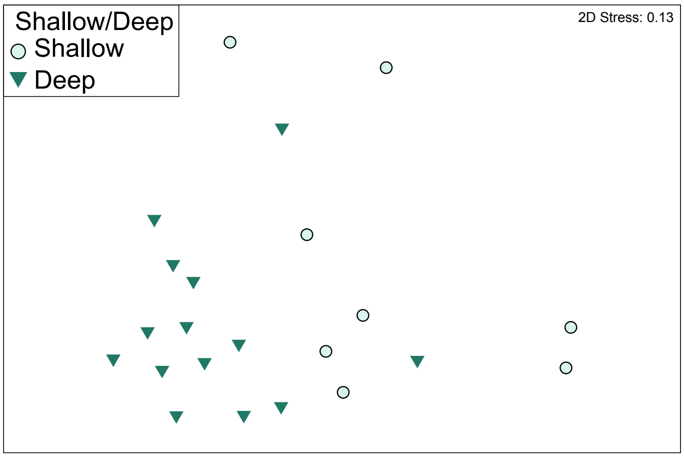
Deep reefs are not refugium for shallow-water fish communities in the southwestern Atlantic

Aline P. M. Medeiros[1], Beatrice P. Ferreira[2], Fredy Alvarado[3], Ricardo Betancur-R[4,5], Marcelo O. Soares[6,7,8], Bráulio A. Santos[9]*

[1] Programa de Pós-Graduação em Ciências Biológicas, Universidade Federal da Paraíba, Cidade Universitária, Castelo Branco, 58051-900, João Pessoa, PB, Brazil
[2] Departamento de Oceanografia, Centro de Tecnologia, Universidade Federal de Pernambuco, Cidade Universitária, 50670-901, Recife, PE, Brazil
[3] Departamento de Agricultura, Centro de Ciências Humanas, Sociais e Agrárias, Universidade Federal da Paraíba, Campus Universitário III, R. João Pessoa, S/N, 58220-000, Bananeiras, PB, Brazil
[4] Department of Biology, The University of Oklahoma, 730 Van Vleet Oval, Room 314, Norman, OK 73019, USA
[5] Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington DC 20560, USA
[6] Instituto de Ciências do Mar-LABOMAR, Universidade Federal do Ceará, Av. da Abolição, 3207, Meireles, 60165-081, Fortaleza, CE, Brazil
[7] Institut de Ciència i Tecnologia Ambientals (ICTA), Universitat Autònoma de Barcelona (UAB), Carrer de les Columnes, Edifici Z, Barcelona, Spain
[8] Dipartimento di Scienze e Tecnologie Biologiche e Ambientali (DISTEBA), Università del Salento, Lecce, Italy
[9] Departamento de Sistemática e Ecologia, Centro de Ciências Exatas e da Natureza, Universidade Federal da Paraíba, Cidade Universitária, Castelo Branco, 58051-900, João Pessoa, PB, Brazil.
*Corresponding author: braulio@dse.ufpb.br

Appendix S1. Complementary species composition analyses

We carried out species preliminary species composition analyses according to depth categories and geographic distance. Prior to these analyses, data were log(x + 1) transformed to reduce discrepancies caused by rare and abundant species and then used in the construction of similarity matrices (Bray–Curtis index) in PRIMER 6.0 Software (Clarke & Warwick, 2001). To assess the relationship between species composition and depth categories, we performed an ANOSIM test and a non-metric dimensional scaling (NMDS). Mantel test was applied to assess if geographic distance and depth difference between reefs were correlated with species similarity. While species composition was not correlated with geographic distance between reefs (Rho= 0.098; p> 0.05), depth presented a significant correlation with species similarity (Rho= 0.542; p= 0.001), indicating that reefs at similar depth tended to be more taxonomically similar than reefs at different depths. This effect of depth on species composition was visible in the NMDS and supported by the ANOSIM (Global_R= 0.439, p= 0.001). The functional distance between reefs was not related to difference in depth (Rho= 0.026; p> 0.05) or geographical distance (Rho= -0.154; p> 0.05).



Non-metric multidimensional scaling (NMDS) applied to the reef fish communities of shallow (< 30 m) and deep (> 30 m) reefs in Northeast Brazil.

Appendix S2. Generalized least square modelling applied to test the effect of depth on diversity metrics

Besides testing whether species, functional and phylogenetic alpha diversity were related to depth categories (shallow vs. deep), we performed generalized least square (GLS) analyses treating depth as a continuous variable. Depth and diversity values were log-transformed (natural log) prior to the analyses. The results we obtained using Wilcox tests were similar to the GLS outcomes, with alpha diversity being positively correlated to the increase in depth for ^{0}D in species diversity; ^{0}D, ^{1}D and ^{2}D in functional diversity; ^{0}D, ^{1}D and ^{2}D in phylogenetic diversity.

Results of the GLSs applied to taxonomic, functional and phylogenetic alpha diversity according to reef depth. The level of significance is indicated as follows: *< 0.05; **< 0.01; NS – not significant.

Diversity type	*q* order	R-square	*P*	Significance
Taxonomic	^{0}D	0.2668	0.01385	*
Taxonomic	^{1}D	0.06745	0.243121	NS
Taxonomic	^{2}D	0.01669	0.5667	NS
Functional	^{0}D	0.2829	0.0108	*
Functional	^{1}D	0.2431	0.01971	*
Functional	^{2}D	0.1875	0.04410	*
Phylogenetic	^{0}D	0.3602	0.00315	**
Phylogenetic	^{1}D	0.2452	0.0191	*
Phylogenetic	^{2}D	0.1855	0.0454	*

Table S1. Species included in the time-calibrated tree, estimated using maximum likelihood and backbone constraint analyses. The source (B17) corresponds to species already placed in the backbone tree (Betancur-R et al., 2017); the remaining species (GenBank) were placed based on *cytochrome oxidase subunit I* (COI) and *cytochrome b* (Cytb) sequences obtained from NCBI. NCBI accession numbers are provided.

Species (as in GenBank)	Species	Source	COI	Cytb
Abudefduf saxatilis	*Abudefduf saxatilis*	B17		
Acanthostracion polygonius	*Acanthostracion polygonius*	GenBank	JQ861011.1	JQ861154.1
Acanthurus bahianus	*Acanthurus bahianus*	B17		
Acanthurus chirurgus	*Acanthurus chirurgus*	GenBank	JQ842356.1	KC623696.1
Acanthurus coeruleus	*Acanthurus coeruleus*	GenBank	JQ842776.1	KC623697.1
Alphestes afer	*Alphestes afer*	GenBank	JQ840759.1	AY313996.1
Amblycirrhitus pinos	*Amblycirrhitus pinos*	B17		
Anisotremus moricandi	*Anisotremus moricandi*	GenBank	JQ741142.1	EU694316.1
Anisotremus surinamensis	*Anisotremus surinamensis*	B17		
Anisotremus virginicus	*Anisotremus virginicus*	B17		
Balistes vetula	*Balistes vetula*	B17		
Bodianus rufus	*Bodianus rufus*	GenBank	JQ839717.1	
Calamus pennatula	*Calamus pennatula*	GenBank	KY402425.1	
Cantherhines macrocerus	*Cantherhines macrocerus*	GenBank	JQ842801.1	
Cantherhines pullus	*Cantherhines pullus*	GenBank	MF041486.1	KF025770.1
Canthigaster figueiredoi	*Canthigaster figueiredoi*	GenBank	JQ681776.1	JQ681871.1
Carangoides bartholomaei	*Carangoides bartholomaei*	GenBank	JQ841092.1	AY050728.1
Caranx latus	*Caranx latus*	GenBank	JQ841100.1	AY050724.1
Caranx lugubris	*Caranx lugubris*	GenBank	MK566835.1	
Cephalopholis fulva	*Cephalopholis fulva*	B17		
Chaetodon ocellatus	*Chaetodon ocellatus*	B17		
Chaetodon striatus	*Chaetodon striatus*	B17		
Chromis multilineata	*Chromis multilineata*	GenBank	JQ842056.1	EU431997.1
Cryptotomus roseus	*Cryptotomus roseus*	B17		
Echeneis naucrates	*Echeneis naucrates*	B17		
Elacatinus figaro	*Elacatinus figaro*	GenBank	KM987237.1	AY846438.1
Elagatis bipinnulata	*Elagatis bipinnulata*	B17		

Species (as in GenBank)	Species	Source	COI	Cytb
Epinephelus adscensionis	*Epinephelus adscensionis*	GenBank	FJ583396.1	
Equetus lanceolatus	*Equetus lanceolatus*	GenBank	KP722721.1	KP722629.1
Fistularia tabacaria	*Fistularia tabacaria*	B17		
Gymnothorax funebris	*Gymnothorax funebris*	GenBank	JQ842871.1	
Haemulon aurolineatum	*Haemulon aurolineatum*	B17		
Haemulon parra	*Haemulon parra*	GenBank	JQ841906.1	EU697512.1
Haemulon plumieri	*Haemulon plumieri*	B17		
Haemulon squamipinna	*Haemulon squamipinna*	GenBank	EU697544.1	EU697517.1
Halichoeres brasiliensis	*Halichoeres brasiliensis*	GenBank		AY823576.1
Halichoeres cyanocephalus	*Halichoeres dimidiatus*	GenBank	JQ841215.1	AY591376.1
Halichoeres maculipinna	*Halichoeres penrosei*	GenBank	JQ840106.1	AY591354.1
Halichoeres poeyi	*Halichoeres poeyi*	GenBank	JQ841595.1	AY823578.1
Holacanthus ciliaris	*Holacanthus ciliaris*	B17		
Holacanthus tricolor	*Holacanthus tricolor*	B17		
Holocentrus adscensionis	*Holocentrus adscensionis*	GenBank	JQ842166.1	KX961691.1
Kyphosus incisor	*Kyphosus incisor*	B17		
Labrisomus nuchipinnis	*Labrisomus nuchipinnis*	GenBank	GU225343.1	
Lutjanus alexandrei	*Lutjanus alexandrei*	GenBank	MG575213.1	
Lutjanus apodus	*Lutjanus* cf. *apodus*	GenBank	JQ842558.1	U26957.1
Lutjanus jocu	*Lutjanus jocu*	GenBank	KF633372.1	HQ162442.1
Lutjanus synagris	*Lutjanus synagris*	GenBank	KF633283.1	HQ162427.1
Malacanthus plumieri	*Malacanthus plumieri*	B17		
Mulloidichthys martinicus	*Mulloidichthys martinicus*	B17		
Mycteroperca bonaci	*Mycteroperca bonaci*	B17		
Myrichthys ocellatus	*Myrichthys ocellatus*	GenBank	JQ842250.1	
Myripristis jacobus	*Myripristis jacobus*	GenBank	JQ842252.1	DQ379998.1
Ocyurus chrysurus	*Ocyurus chrysurus*	B17		
Odontoscion dentex	*Odontoscion dentex*	B17		
Ophioblennius trinitatis	*Ophioblennius trinitatis*	GenBank		MF990196.1
Paranthias furcifer	*Paranthias furcifer*	GenBank	JQ365485.1	
Pareques acuminatus	*Pareques acuminatus*	B17		
Pempheris schomburgki	*Pempheris schomburgki*	B17		
Pomacanthus paru	*Pomacanthus paru*	GenBank	JQ840654.1	

Species (as in GenBank)	Species	Source	COI	Cytb
Pseudocaranx dentex	*Pseudocaranx dentex*	GenBank	EF609442.1	DQ197985.1
Pseudupeneus maculatus	*Pseudupeneus maculatus*	B17		
Rypticus saponaceus	*Rypticus saponaceus*	B17		
Scarus trispinosus	*Scarus trispinosus*	GenBank	MF999162.1	
Scomberomorus regalis	*Scomberomorus regalis*	B17		
Scorpaena plumieri	*Scorpaena plumieri*	GenBank	JQ365552.1	
Selar crumenophthalmus	*Selar crumenophthalmus*	B17		
Sparisoma amplum	*Sparisoma amplum*	GenBank		DQ457024.1
Sparisoma axillare	*Sparisoma axillare*	GenBank		DQ457034.1
Sparisoma frondosum	*Sparisoma frondosum*	GenBank		DQ457032.1
Sphoeroides spengleri	*Sphoeroides spengleri*	GenBank	JQ681816.1	JQ681909.1
Sphyraena barracuda	*Sphyraena barracuda*	B17		
Stegastes fuscus	*Stegastes fuscus*	B17		
Stegastes pictus	*Stegastes pictus*	GenBank	KM077183.1	KM077201.1
Stegastes variabilis	*Stegastes variabilis*	GenBank	JQ841972.1	KM077204.1
Thalassoma noronhanum	*Thalassoma noronhanum*	GenBank	JQ839625.1	AY328876.1
Xyrichtys martinicensis	*Xyrichtys martinicensis*	GenBank	JQ839657.1	U92005.1

Table S2. Community trait weighted mean (CWM) for each state of the six functional traits evaluated in Northeast Brazil. We compared all attributes between shallow and deep reefs using one-way Wilcox-tests. Seven trait states were significantly different between depth categories. Level of significance (*p*): *< 0.05.

Trait	State	CWM average		U	*p*	
		Shallow (min, max)	Deep (min, max)			
Water column position	Benthic	0.05 (0, 0.14)	0.2 (0.03, 0.8)	27.5	0.028	*
	Benthopelagic	0.9 (0.86, 1.0)	0.7 (0.15, 0.96)	103	0.999	
	Pelagic	0.01 (0, 0.03)	0.12 (0, 0.62)	32.5	0.049	*
Habitat use	Specialist	0.17 (0, 0.7)	0.08 (0, 0.58)	63	0.71	
	Intermediate	0.18 (0.08, 0.3)	0.31 (0.01, 0.76)	43.5	0.21	
	Generalist	0.65 (0.18, 0.93)	0.61 (0.24, 0.91)	61	0.65	
Body size	0 - 7 cm	0.01 (0, 0.09)	0.005 (0, 0.03)	45.5	0.19	
	7.1 - 15 cm	0.25 (0, 0.73)	0.14 (0, 0.57)	56	0.76	
	15.1 - 30 cm	0.48 (0.11, 0.66)	0.27 (0.01, 0.61)	83	0.97	
	30.1 - 50 cm	0.23 (0, 0.51)	0.41 (0.08, 0.87)	36	0.092	
	50.1 - 80 cm	0.006 (0, 0.028)	0.08 (0, 0.53)	27.5	0.025	*
	> 80 cm	0.02 (0, 0.11)	0.1 (0, 0.41)	17	0.004	*
Mobility	High mobility	0.007 (0, 0.036)	0.06 (0, 0.26)	33.5	0.057	
	Roving	0.89 (0.66, 1)	0.89 (0.71, 1)	58.5	0.58	
	Sedentary	0.11 (0, 0.33)	0.05 (0, 0.21)	72.5	0.27	
Trophic category	Herbivore	0.24 (0, 0.61)	0.19 (0, 0.5)	67	0.78	
	Macro carnivore	0.096 (0, 0.011)	0.19 (0.05, 0.49)	29	0.035	*
	Macro invertivore	0.56 (0.16, 0.76)	0.47 (0.09, 0.87)	64.5	0.73	
	Omnivore	0.01 (0, 0.067)	0.03 (0, 0.136)	42	0.17	
	Planktivore	0.05 (0, 0.33)	0.07 (0, 0.21)	31	0.044	*
	Small invertivore	0.03 (0, 0.07)	0.04 (0, 0.14)	45.5	0.25	
Larval dispersion	Balistidae type	0.014 (0, 0.06)	0.015 (0, 0.07)	50	0.34	
	Brooding	0 (0, 0)	0.0004 (0, 0.006)	52	0.25	
	Demersal eggs	0.11 (0, 0.3)	0.075 (0, 0.24)	64	0.72	
	Pelagic eggs	0.88 (0.66, 1)	0.9 (0.71, 1)	48.5	0.32	
	Ovoviviparous	0 (0, 0)	0.0046 (0, 0.03)	28	0.011	*

5 CAPÍTULO III – CENTENARY SHIPWRECKS REVEAL THE LIMITS OF ARTIFICIAL HABITATS IN PROTECTING REGIONAL FISH DIVERSITY

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RESEARCH ARTICLE

Centenary shipwrecks reveal the limits of artificial habitats in protecting regional reef fish diversity

Aline P. M. Medeiros[1] | **Beatrice P. Ferreira**[2] | **Ricardo Betancur-R**[3,4] | **Aiara P. L. R. Cardoso**[1] | **Marcello R. S. B. C. Matos**[1] | **Bráulio A. Santos**[5]

[1]Programa de Pós-Graduação em Ciências Biológicas, Universidade Federal da Paraíba, Cidade Universitária, João Pessoa, Brazil

[2]Departamento de Oceanografia, Centro de Tecnologia, Universidade Federal de Pernambuco, Cidade Universitária, Recife, Brazil

[3]Department of Biology, The University of Oklahoma, Norman, OK, USA

[4]Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA

[5]Departamento de Sistemática e Ecologia, Centro de Ciências Exatas e da Natureza, Universidade Federal da Paraíba, Cidade Universitária, João Pessoa, Brazil

Correspondence
Bráulio A. Santos
Email: braulio@dse.ufpb.br

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Abstract

1. The sinking of artificial structures has become increasingly common around the world, but whether the artificial structures favour or disfavour fish diversity remain under debate. Sinking may empty the nearby natural reefs locally and regionally by attracting their biota. Conversely, it may improve environmental conditions for species survival and reproduction, acting as source of diversity at the local and regional levels.
2. We tested these contrasting hypotheses by assessing the taxonomic, functional and phylogenetic diversity of 12 fish communities in Northeast Brazil: four ageing (>100-year-old) shipwrecks and eight surrounding natural reefs at comparable depths and distances. We partitioned the gamma diversity of artificial and natural reef communities into independent alpha and beta components, accounted for species' abundance and assessed whether beta patterns were mostly driven by spatial turnover or nestedness.
3. We recorded 6,335 individuals distributed in 88 fish species and 38 families. While artificial and natural reefs shared 50 species (57%), 21 species (24%) were exclusive to the artificial reefs, suggesting that the nearby natural reefs—the most likely original source of these exclusive species—do not harbour them anymore. Alpha diversity of typical and dominant species did not significantly differ between the reef types, but alpha diversity of rare species was taxonomically, functionally and phylogenetically higher in artificial reefs, indicating positive effects of the structures at the local scale.
4. By contrast, regional beta diversity was higher in natural reefs in terms of taxonomic and functional diversity, regardless of species abundance. Pairwise beta diversity indicated that turnover had a large effect on the compositional dissimilarity in both reef types, whereas nestedness was almost irrelevant in artificial reefs.
5. *Synthesis and applications*. Artificial structures such as shipwrecks may promote the co-occurrence of rare species, but they are unable to produce the beta diversity patterns that natural reefs do, even following many decades of colonization. Although artificial habitats host a significant portion of the regional reef fish diversity, they may have also contributed to the degradation of nearby natural reefs.

We recommend the establishment of regulated diving spots, fishing grounds and no-take areas as a strategy to conserve regional fish diversity.

KEYWORDS
Atlantic, beta diversity, Brazil, functional diversity, Hill numbers, phylogenetic diversity, reef fishes, species diversity

1 | INTRODUCTION

As human activities sprawl over natural ecosystems and transform biomes into anthromes (Ellis et al., 2010), countless artificial structures are left behind or intentionally introduced in the altered ecosystems (Davis et al., 1982; Lynn et al., 2021; Northrup et al., 2021). These artificial structures vary enormously in terms of their composition, size, shape, location, density, age, origin, polluting potential and residence time in nature. Examples are energy towers in pristine forests, abandoned roads in agroecosystems, buried war explosives, lost fishing tackles, sunken vessels and aircrafts on ocean floor and entire cities inundated by artificial freshwater reservoirs. The structures may be beneficial to some species and detrimental to others. Additionally, they can disrupt species interactions, favour biological invasion and create novel ecosystems (Connell & Glasby, 1999; Manzotti et al., 2020; Mercader et al., 2019; Palmer et al., 2010). From an ecological perspective, it is critical to understand how these structures interact with the remaining biota and the spatial and temporal scales at which their positive and negative effects disappear.

The impact of artificial habitats on ecosystems has attracted particular attention among marine and freshwater ecologists (Bohnsack, 1989; Carr & Hixon, 1997; Folpp et al., 2013; Grossman et al., 1997). In marine ecosystems, artificial structures have been deliberately submerged for the establishment of marine aquafarms, fishing zones, tourism sites, oil and gas exploitation, among other goals. Accidental collision, unsuitable conditions for navigation, human and mechanical failures have also resulted in the unplanned sinking of artificial structures in marine environments (Cardoso et al., 2020). The Mediterranean Sea, for instance, has 4% of the world's sunken wrecks (i.e. thousands of vessels, aircrafts and other commercial and military devices), which date back to Second World War and still promote uncontrolled leakage of toxic material and organic/inorganic pollutants (Parliamentary Assembly of the Council of Europe, 2012). In other regions of the Mediterranean basin, the alliance between professional diving schools and Malta government has engaged in the intentional scuttling of decommissioned vessels at suitable locations for diving activities, making Malta as one of the most popular wreck-dive destinations in Europe (Consoli et al., 2015). In Northeast Brazil and other coastal regions where fish stocks have depleted, traditional fishermen illegally sink pieces of car, fridge and similar objects as their only alternative to attract the remaining fish schools (Araújo, 2017).

The ecological motivation behind fishermen and divers' decision is to increase the area of inhabitable space at the sea bottom, increase environmental heterogeneity and aggregate fishes around the artificial structures. Habitat limitation and complexity has long been one of the cornerstones of community ecology (Hortal et al., 2009; MacArthur & Wilson, 1967; Simpson, 1949; Tews et al., 2004). The higher the habitat complexity and heterogeneity, the higher the diversity an ecosystem can harbour (Bejarano et al., 2011; Galzin et al., 1994; Luckhurst & Luckhurst, 1978). Richness, abundance, biomass and trophic structure of fish communities, for instance, have been linked to the structural complexity of natural reefs, which provide shelter, refuge and foraging area at some stage of species development (Beukers & Jones, 1998; Böhm & Hoeksema, 2017; Brandl et al., 2018; Cowman et al., 2017; Darling et al., 2017; Davis & Smith, 2017; Rilov & Benayahu, 2000). Even within artificial reefs, more complex sites host more fish diversity than less complex sites (Cardoso et al., 2020). Furthermore, artificial reefs may reduce human pressure on natural reefs by serving as fishery enhancement tool and recreational diving spots (Bohnsack, 1989; Hall et al., 2021; Santos et al., 2013), potentially favouring fish diversity locally and regionally ('production hypothesis' sensu Wilson et al., 2001 and references therein).

An important factor that is typically not accounted for in the creation of artificial reefs is habitat selection (Mercader et al., 2019; Nicholls & Racey, 2006). By introducing artificial structures at the sea bottom, species from nearby natural habitats may leave them definitively and select a new environment to establish ('attraction hypothesis' sensu Wilson et al., 2001). This process is gradual and depends on the dispersal and colonization abilities of each species. It usually starts with a few immigrants in a source–sink dynamics, but if conditions at the new environment are better for survival and reproduction, the population of the old environment will gradually disappear (Leibold et al., 2004). Such change in spatial distribution is indeed the rule in nature, even for sessile organisms such as plants and corals, and may take decades to be detected (Bellard et al., 2012). In the long run, artificial reefs may silently degrade the surrounding reefs by 'stealing' their inhabitants. Furthermore, exotic invasive species may follow the same pathway and use the artificial reefs as stepping stones to spread their distribution over the natural

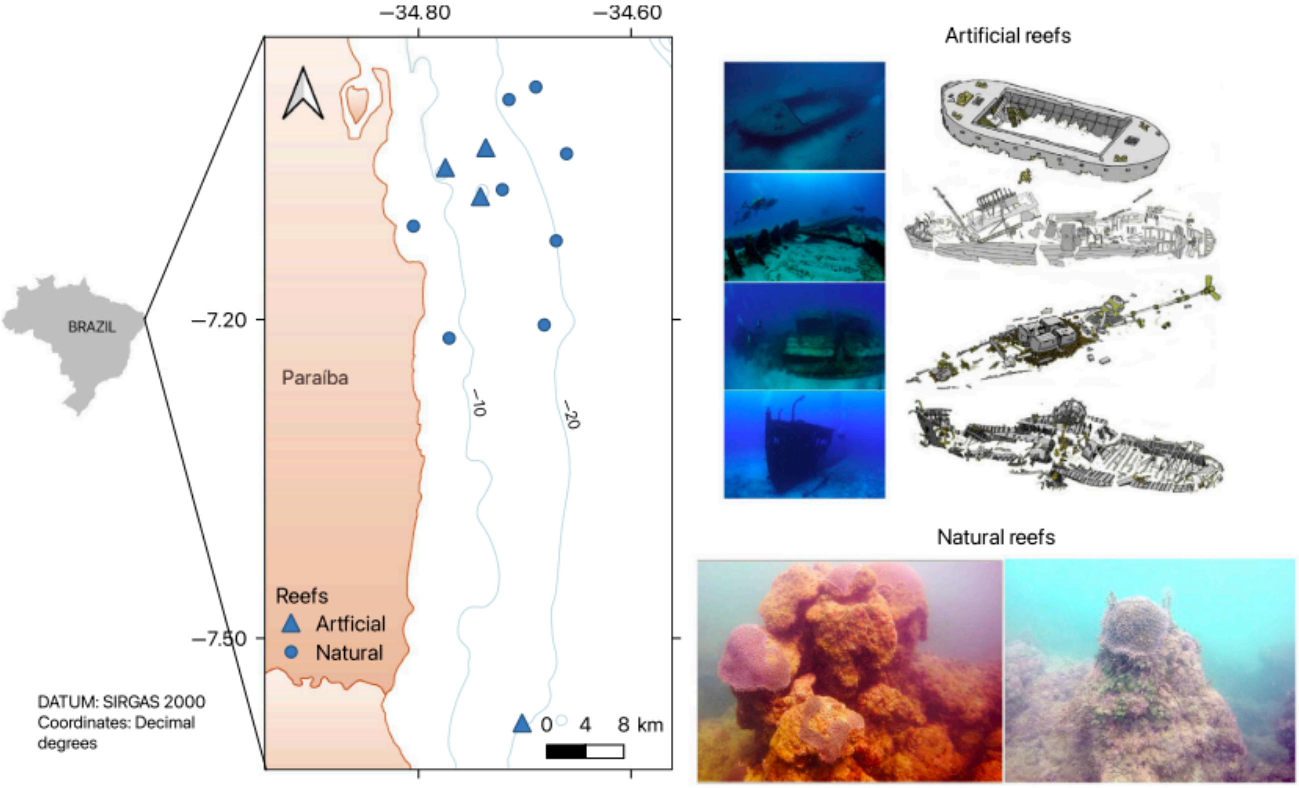

FIGURE 1 Study area in the continental shelf of Paraiba state, Northeast Brazil. Blue triangles and blue circles depict artificial and natural reefs respectively. Blue lines indicate bathymetric curves. Photographs of artificial reefs by Diego Luna and Max Glegiston, sketches by Maurício de Carvalho and Bertran Feitoza

reefs. Soares et al. (2020) have demonstrated the role of shipwrecks as a network of stepping stones for the sun coral *Tubastraea tagusensis* spread in the Atlantic Ocean, creating complementary paths for the invasiveness by overcoming physiological traits and the short life span of the coral larvae. Artificial structures may also favour the overexploitation of fishing stocks, drive species to local extinction and cause chemical pollution (Grossman et al., 1997), eroding diversity at both local and regional scales.

In this work, we compared four artificial and eight natural reefs of Northeast Brazil to test these divergent hypotheses on the role of artificial reefs on local and regional patterns of fish diversity. Our goal was to assess the hypotheses at the community level by comparing diversity and compositional patterns between artificial and natural reefs and complement the valuable studies that have been conducted at the population and individual levels (e.g. Brown-Peterson et al., 2021). These studies usually focus on the relative abundance of ontogenetic stages, biometrical, gonadal and/or larval data of target species to make natural versus artificial comparisons and draw conclusions for the species studied. Here, we employed a community-level approach aimed at partitioning the taxonomic, functional and phylogenetic gamma diversity into independent alpha and beta components (Jost, 2007). We classified the species into six complementary functional traits to examine the functional profiles of communities in artificial and natural reefs. We also calculated phylogenetic diversity based on a newly estimated phylogeny. If the artificial reefs favour diversity by providing new habitats for colonization ('production hypothesis'), we expect higher values of alpha and beta diversity in artificial reefs relative to natural reefs. We also expect that gamma diversity of artificial reefs is smaller than that of natural reefs, as all species, functions and linages found on the artificial structures are expected to come from natural reefs. In contrast, if the artificial reefs disfavour diversity by gradually subtracting individuals and species from the surrounding reefs ('attraction hypothesis'), we expect greater alpha diversity in artificial reefs (the same prediction from the 'production hypothesis'), but smaller beta diversity across the artificial structures as similar subsets of species will be attracted and establish in the man-made environment. Under this scenario, gamma diversity of artificial reefs should be similar or even greater than that of natural reefs.

2 | MATERIALS AND METHODS

2.1 | Study area

We conducted this study in the coast of Paraiba state, which is located in the Southwestern Atlantic region and the Northeastern Brazilian subprovince (sensu Pinheiro et al., 2018; between 7°0′0″S 34°50′0″W and 7°15′0″S 34°30′0″W; Figure 1). This subprovince is known for having a relatively short continental shelf (35 km wide), with rock-based reefs parallel to the coast line and break at around 70–75 m depth (Feitoza et al., 2005; Leão & Dominguez, 2000; Morais & Santos, 2018). Natural reefs are known for having benthic organisms such as calcareous algae, macroalgae and macrobenthos (i.e. Zoanthidae and sponges) associated with their three-dimensional structures (Honório et al., 2010). Coral cover is low, averaging 3.4% (0.3%–20%), while rock dominates the reef cover, averaging 38.9% (1.4%–79.5%; Morais & Santos, 2018). Water temperature varies from 23 to 30°C up to 50 m depth, and visibility ranges from 20 to 50 m (Feitoza et al., 2005; Maida & Ferreira, 1997; Rocha, 2003).

2.2 | Data survey

We surveyed 12 reefs ranging from 9.1 to 30 m mean depth (Figure 1). Reefs were categorized into artificial and natural (see Table 1; Table S1; Medeiros, Ferreira, Betancur-R, et al., 2021 for details on reef description). Natural reefs were selected based on proximity of their artificial counterparts to ensure similar environmental features (e.g. depth range). The reef fish communities were sampled with diurnal SCUBA dives in 2015, 2017 and 2018 (one dive per reef, see details in Table S1). During this period, both types of reef were sampled as permitted by navigation conditions. Sampling effort was measured as the total time recorded for each reef area (Table S1). We recorded the fish community from each artificial and natural reef at approximately 1 m above the bottom using high-resolution videos (GoPro Hero 4), and following the browsing trajectory methodology (Mallet & Pelletier, 2014; Mallet et al., 2016; more details can be found in Cardoso et al., 2020; Medeiros, Ferreira, Betancur-R, et al., 2021). Assuming that each natural reef has different shapes and features (e.g. number of crevices), as well as each artificial reef has different conditions (e.g. shipwrecks dismantled or whole; see Table 1), recording times and trajectories were different as well (Table S1). To account for this, we standardized samples by completeness rather than size as recommend by Chao and Jost (2012), which is indeed the most reliable way of making statistical comparisons between communities (see also Cardoso et al., 2020; Medeiros, Ferreira, Betancur-R, et al., 2021). Next, we examined the videos to identify fish species and estimate their abundances. Abundance was measured as the maximum number of conspecifics seen simultaneously in the same frame (Barley et al., 2017; Lindfield et al., 2016).

After identifying each species to the lowest possible taxonomic level, we categorized them into six functional traits. These traits were chosen based on the complementary function they represent for ecosystem processes, including habitat use, food acquisition, mobility, nutrient budget and reproduction strategies (see Villéger et al., 2017). We classified the traits as follows: (a) water column position trait (benthic, pelagic and benthopelagic states); (b) habitat use (generalist, intermediate generalist and specialist); (c) body size based on total length reported in literature (0–7 cm; 7.1–15 cm; 15.1–30 cm; 30.1–50 cm; 50.1–80 cm; >80 cm); (d) mobility (high mobility, roving and sedentary); (e) trophic categories (herbivore, macro carnivore, macro invertivore, small invertivore, omnivore and planktivore); and (f) spawning mode (Balistidae type, brooding, demersal eggs, pelagic eggs and ovoviviparous). We obtained functional trait data from the study by Pinheiro et al. (2018, available at https://swatlanticreeffishes.wordpress.com) and complemented it with our own field records (e.g. water column position).

Prior to measuring phylogenetic diversity, we estimated a community-based phylogenetic tree including 83 of the 86 teleost fish species recorded in artificial and natural reefs (Figure 2). We used a multi-locus phylogenetic tree of ray-finned fishes dated with multiple fossil calibration points, which comprised 1,661 species, as a backbone tree for this analysis (Betancur-R et al., 2017). First, we retrieved *cytochrome oxidase subunit I* (COI) and *cytochrome b* (Cytb) sequences for the target taxa from NCBI, and aligned the sequences using MUSCLE v3.8.425 (Edgar, 2004) as implemented in Geneious Prime 2019.1.1 (https://www.geneious.com). Of the 83 target species with COI and/or Cytb data, 29 were previously placed in the backbone tree (accession numbers are given in Table S2). Our goal was to obtain phylogenetic placement for the remaining, previously unexamined 54 species. The community-based phylogenetic tree inferred for this study was estimated after implementing a series of quality-control steps to avoid misidentifications or

TABLE 1 General characteristics of the four shipwrecks classified as artificial reefs in this study and located along the coast of Paraiba, Northeast Brazil (Cardoso et al., 2020; Carvalho & Accioly, 2019; Oliveira, 2010)

General characteristics	Alice	Alvarenga	Queimado	Vapor Bahia
Type of vessel	Steamship	Barge	Steamship	Steamship
Material	Steel	Iron	Wood and metal	Iron
Condition	Dismantled	Whole	Dismantled	Dismantled
Year sunk	1911	1926	1873	1887
Distance from the coast (nmi)	3.5	6	5	8
Overall length (m)	53	20	103	80
Greatest breadth (m)	6.7	5	13	10
Depth (m)	7–12	18–20	12–18	18–25

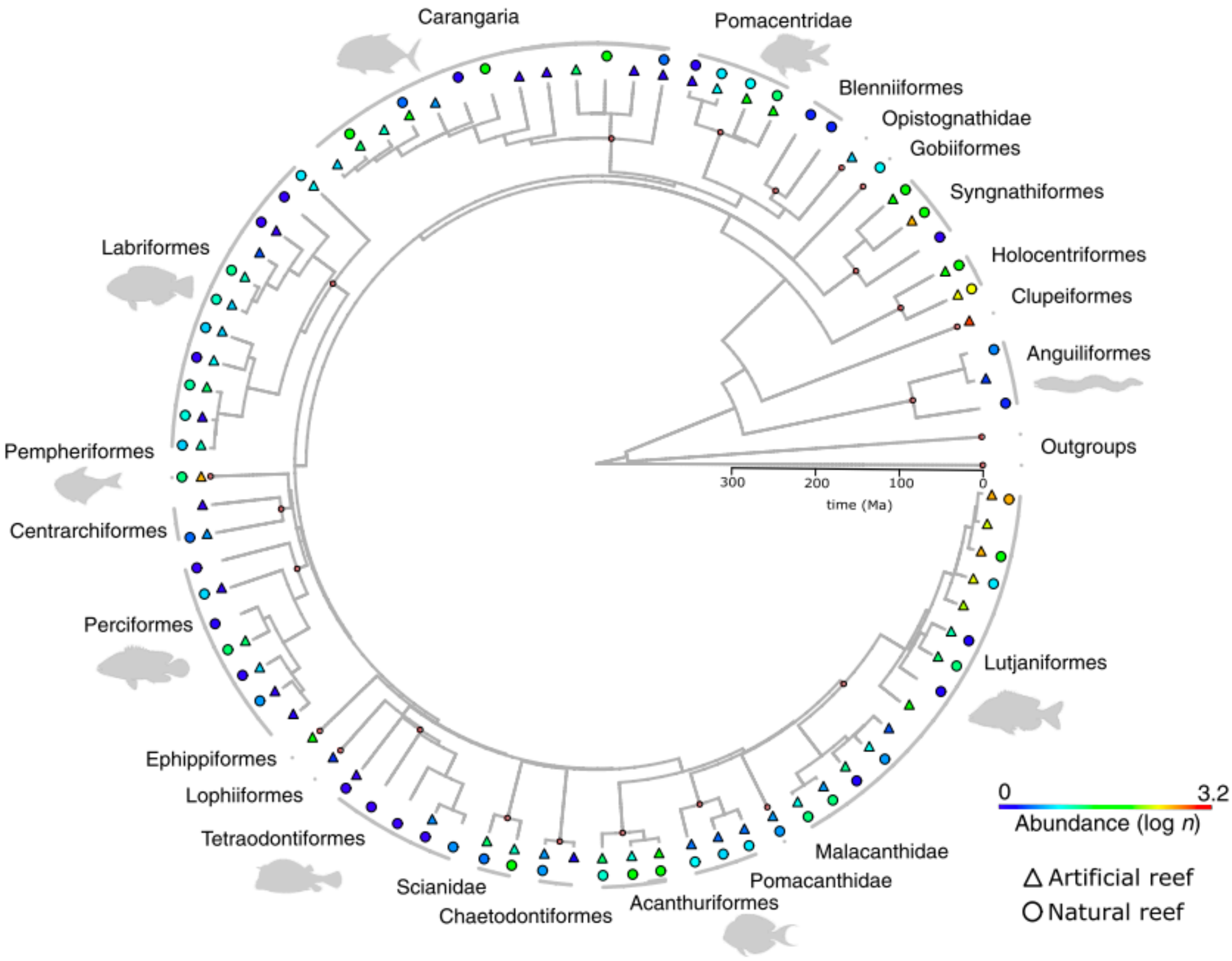

FIGURE 2 Time-calibrated phylogeny encompassing 83 of the 88 species recorded in this study. Internal red nodes indicate taxonomic annotations (e.g. family, order) clades of Teleostei and the two outgroups. Triangle and circle symbols represent whether the species was registered in artificial and natural reefs respectively; symbol colour indicates species' log-transformed abundance

any discrepancies in sequence selection (see Medeiros, Ferreira, Betancur-R, et al., 2021). Two elasmobranchs and three teleosts recorded in our survey, which accounted for 0.3% of the total abundance registered, were not included in the community-based tree. We also replaced two taxonomic entities registered herein, and not identified as species, with confamiliars/congeners that had sequence data available in NCBI (see details in Table S2). Then, we performed backbone-constrained maximum likelihood (ML) searches in RAxML v8.1.20 using by-codon partitions and 10 independent iterations (Stamatakis, 2006; Stamatakis et al., 2008). Next, the resulting ML phylogram was time-calibrated using secondary calibrations, extracted from the reference backbone tree via 'congruification' (Eastman et al., 2013) and used in TreePL v1.0 to date our phylogenetic tree (Smith & O'Meara, 2012). We then pruned the resulting tree to retain the 83 target species using the R package PHYTOOLS (Revell, 2012), which was used for downstream phylogenetic diversity estimations.

2.3 | Diversity estimation

Prior to diversity estimation for artificial and natural reefs, we standardized the 12 reefs by sample coverage rather than size (Chao & Jost, 2012). This way, sample coverage was measured for each reef and for both artificial and natural reef categories using the formulae:

$$\hat{C}_n = 1 - \frac{f_1}{n}\left[\frac{(n-1)f_1}{(n-1)f_1 + 2f_2}\right],$$

where f_1 and f_2 represent the singletons (i.e. species in which only one individual was recorded) and doubletons (i.e. species in which two individuals were recorded) in the sample, respectively, and n is the original sample size (total fish abundance in each reef). Sample coverage ranged from 72 to 99% (mean value 91%) when each reef was analysed separately and was nearly complete when reefs were analysed in both artificial and natural categories (99.7 and 99% respectively) (Table S1). Sample coverage was estimated using the R package INEXT (Hsieh et al., 2016).

Gamma and alpha diversity of species, functions and lineages (i.e. taxonomic, functional and phylogenetic diversity) was measured using Hill numbers (Hill, 1973), which quantify diversity in units of equivalent numbers of equally abundant species (Gotelli & Chao, 2013). The equations allow to weight species abundance exponentially by a q factor and satisfy the mathematical replication principle (Chao et al., 2014; Jost, 2010).

Gamma and alpha taxonomic diversity of order q were calculated following the equation:

$$D^q \left(\sum_{i=1}^{S} p_i^q \right)^{1/(1-q)},$$

where S represents the number of fish species in a reef, p_i is the abundance of the ith species and q is the order that controls the sensitivity to species abundance. When $q = 0$ (^0D), all abundances return to 1 and the index is equivalent to species richness (also known as the diversity of rare species); when $q = 1$ (^1D), the index keeps the relative abundance of each species and describes the diversity of typical species; when $q = 2$ (^2D), all abundances are squared, favouring the more abundant species and expressing the diversity of dominant species (Chao et al., 2014).

Alpha and gamma functional diversity are expressed as the total functional distance between the pairs of species in the community and is measured as:

$$\mathrm{FD}(Q)^q = \left[\sum_{i=1}^{S} \sum_{j=1}^{S} d_{ij} \left(\frac{pipj}{Q} \right)^q \right]^{1/(1-q)},$$

where d_{ij} corresponds to the functional distance (Gower distance matrix herein) between the ith and jth species, $p_i p_j/Q$ represents the Rao's quadratic entropy and q weights the species abundances (Chao et al., 2014; Chiu & Chao, 2014). Functional diversity is based on the functional distance built from all traits and their states. To identify which state of each trait differed between artificial and natural reefs, we estimated the community-weighted trait means (CWM hereafter). CWM corresponds to the mean values of each trait state in the community weighted by their abundance (Lavorel et al., 2008).

Alpha and gamma phylogenetic diversity, expressed as the effective number of maximally distinct lineages over a time interval (Chao et al., 2010), was also quantified under the Hill number framework (Chao et al., 2014) as follows:

$$\mathrm{PD}(T)^q = \left\{ \sum_{i \in \boldsymbol{B}_T} L_i \left(\frac{a_i}{T} \right)^q \right\}^{1/(1-q)},$$

where L_i represents the length (or duration) of branch i in the set B_T, a_i is the overall abundance descended from branch i and q weights the species abundances.

Beta diversity was estimated using two different mathematical approaches that yield different aspects of the spatial patterns shaping fish communities. The first approach, regional beta diversity, is given for N sites, considering rare (^0D), typical (^1D) and dominant (^2D) species (Jost, 2007; Jost et al., 2010). A single value is calculated for each type of reef. For the taxonomic regional beta diversity, for instance, the value expresses the effective number of completely distinct communities in the region. The same rationale applied to the functional and phylogenetic regional beta diversity (Chao et al., 2014). We used regional beta diversity to construct the taxonomic, functional and phylogenetic beta profiles of artificial and natural reefs for rare (^0D), typical (^1D) and dominant (^2D) species.

The second approach, pairwise beta diversity, considers the partition of the overall beta into its nestedness and turnover components for every pair of reefs (see details in Baselga, 2010). In this regard, the regional beta measures the diversity itself, while the pairwise beta sheds light into the mechanisms underlying the spatial variation in diversity. To calculate the pairwise beta diversity, we used a presence/absence matrix for species recorded in artificial and natural reefs, which corresponds to Hill numbers taxonomic diversity of order ^0D. Diversity estimations for alpha, beta and gamma were performed in R using the packages ENTROPART for taxonomic diversity (Marcon & Hérault, 2015), HILLR for phylogenetic diversity (Chao et al., 2014) and *betapart* for pairwise beta (Baselga et al., 2018). The function to estimate functional diversity, implemented in R, is available in the study by Chiu and Chao (2014).

Finally, we performed nonparametric Wilcoxon tests to check whether alpha diversity metrics of the three dimensions and the components of pairwise beta diversity, nestedness and turnover differed between artificial and natural reefs. We also used a non-metric multidimensional scaling based on Bray–Curtis dissimilarity index and an analysis of similarity to explore compositional differences between the reef types. This analysis is presented as Supporting Information. Natural versus artificial comparisons of gamma and regional beta diversity did not require statistical tests as only one value is given for these metrics.

3 | RESULTS

We recorded 6,335 individuals distributed in 88 fish species and 38 families (Table S3). The 10 most representative families were Haemulidae (9 species), Carangidae (8), Labridae (6), Labridae: Scarinae (6), Serranidae (6), Pomacentridae (4), Lutjanidae (5), Acanthuridae (3), Pomacanthidae (3) and Muraenidae (3). Seven species represented 70% of individuals: *Haemulon squamipinna* (26%), Clupeidae sp. (14%), *Haemulon aurolineatum* (8%), *Pempheris schomburgkii* (8%), *Mulloidichthys martinicus* (8%), *Holocentrus adscensionis* (5%) and *Haemulon plumieii* (4%). In terms of spatial distribution, 50 species occurred in both artificial and natural reefs, while 21 species occurred only in artificial reefs and 17 only in natural reefs (Table S3). Seven species were listed in the IUCN Red

List (Table S3), including *Scarus trispinosus* (endangered) and other three Scarinae species (vulnerable), *Ginglymostoma cirratum* (vulnerable), *Elacatinus figaro* (vulnerable; recorded only in natural reefs) and *Epinephelus itajara* (vulnerable; recorded only in artificial reefs). No non-indigenous or invasive were recorded.

3.1 | Gamma diversity

Gamma diversity of rare, typical and dominant species produced contrasting results, with artificial reefs showing greater diversity of rare species and smaller diversity of typical and dominant species than their natural counterparts (^0D Gamma$_{\text{Artificial}}$ = 71 vs. Gamma$_{\text{Natural}}$ = 67; ^1D Gamma$_{\text{Artificial}}$ = 17.6 vs. Gamma$_{\text{Natural}}$ = 23.3; and ^2D Gamma$_{\text{Artificial}}$ = 10.9 vs. Gamma$_{\text{Natural}}$ = 13.7). Following the same trend, gamma functional diversity was higher in artificial reefs for ^0D (Gamma$_{\text{Artificial}}$ = 2,519 vs. Gamma$_{\text{Natural}}$ = 2,274) and ^2D (Gamma$_{\text{Artificial}}$ = 42 vs. Gamma$_{\text{Natural}}$ = 37), but smaller for ^1D (Gamma$_{\text{Artificial}}$ = 113 vs. Gamma$_{\text{Natural}}$ = 126). Conversely, gamma phylogenetic diversity was consistently higher for artificial reefs in all scenarios (^0D Gamma$_{\text{Artificial}}$ = 3,867 vs. Gamma$_{\text{Natural}}$ = 3,666; ^1D Gamma$_{\text{Artificial}}$ = 815 vs. Gamma$_{\text{Natural}}$ = 729; and ^2D Gamma$_{\text{Artificial}}$ = 528 vs. Gamma$_{\text{Natural}}$ = 435). Although taxonomic and functional diversity showed contrasting results within their typical and dominant species levels, the overall gamma diversity showed higher values in artificial than natural reefs, which supports the 'attraction hypothesis'.

3.2 | Alpha diversity

The average effective number of rare (^0D) species was greater in artificial than natural reefs for the three types of diversity measured: taxonomic ($U = 30$, $p = 0.021$), functional ($U = 30$, $p = 0.022$) and phylogenetic ($U = 30$, $p = 0.022$) (Figure 3), supporting both hypotheses. The functional diversity varied more within the reef types than between them (Figure 3), with no statistical difference between artificial and natural reefs. When we analysed the data separately by functional trait, differences between the reef types raised for five trait states (Table S4). Significant traits included water column position, mobility, trophic category and larval dispersion, which helped to build a functional profile highlighting the differences between artificial and natural reefs (Figure S1). Artificial reefs showed a greater abundance of pelagic ($U = 31$, $p = 0.012$), planktivore ($U = 29$, $p = 0.031$), high mobility species ($U = 31$, $p = 0.012$), and also of species that produce pelagic larvae ($U = 29$, $p = 0.034$). Conversely, natural reefs harboured a higher abundance of herbivore species ($U = 3$, $p = 0.034$) (Figure S2).

3.3 | Beta diversity

Taxonomic and functional regional beta diversity were higher in natural than artificial reefs (Figure 4), supporting the 'attraction hypothesis'. In the natural reefs, rare, typical and dominant species showed similar levels of beta diversity, with values around 3.0–3.5 completely distinct communities (Figure 4). Regional beta diversity of species in artificial reefs produced a similar trend, but with values oscillating around 1.6–2.0 completely distinct communities. These same trends were observed for functional regional beta diversity, indicating that large aggregations or solitary fishes of natural reefs are not only more taxonomically distinct than those of artificial reefs, but also have different functional profiles (Figure 4).

The phylogenetic regional beta profile revealed a higher beta diversity for rare species in natural reefs, but similar values for typical and dominant, suggesting that typical and dominant species are phylogenetically more similar than rare species. The phylogenetic profile also indicated that large aggregations belong to close evolutionary lineages in both reef types, while solitary fishes tend to belong to more distant related lineages in natural reefs.

When the pairwise beta diversity of species was decomposed into nestedness and turnover components, the spatial variation in species composition was more explained by turnover than nestedness for both artificial and natural reefs (Figure 5; see also Figure S1 for a classical NMDS ordination with the 12 reefs). In artificial reefs, turnover accounted on average for 0.49, while nestedness accounted for only 0.02 of the overall beta diversity (Figure 5). Natural reefs produced similar pairwise beta outcomes, with turnover averaging 0.57 and nestedness 0.21 (Figure 5). Considering the median values of overall pairwise beta diversity, the natural reefs (0.62) were about 50% more diverse than the artificial ones (Figure 5), reinforcing the pattern of regional homogenization across the artificial structures and the 'attraction hypothesis'.

4 | DISCUSSION

Following more than a century of shipwreck colonization, our findings support only a few predictions from the 'production hypothesis' and numerous predictions from the 'attraction hypothesis'. Locally, the artificial reefs do have the potential to host a greater diversity of species, functions and lineages of rare fishes than the natural reefs currently do. They also exhibit similar levels of local diversity considering typical and dominant species, indicating that their attractiveness is a community-wide phenomenon (Rilov & Benayahu, 2000; Tews et al., 2004; Zhang et al., 2021). If one stops the interpretation at this stage (local scale) and ignores what happens in the surrounding seascape, the conclusion is that sinking artificial reefs is beneficial to fish diversity. However, when we interpret the patterns of beta and gamma diversity, we conclude the contrary. The shipwrecks are taxonomically and functionally more homogeneous to each other than the natural reefs are. They show greater values of gamma diversity for many taxonomic, functional and phylogenetic metrics, which was likely constructed at the expense of the natural reefs (Bohnsack, 1989; Consoli et al., 2015). Furthermore, a quarter of their species does not occur in the nearby natural reefs. As we discuss below, the success of shipwreck colonization at the local

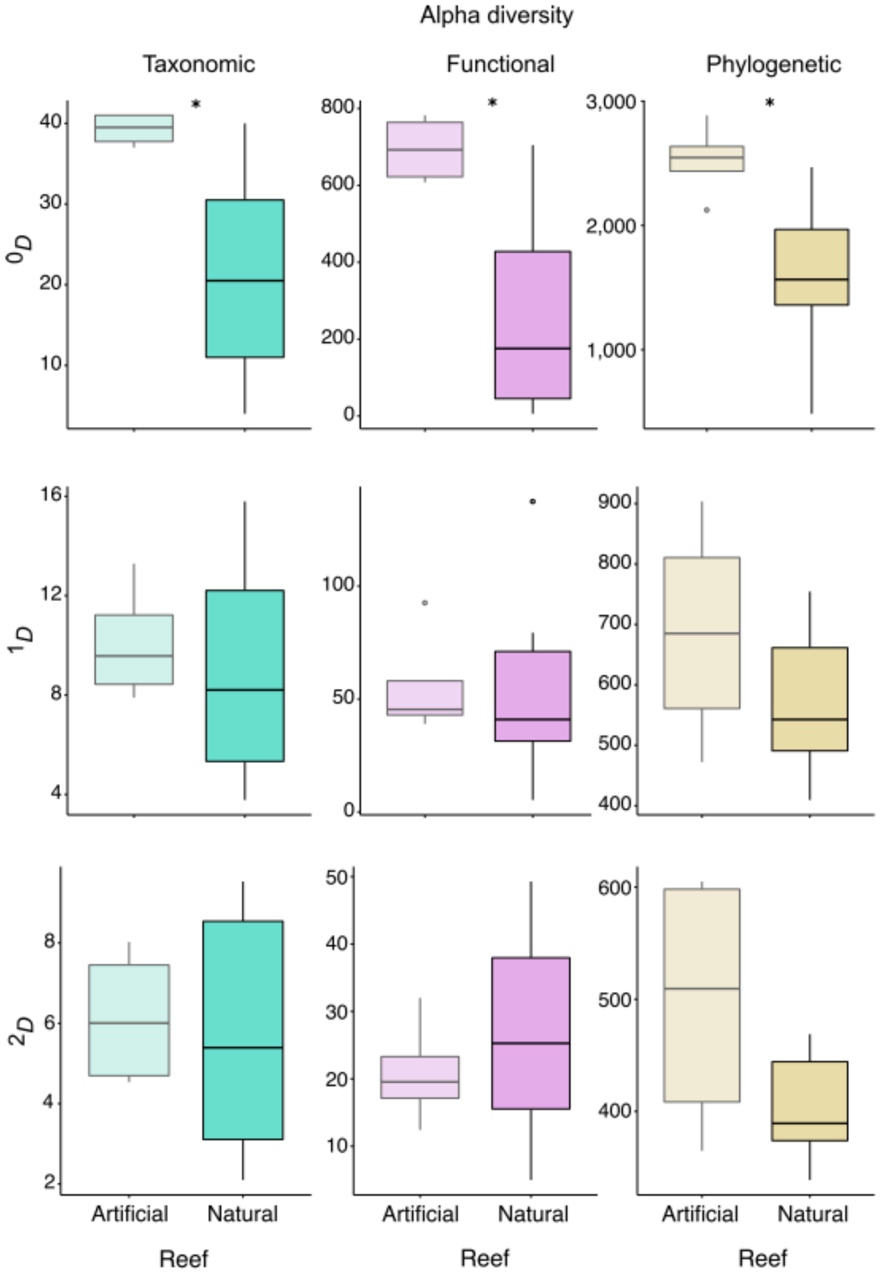

FIGURE 3 Alpha taxonomic, functional and phylogenetic diversity of rare (^{0}D), typical (^{1}D) and dominant (^{2}D) fish species between artificial ($n = 4$) and natural ($n = 8$) reefs distributed along the coast of Paraiba, Northeast Brazil. Median is shown as the horizontal line within the box; lower and upper ends of the box define the first and third quartiles respectively; whiskers represent the interquartile range and circular dots indicate extreme values. Significant differences between reef types are indicated by asterisks ($p < 0.05$)

scale has possibly triggered a silent degradation of the surrounding natural reefs.

To understand this process and do not totally attribute the degradation of natural reefs to the shipwrecks, we should go back to 1873–1926, when the four vessels accidentally became part of the study region (Oliveira, 2010). At that moment, the natural reefs were virtually pristine and provided the majority, if not all, the species that compose the shipwreck fish communities. The three-dimensional shape and complex physical structure of the vessels offered suitable conditions for the establishment of dozens of invertebrate and vertebrate species over the subsequent decades, increasing the density of species per unit of volume (Zhang et al., 2021). The cryptic, rare fish species benefited even more from the new artificial conditions (Brandl et al., 2017). During the early 1960s, the naturalist Jacques Laborel pioneered the study of the Brazilian reefs, examining the ecology, evolution and biogeography of the coral reef communities. The natural reefs of our study region, which was among the Laborel's diving spots, were firstly described in their original, conserved shape (see p. 59 of Laborel, 1970, traduced from French to Portuguese by Laborel-Deguen et al., 2019). After his work, the coastal city of João Pessoa—capital of Paraiba state—and vast sugarcane plantations rapidly expanded over the Atlantic forest and increased pressure on the marine ecosystems (Stevens, 2014), exponentially incrementing the exploitation of fishery resources and the agricultural, industrial and urban runoff into the sea. From 2000s and on, and especially in the last decade, mass tourism in the shallowest reefs located near the urban beaches of João Pessoa have accelerated and imposed additional pressure to the remaining marine biota (Medeiros

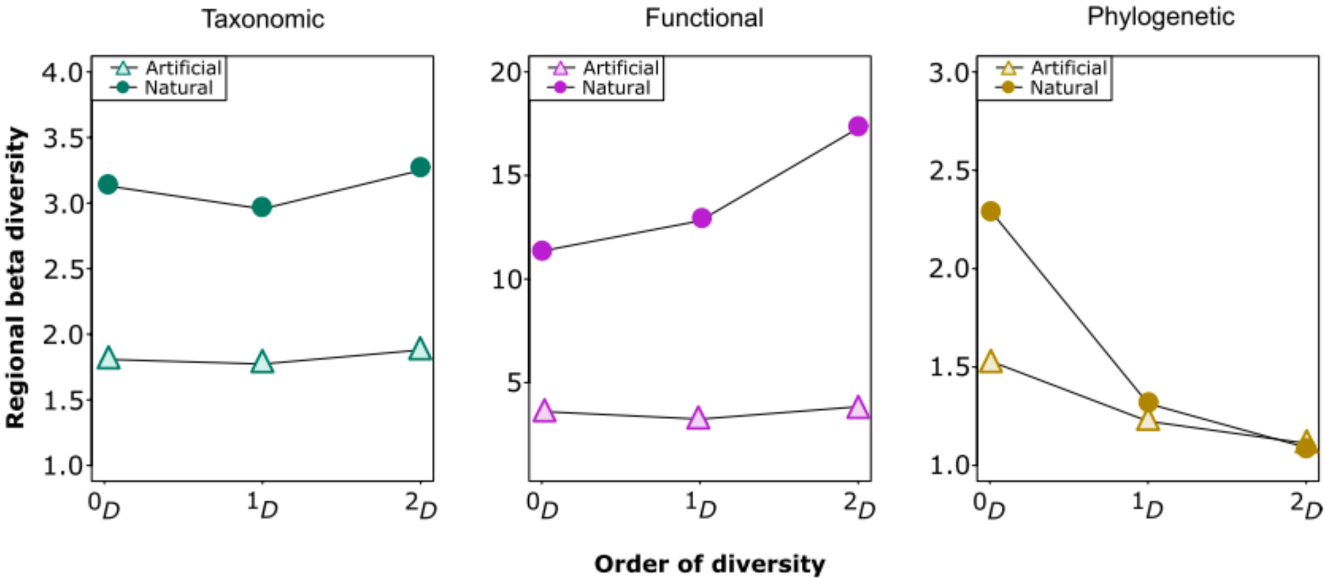

FIGURE 4 Profiles of taxonomic, functional and phylogenetic regional beta diversity of rare (^{0}D), typical (^{1}D) and dominant (^{2}D) fish species recorded in artificial ($n = 4$) and natural ($n = 8$) reefs distributed along the coast of Paraiba, Northeast Brazil

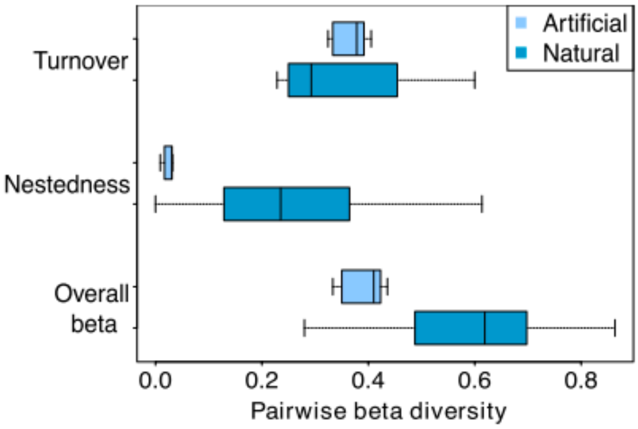

FIGURE 5 Pairwise beta diversity of artificial ($n = 4$) and natural ($n = 8$) reefs decomposed into turnover and nestedness components. Vertical bars inside each horizontal boxplot represent the median values; left and right limits of each box represent the first and third quantiles respectively; left and right error bars indicate 95% confidence interval. Overall beta refers to the sum of turnover and nestedness components. Reef types differ statistically in terms of overall beta and nestedness ($p < 0.05$)

et al., 2007). These impacts affected all reefs in our study region, including artificial and natural ones.

Overfishing, the most dangerous threat for fish diversity, followed the same trajectory and has not been restricted to the natural reefs (Floeter et al., 2006; Grossman et al., 1997). Local fishermen, artisanal or not, continue to fishing in the shipwrecks, just like they fish in the artificial structures they have illegally sunken in secret locations (Araújo, 2017). Unfortunately, there is no official database of fishing statistics in Paraiba that allows us to assess the potential confounding effects of fishing on our findings, but our experience in the region working with artisanal fishermen, public agents and diving professionals on marine conservation planning strongly suggests that both reef types are overexploited (see the 13-min documentary *Unidades de Mar* available for free with English subtitles at https://youtu.be/72w4b1ZVBDM). We hypothesize that even the shipwrecks were more diverse in the past, until the 1970s, when most relevant threats intensified. In this sense, the four artificial communities we have studied along with the eight surrounding natural communities are subsets from an impoverished regional pool that still sustains a considerable portion of the Southwestern Atlantic reef fish diversity (Cardoso et al., 2020; Medeiros, Ferreira, Alvarado, et al., 2021; Pinheiro et al., 2018). Coming decades are not optimistic if the levels of (de)protection and non-regulation remain (Bellwood et al., 2019; Hughes et al., 2017).

Taken this history into account, our findings do suggest that the shipwrecks have represented an additional source of degradation to the nearby natural reefs. Three points support our line of argument. First, from those 21 species that were exclusive to the shipwrecks, more than half have been previously reported in nearby natural reefs in the last decades (Feitoza et al., 2005; Honório et al., 2010), and six species were recently registered in other natural reefs of Paraiba coast (Medeiros, Ferreira, Alvarado, et al., 2021). Second, because they are all native and common in other reefs of Northeast Brazil (Freitas & Lotufo, 2015; Pinheiro et al., 2018; Soares et al., 2016), there is no reason to expect they were not present in the eight natural reefs since 1926 when the last vessel wrecked (i.e. no reason for their absence be treated as false negative). It is not a coincidence that the 21 species are absent exactly in the reefs surrounding the shipwrecks. Third, the greater gamma diversity values of artificial reefs could have not been achieved without taking species from the natural reefs, as the only entrance of species into the shipwreck communities is through immigration. We acknowledge that some species could have been imported from natural reefs other than the eight we sampled (via long-distance larval dispersal), but it is quite unlikely that this holds for a quarter of the 88 species recorded in our study. Altogether, these lines of evidence suggest that the artificial structures have contributed for degradation of fish diversity at their surrounding seascape.

Our analyses on the compositional dissimilarity and beta diversity patterns also reinforce the notion that the positive effects of shipwrecks are limited to the local (alpha) scale. There are numerous examples in the literature showing how species composition of artificial structures differ from those of nearby natural ecosystems (Burt et al., 2009; Clynick et al., 2008; Clark & Edwards, 1999; Folpp et al., 2013, 2020; Rilov & Benayahu, 2000). Our study supports these previous works by demonstrating that the communities established in the artificial structures diverge taxonomically and functionally from the natural communities of the original ecosystem. Although spatially close, artificial and natural reefs shared only 57% of their species. Fortunately, the shipwreck communities maintain similar levels of phylogenetic beta diversity when compared to their natural counterparts, but the benefits for conservation at larger spatial scales finish here. If we are interested in fully conserving the original diversity of reef fishes, we must protect the natural reefs, develop techniques to restore them and leave the sinking of artificial structures as the last strategy and with specific goals [but see Folpp et al. (2020) and Rilov and Benayahu (2000) for contrasting recommendation in estuaries and Rilov & Benayahu (2000) for restoration of reef areas respectively].

The role of spatial turnover in determining the beta diversity patterns across the study region also calls attention for going beyond the interpretation of what happens at the local scale. When turnover is more important than nestedness—our case—the regional diversity is spread across the region instead of being concentrated in particular sites (Baselga, 2010). This pattern emerges because species are sorted across space according to site's environmental quality, which must be suitable for survival and reproduction (Leibold et al., 2004). If some immigrants from a colonized site arrive at a new uncolonized site, but conditions (biotic and abiotic) are not suitable for the establishment of a new population, colonization fails. The new site results in a sort of ecological trap that invalidates the immigration event and disrupts the source–sink dynamics, precluding the expansion of species' geographic distribution and increasing compositional dissimilarity across sites (Baselga, 2010; Bellard et al., 2012; Leibold et al., 2004). In the long run, both sites will account for a unique portion of the regional diversity, making each site equally important for the structure of the fish metacommunity. In practical terms, the greater importance of turnover indicates that any attempt to manage or conserve the shipwrecks or the natural reefs should encompass them all and not being focused on one or another (Medeiros, Ferreira, Betancur-R, et al., 2021; Morais & Santos, 2018).

In summary, our findings indicate that artificial structures such as centenary shipwrecks have limits as a long-term repository of marine fish diversity. Their benefits at the local scale may hide disadvantages at the regional level. The deliberate sinking of new artificial structures at the sea bottom should be done with caution after exhausting all possibilities of conserving and restoring the natural reefs (Carr & Hixon, 1997; Manzotti et al., 2020). Artificial reefs should not be implanted close to natural reefs, rocky shores or in islands with pristine reef ecosystems. The federal government of Brazil is following the opposite direction and putting in place a large-scale project of sinking artificial structures. They plan to sink at least 73 vessels, aircrafts and other military devices in 15 regions, including the coast of Paraiba (Estadão, 2020). The criteria for choosing the sinking locations were not divulgated, neither the conservation status of the surrounding natural reefs. We strongly recommend a comprehensive analysis of the physical and biological conditions of the locations to estimate potential impacts on the remaining biota. That should be conducted as soon as possible, before sinking any structure. Regions with highly diverse and vulnerable communities, such as the oceanic islands, must not be part of the project as wreck-driven degradation of the natural reefs is likely to be immense. The same applies to regions with high susceptibility to biological invasion, where exotic invasive species have been already reported or are about to be reported (Soares et al., 2020). In the regions where sinking is technically possible, a permanent program of biodiversity monitoring should be implemented at each artificial structure and its surrounding seascape to estimate the level of degradation in nearby natural reefs and implement actions to revert it. This Brazilian initiative is not unique around the world (Fabi et al., 2011; Folpp et al., 2013). Thus, further studies should examine the generalization of our findings and recommendations in other countries.

As demonstrated in the Mediterranean Sea, despite their impact, shipwrecks may be included in management and conservation strategies (Renzi et al., 2017). Economic activities (e.g. diving tourism) can generate direct revenue of more than US$ 14 million per year (Zimmerhackel et al., 2019). This recreational activity can also benefit local businesses and work as financing mechanisms for conservation strategies (Vianna et al., 2018). On this regard, shipwrecks can be a useful source to increase revenue and mitigate the human pressure on natural reefs (Shani et al., 2012). Moreover, diversity, biomass and trophic structure have been negatively related to fishing pressure (Jennings et al., 1995). This way, the establishment of regulated fishing grounds and no-take zones may improve diversity and fish stocks (Tyler et al., 2011). In this sense, previously established artificial structures such as the shipwrecks in our study region could be used as diving spots and, possibly, fishing grounds for recreational activities since regulation policies were applied and monitored. Once properly managed, these reefs could contribute to maintain part of the regional taxonomic, functional and phylogenetic fish diversity.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

A.P.M.M. and B.A.S. conceived the ideas and designed the methodology; A.P.L.R.C., M.R.S.B.C.M., A.P.M.M. and B.A.S. collected the data; A.P.M.M. and B.A.S. analysed the data; A.P.M.M. and B.A.S. led the writing of the manuscript; A.P.M.M. and R.B.-R. assembled the gene data to phylogenetic inference. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via Dryad Digital Repository https://doi.org/10.5061/dryad.76hdr7sx6 (Medeiros, Ferreira, Betancur-R, et al., 2021).

ORCID

Aline P. M. Medeiros https://orcid.org/0000-0002-7272-4441
Beatrice P. Ferreira https://orcid.org/0000-0001-6315-9834
Brálio A. Santos https://orcid.org/0000-0001-6046-4024

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Centenary shipwrecks reveal the limits of artificial habitats in protecting regional fish diversity

Aline P. M. Medeiros[1], Beatrice P. Ferreira[2], Ricardo Betancur-R[3,4], Aiara P. L. R. Cardoso[1], Marcello R. S. B. C. Matos[1], Bráulio A. Santos[5]*

[1] Programa de Pós-Graduação em Ciências Biológicas, Universidade Federal da Paraíba, Cidade Universitária, Castelo Branco, 58051-900, João Pessoa, PB, Brazil

[2] Departamento de Oceanografia, Centro de Tecnologia, Universidade Federal de Pernambuco, Cidade Universitária, 50670-901, Recife, PE, Brazil

[3] Department of Biology, The University of Oklahoma, 730 Van Vleet Oval, Room 314, Norman, OK 73019, USA

[4] Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington DC 20560, USA

[5] Departamento de Sistemática e Ecologia, Centro de Ciências Exatas e da Natureza, Universidade Federal da Paraíba, Cidade Universitária, Castelo Branco, 58051-900, João Pessoa, PB, Brazil.

*****Corresponding author: braulio@dse.ufpb.br

S1 – Extended materials and methods

Table S1. Information on reef category, name, mean depth, sampling effort and sample coverage of each reef surveyed in the coast of Paraiba, Northeast Brazil.

Reef Category	**Reef name**	**Mean depth (m)**	**Sampling effort (min)**	**Sample coverage**	**Sample coverage by reef category**
Artificial	Alice	13	42'	99%	Artificial 99.7%
Artificial	Alvarenga	19	42'	99%	
Artificial	Queimado	15	42'	99%	
Artificial	Vapor Bahia	21.5	42'	98%	
Natural	S9 (Chapeirões)	9.1	44'30''	75%	Natural 99%
Natural	S10 (Cabeço Ninho)	9.3	33'53''	96%	
Natural	S11 (Sapata Brau)	20.1	28'09''	99%	
Natural	S13 (Cangulo)	24.5	24'19''	91%	
Natural	S22 (Estação 2)	18	19'41''	98%	
Natural	D14 (Ponto 216)	30	23'03''	72%	
Natural	D15 (Caial)	27	26'16''	86%	
Natural	D16 (Pedra Baixo)	30	31'50''	80%	

Table S2. Species included in the time-calibrated tree, estimated using maximum likelihood and backbone constraint analyses. The source (B17) corresponds to species already placed in the backbone tree (Betancur-R et al., 2017); the remaining species (GenBank) were placed based on *cytochrome oxidase subunit I* (COI) and *cytochrome b* (Cytb) sequences obtained from NCBI. NCBI accession numbers are provided in 'COI' and 'Cytb' columns.

Species (as in GenBank)	Species	Source	COI	Cytb
Abudefduf saxatilis	*Abudefduf saxatilis*	B17		
Acanthostracion polygonius	*Acanthostracion polygonius*	GenBank	JQ861011.1	JQ861154.1
Acanthurus bahianus	*Acanthurus bahianus*	B17		
Acanthurus chirurgus	*Acanthurus chirurgus*	GenBank	JQ842356.1	KC623696.1
Acanthurus coeruleus	*Acanthurus coeruleus*	GenBank	JQ842776.1	KC623697.1
Alphestes afer	*Alphestes afer*	GenBank	JQ840759.1	AY313996.1
Amblycirrhitus pinos	*Amblycirrhitus pinos*	B17		
Anisotremus moricandi	*Anisotremus moricandi*	GenBank	JQ741142.1	EU694316.1
Anisotremus surinamensis	*Anisotremus surinamensis*	B17		
Anisotremus virginicus	*Anisotremus virginicus*	B17		
Balistes vetula	*Balistes vetula*	B17		
Bodianus rufus	*Bodianus rufus*	GenBank	JQ839717.1	
Cantherhines macrocerus	*Cantherhines macrocerus*	GenBank	JQ842801.1	
Cantherhines pullus	*Cantherhines pullus*	GenBank	MF041486.1	KF025770.1
Carangoides bartholomaei	*Carangoides bartholomaei*	GenBank	JQ841092.1	AY050728.1
Carangoides ruber	*Carangoides ruber*	GenBank	JQ841490.1	AY050723.1
Caranx crysos	*Caranx crysos*	GenBank	JQ841093.1	EF392574.1
Caranx latus	*Caranx latus*	GenBank	JQ841100.1	AY050724.1
Cephalopholis fulva	*Cephalopholis fulva*	B17		
Chaetodipterus faber	*Chaetodipterus faber*	GenBank	KT367891.1	
Chaetodon ocellatus	*Chaetodon ocellatus*	B17		
Chaetodon striatus	*Chaetodon striatus*	B17		
Chromis multilineata	*Chromis multilineata*	GenBank	JQ842056.1	EU431997.1
Harengula clupeola	Clupeidae sp	GenBank	JQ840529.1	
Cryptotomus roseus	*Cryptotomus roseus*	B17		

Echeneis naucrates	*Echeneis naucrates*	B17		
Elacatinus figaro	*Elacatinus figaro*	GenBank	KM987237.1	AY846438.1
Elagatis bipinnulata	*Elagatis bipinnulata*	B17		
Epinephelus adscensionis	*Epinephelus adscensionis*	GenBank	FJ583396.1	
Epinephelus itajara	*Epinephelus itajara*	GenBank	JQ841167.1	EU823103.1
Fistularia tabacaria	*Fistularia tabacaria*	B17		
Gymnothorax funebris	*Gymnothorax funebris*	GenBank	JQ842871.1	
Gymnothorax vicinus	*Gymnothorax vicinus*	GenBank	JQ841585.1	HQ122505.1
Haemulon aurolineatum	*Haemulon aurolineatum*	B17		
Haemulon parra	*Haemulon parra*	GenBank	JQ841906.1	EU697512.1
Haemulon plumieri	*Haemulon plumieri*	B17		
Haemulon squamipinna	*Haemulon squamipinna*	GenBank	EU697544.1	EU697517.1
Haemulon steindachneri	*Haemulon steindachneri*	GenBank	EU697545.1	EU697518.1
Halichoeres brasiliensis	*Halichoeres brasiliensis*	GenBank		AY823576.1
Halichoeres cyanocephalus	*Halichoeres dimidiatus*	GenBank	JQ841215.1	AY591376.1
Halichoeres maculipinna	*Halichoeres penrosei*	GenBank	JQ840106.1	AY591354.1
Halichoeres poeyi	*Halichoeres poeyi*	GenBank	JQ841595.1	AY823578.1
Holacanthus ciliaris	*Holacanthus ciliaris*	B17		
Holacanthus tricolor	*Holacanthus tricolor*	B17		
Holocentrus adscensionis	*Holocentrus adscensionis*	GenBank	JQ842166.1	KX961691.1
Kyphosus incisor	*Kyphosus incisor*	B17		
Labrisomus nuchipinnis	*Labrisomus nuchipinnis*	GenBank	GU225343.1	
Lutjanus alexandrei	*Lutjanus alexandrei*	GenBank	MG575213.1	
Lutjanus analis	*Lutjanus analis*	GenBank	KF633343.1	HQ162430.1
Lutjanus jocu	*Lutjanus jocu*	GenBank	KF633372.1	HQ162442.1
Lutjanus synagris	*Lutjanus synagris*	GenBank	KF633283.1	HQ162427.1
Malacanthus plumieri	*Malacanthus plumieri*	B17		
Mulloidichthys martinicus	*Mulloidichthys martinicus*	B17		
Myrichthys ocellatus	*Myrichthys ocellatus*	GenBank	JQ842250.1	
Myripristis jacobus	*Myripristis jacobus*	GenBank	JQ842252.1	DQ379998.1
Ocyurus chrysurus	*Ocyurus chrysurus*	B17		
Odontoscion dentex	*Odontoscion dentex*	B17		

Ogcocephalus vespertilio	*Ogcocephalus vespertilio*	GenBank	JQ365464.1	
Ophioblennius trinitatis	*Ophioblennius trinitatis*	GenBank		MF990196.1
Opistognathus brasiliensis	*Opistognathus* sp	GenBank	MH751525.1	
Orthopristis ruber	*Orthopristis ruber*	GenBank	GU702465.1	JQ741531.1
Paralichthys brasiliensis	*Paralichthys brasiliensis*	GenBank	MF999166.1	
Paranthias furcifer	*Paranthias furcifer*	GenBank	JQ365485.1	
Pareques acuminatus	*Pareques acuminatus*	B17		
Pempheris schomburgki	*Pempheris schomburgki*	B17		
Pomacanthus paru	*Pomacanthus paru*	GenBank	JQ840654.1	
Pseudocaranx dentex	*Pseudocaranx dentex*	GenBank	EF609442.1	DQ197985.1
Pseudupeneus maculatus	*Pseudupeneus maculatus*	B17		
Rypticus saponaceus	*Rypticus saponaceus*	B17		
Scarus trispinosus	*Scarus trispinosus*	GenBank	MF999162.1	
Scorpaena plumieri	*Scorpaena plumieri*	GenBank	JQ365552.1	
Selar crumenophthalmus	*Selar crumenophthalmus*	B17		
Selene vomer	*Selene vomer*	GenBank	JQ365562.1	AF363746.1
Sparisoma axillare	*Sparisoma axillare*	GenBank		DQ457034.1
Sparisoma frondosum	*Sparisoma frondosum*	GenBank		DQ457032.1
Sparisoma radians	*Sparisoma radians*	GenBank	JQ841825.1	DQ457028.1
Sphoeroides spengleri	*Sphoeroides spengleri*	GenBank	JQ681816.1	JQ681909.1
Sphyraena barracuda	*Sphyraena barracuda*	B17		
Sphyraena guachancho	*Sphyraena guachancho*	GenBank	KF461240.1	
Sphyraena picudilla	*Sphyraena picudilla*	GenBank	JQ843068.1	
Stegastes fuscus	*Stegastes fuscus*	B17		
Stegastes pictus	*Stegastes pictus*	GenBank	KM077183.1	KM077201.1
Thalassoma noronhanum	*Thalassoma noronhanum*	GenBank	JQ839625.1	AY328876.1

S2 – Extended results

Table S3. Fish species recorded in the 12 reefs (n = 4 artificial, n = 8 natural) studied in the coast of Paraiba, Northeast Brazil. Numbers represent species abundance. The last column on the right identifies threatened species according to IUCN's (The International Union for Conservation of Nature) red list (available at https://www.iucnredlist.org). EN: endangered; VU: vulnerable.

Family	Species Scientific Name	Artificial Reefs	Natural Reefs	IUCN
Ginglymostomatidae	*Ginglymostoma cirratum* (Bonnaterre 1788)	5	1	VU
Dasyatidae	*Hypanus* sp	0	1	
Muraenidae	*Gymnothorax funebris* Ranzani 1839	0	4	
Muraenidae	*Gymnothorax vicinus* (Castelnau 1855)	2	0	
Muraenidae	*Muraena pavonina* Richardson 1845	1	2	
Ophichthidae	*Myrichthys ocellatus* (Lesueur, 1825)	0	2	
Clupeidae	Clupeidae sp	886	0	
Ogcocephalidae	*Ogcocephalus vespertilio* (Linnaeus 1758)	2	0	
Fistulariidae	*Fistularia tabacaria* Linnaeus 1758	0	1	
Scorpaenidae	*Scorpaena plumieri* Bloch 1789	0	1	
Holocentridae	*Holocentrus adscensionis* (Osbeck 1765)	172	166	
Holocentridae	*Myripristis jacobus* Cuvier 1829	58	43	
Serranidae: Epinephelinae	*Alphestes afer* (Bloch 1793)	2	4	
Serranidae: Epinephelinae	*Cephalopholis fulva* (Linnaeus 1758)	23	24	
Serranidae: Epinephelinae	*Epinephelus adscensionis* (Osbeck 1765)	3	2	
Serranidae: Epinephelinae	*Epinephelus itajara* (Lichtenstein 1822)	1	0	VU
Serranidae: Epinephelinae	*Paranthias furcifer* (Valenciennes 1828)	0	1	
Serranidae: Epinephelinae	*Rypticus saponaceus* (Bloch & Schneider 1801)	2	3	
Malacanthidae	*Malacanthus plumieri* (Bloch 1786)	4	4	

Echeneidae	*Echeneis naucrates* Linnaeus 1758	1	2
Carangidae	*Caranx bartholomaei* Cuvier 1833	22	34
Carangidae	*Caranx ruber* (Bloch 1793)	3	0
Carangidae	*Caranx crysos* (Mitchill 1815)	11	0
Carangidae	*Caranx latus* Agassiz 1831	48	3
Carangidae	*Elagatis bipinnulata* (Quoy & Gaimard 1825)	1	0
Carangidae	*Pseudocaranx dentex* (Bloch & Schneider 1801)	0	1
Carangidae	*Selar crumenophthalmus* (Bloch 1793)	0	57
Carangidae	*Selene vomer* (Linnaeus 1758)	4	0
Lutjanidae	*Lutjanus alexandrei* Moura & Lindeman 2007	9	19
Lutjanidae	*Lutjanus analis* (Cuvier 1828)	2	0
Lutjanidae	*Lutjanus jocu* (Bloch & Schneider 1801)	4	18
Lutjanidae	*Lutjanus synagris* (Linnaeus 1758)	17	1
Lutjanidae	*Ocyurus chrysurus* (Bloch 1791)	9	5
Haemulidae	*Anisotremus moricandi* (Ranzani 1842)	0	1
Haemulidae	*Anisotremus surinamensis* (Bloch 1791)	11	1
Haemulidae	*Anisotremus virginicus* (Linnaeus 1758)	47	21
Haemulidae	*Haemulon aurolineatum* Cuvier 1830	443	63
Haemulidae	*Haemulon parra* (Desmarest 1823)	119	0
Haemulidae	*Haemulon plumierii* (Lacepède 1801)	261	7
Haemulidae	*Haemulon squamipinna* Rocha & Rosa 1999	786	767
Haemulidae	*Haemulon steindachneri* (Jordan & Gilbert 1882)	180	0
Haemulidae	*Orthopristis ruber* (Cuvier 1830)	87	0
Sciaenidae	*Odontoscion dentex* (Cuvier 1830)	25	3
Sciaenidae	*Pareques acuminatus* (Bloch & Schneider 1801)	9	69
Mullidae	*Mulloidichthys martinicus* (Cuvier 1829)	455	33
Mullidae	*Pseudupeneus maculatus* (Bloch 1793)	26	20
Pempheridae	*Pempheris schomburgkii* Müller & Troschel 1848	491	13
Chaetodontidae	*Chaetodon ocellatus* Bloch 1787	1	0
Chaetodontidae	*Chaetodon striatus* Linnaeus 1758	4	4

Pomacanthidae	*Holacanthus ciliaris* (Linnaeus 1758)	3	5	
Pomacanthidae	*Holacanthus tricolor* (Bloch 1795)	2	7	
Pomacanthidae	*Pomacanthus paru* (Bloch 1787)	2	8	
Kyphosidae	*Kyphosus incisor* (Cuvier 1831)	1	0	
Cirrhitidae	*Amblycirrhitus pinos* (Mowbray 1927)	4	3	
Pomacentridae	*Abudefduf saxatilis* (Linnaeus 1758)	38	21	
Pomacentridae	*Chromis multilineata* (Guichenot 1853)	32	10	
Pomacentridae	*Stegastes fuscus* (Cuvier 1830)	9	7	
Pomacentridae	*Stegastes variabilis* (Castelnau 1855)	1	1	
Sphyraenidae	*Sphyraena barracuda* (Edwards 1771)	37	0	
Sphyraenidae	*Sphyraena guachancho* Cuvier 1829	1	0	
Sphyraenidae	*Sphyraena picudilla* Poey 1860	21	0	
Labridae	*Bodianus rufus* (Linnaeus 1758)	13	6	
Labridae	*Halichoeres brasiliensis* (Bloch 1791)	11	6	
Labridae	*Halichoeres dimidiatus* (Agassiz 1831)	2	10	
Labridae	*Halichoeres penrosei* Starks 1913	7	1	
Labridae	*Halichoeres poeyi* (Steindachner 1867)	23	14	
Labridae	*Thalassoma noronhanum* (Boulenger 1890)	5	5	
Scarinae	*Cryptotomus roseus* Cope 1871	0	1	
Scarinae	*Scarus trispinosus* Valenciennes 1840	1	1	EN
Scarinae	*Scarus zelindae* Moura, Figueiredo & Sazima 2001	4	4	VU
Scarinae	*Sparisoma axillare* (Steindachner 1878)	14	18	VU
Scarinae	*Sparisoma frondosum* (Agassiz 1831)	6	11	VU
Scarinae	*Sparisoma radians* (Valenciennes 1840)	2	0	
Opistognathidae	*Opistognathus* sp	6	0	
Labrisomidae	*Labrisomus nuchipinnis* (Quoy & Gaimard 1824)	0	2	
Blenniidae	*Ophioblennius trinitatis* Miranda Ribeiro 1919	0	2	
Gobiidae	*Elacatinus figaro* Sazima, Moura & Rosa 1997	0	8	VU
Microdesmidae	*Ptereleotris randalli* Gasparini, Rocha & Floeter 2001	0	2	
Ephippidae	*Chaetodipterus faber* (Broussonet 1782)	83	0	

Paralichthyidae	*Paralichthys brasiliensis* (Ranzani 1842)	1	0
Acanthuridae	*Acanthurus bahianus* Castelnau 1855	10	41
Acanthuridae	*Acanthurus chirurgus* (Bloch 1787)	39	50
Acanthuridae	*Acanthurus coeruleus* Bloch & Schneider 1801	47	16
Balistidae	*Balistes vetula* Linnaeus 1758	0	1
Monacanthidae	*Cantherhines macrocerus* (Hollard 1853)	0	4
Monacanthidae	*Cantherhines pullus* (Ranzani 1842)	3	1
Ostraciidae	*Acanthostracion polygonius* Poey 1876	1	1
Tetraodontidae	*Sphoeroides spengleri* (Bloch 1785)	0	1

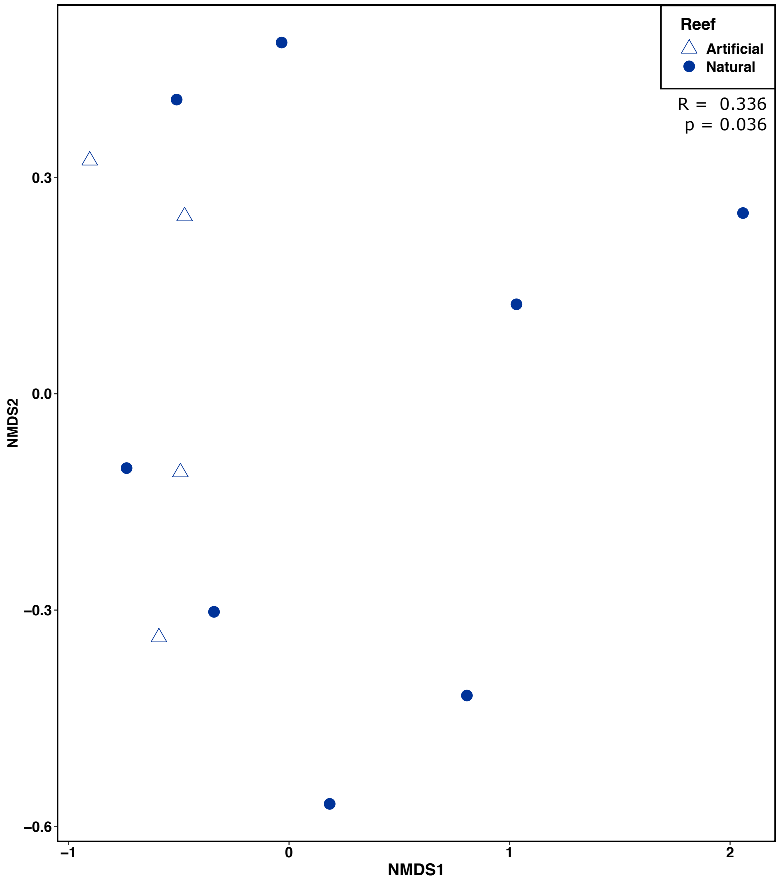

Figure S1. Non-metric multidimensional scaling (NMDS) applied to the reef fish communities of artificial and natural reefs in Northeast Brazil. Global R and significance level (p) of the Analysis of Similarity (ANOSIM) are also provided.

Table S4. Community weighted mean (CWM) for each trait state of the six functional traits evaluated for fish species from Northeast Brazil. We compared all attributes between artificial and natural reefs using two-tailed Wilcox-tests. Five trait states were significantly different between reef categories. Level of significance (*p*): *< 0.05.

Trait	**State**	**CWM average**		**U**	***p***	
		Artificial (min, max)	**Natural (min, max)**			
Water column position	Benthic	0.098 (0.01, 0.2)	0.084 (0, 0.2)	18	0.799	
	Benthopelagic	0.679 (0.5, 0.9)	0.896 (0.8, 1)	6	0.107	
	Pelagic	0.222 (0.05, 0.4)	0.02 (0, 0.1)	31	0.012	*
Habitat use	Specialist	0.182 (0.04, 0.4)	0.183 (0, 0.7)	21	0.442	
	Intermediate	0.173 (0.04, 0.3)	0.184 (0.07, 0.3)	14	0.799	
	Generalist	0.645 (0.3, 0.8)	0.633 (0.2, 0.9)	17	0.932	
Body size	0 - 7 cm	0 (0, 0)	0.012 (0, 0.1)	12	0.361	
	7.1 - 15 cm	0.278 (0.04, 0.6)	0.242 (0, 0.7)	20	0.552	
	15.1 - 30 cm	0.352 (0.1, 0.5)	0.441 (0.1, 0.8)	13	0.671	
	30.1 - 50 cm	0.306 (0.2, 0.5)	0.251 (0, 0.5)	22	0.350	
	50.1 - 80 cm	0.016 (0.01, 0.04)	0.014 (0, 0.06)	22	0.342	
	> 80 cm	0.048 (0.02, 0.07)	0.041 (0, 0.1)	20	0.552	
Mobility	High mobility	0.222 (0.05, 0.4)	0.02 (0, 0.1)	31	0.012	*
	Roving	0.667 (0.4, 0.9)	0.89 (0.7, 1)	4	0.051	
	Sedentary	0.111 (0.01, 0.3)	0.09 (0, 0.3)	18	0.799	
Trophic category	Herbivore	0.034 (0.01, 0.06)	0.235 (0.02, 0.6)	3	0.034	*
	Macro carnivore	0.065 (0.03, 0.1)	0.13 (0.07, 0.3)	6	0.107	
	Macro invertivore	0.601 (0.3, 0.9)	0.523 (0.2, 0.8)	19	0.671	
	Omnivore	0.013 (0, 0.04)	0.016 (0, 0.06)	16	1.000	
	Planktivore	0.283 (0.08, 0.6)	0.06 (0, 0.3)	29	0.031	*
	Small invertivore	0.003 (0, 0.003)	0.037 (0, 0.1)	8	0.202	
Larval dispersal	Balistidae type	0.002 (0, 0.007)	0.015 (0, 0.06)	8.5	0.204	
	Brooding	0.003 (0, 0.01)	0 (0, 0)	20	0.216	
	Demersal eggs	0.022 (0.01, 0.04)	0.086 (0, 0.3)	8	0.202	

Pelagic eggs	0.973 (0.9, 0.9)	0.899 (0.7, 0.9)	29	0.034	*
Ovoviviparous	0.001 (0, 0.003)	0.001 (0, 0.004)	16	1.000	

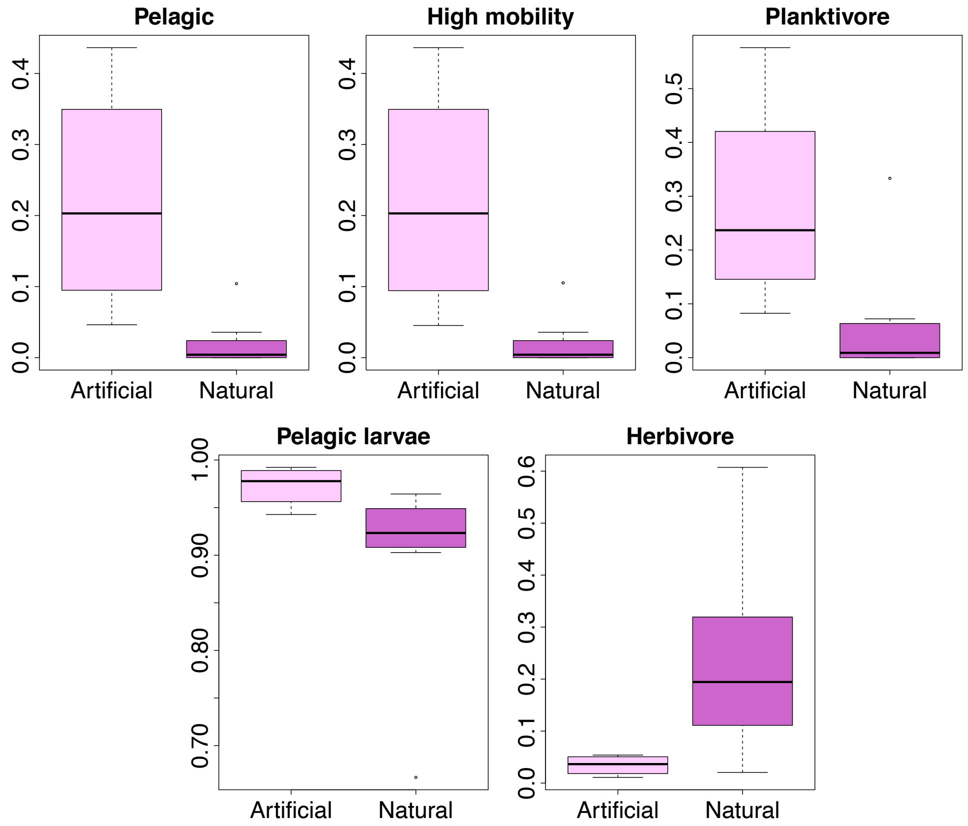

Figure S2. Community trait weighted mean (CWM) for each trait state that produced significant results when compared between artificial and natural reefs (see Table S4).

References

Betancur-R, R., Wiley, E. O., Arratia, G., Acero, A., Bailly, N., Miya, M., … Ortí, G. (2017). Phylogenetic classification of bony fishes. BMC Evolutionary Biology, 17(1), 162. doi: 10.1186/s12862-017-0958-3

6 CONSIDERAÇÕES FINAIS E CONCLUSÃO

Embora a abordagem metodológica para coleta e análise de dados tenha sido a mesma para os capítulos II e III, as áreas recifais utilizadas nesses capítulos foram diferentes. No segundo capítulo, foram analisados 22 recifes naturais distribuídos ao longo do gradiente de profundidade e classificados como rasos (<30 m de profundidade; n=8) e profundos (>30 m de profundidade; n=14). No terceiro capítulo foram analisados recifes artificiais (i.e. naufrágios; n=4) e recifes naturais (n=8) com características de distância da costa e profundidade similares aos naufrágios. Ao todo, foram registradas 99 espécies de peixes recifais distribuídas em 40 famílias. A Tabela 1 lista as espécies registradas nos recifes artificiais e naturais ao longo do estudo.

Tabela 1. Distribuição das espécies de peixes registradas nos recifes artificiais (n=4) e naturais (n=22) da Paraíba, Brasil. Recifes artificiais correspondem aos naufrágios centenários Alice, Alvarenga, Queimado e Vapor Bahia (Cardoso *et al.*, 2020; Oliveira 2010). Recifes naturais estão divididos em rasos (<30 m de profundidade; n=8) e profundos (>30 m de profundidade; n=14) (Medeiros *et al.*, 2021). Números indicam abundância das espécies.

			Recifes Naturais	
Família	**Espécie**	**Recifes Artificiais**	**Rasos (<30 m)**	**Profundos (>30 m)**
Ginglymostomatidae	*Ginglymostoma cirratum*	5	0	5
Dasyatidae	*Hypanus americanus*	0	0	2
Dasyatidae	*Hypanus* sp	0	0	1
Muraenidae	*Gymnothorax funebris*	0	1	5
Muraenidae	*Gymnothorax vicinus*	2	0	0
Muraenidae	*Muraena pavonina*	1	2	1
Ophichthidae	*Myrichthys ocellatus*	0	1	1
Clupeidae	*Clupeidae* sp	886	0	0
Ogcocephalidae	*Ogcocephalus vespertilio*	2	0	0
Fistulariidae	*Fistularia tabacaria*	0	1	0
Scorpaenidae	*Scorpaena plumieri*	0	0	1
Holocentridae	*Holocentrus adscensionis*	172	22	211
Holocentridae	*Myripristis jacobus*	58	0	64
Serranidae	*Alphestes afer*	2	3	2
Serranidae	*Cephalopholis fulva*	23	14	68

			Recifes Naturais	
Família	**Espécie**	**Recifes Artificiais**	**Rasos (<30 m)**	**Profundos (>30 m)**
Serranidae	*Epinephelus adscensionis*	3	1	11
Serranidae	*Epinephelus itajara*	1	0	0
Serranidae	*Mycteroperca bonaci*	0	0	2
Serranidae	*Paranthias furcifer*	0	0	38
Serranidae	*Rypticus saponaceus*	2	1	2
Malacanthidae	*Malacanthus plumieri*	4	0	5
Echeneidae	*Echeneis naucrates*	1	2	0
Carangidae	*Carangoides bartholomaei*	22	0	129
Carangidae	*Carangoides ruber*	3	0	0
Carangidae	*Caranx crysos*	11	0	0
Carangidae	*Caranx latus*	48	3	0
Carangidae	*Caranx lugubris*	0	0	2
Carangidae	*Elagatis bipinnulata*	1	0	13
Carangidae	*Pseudocaranx dentex*	0	0	2
Carangidae	*Selar crumenophthalmus*	0	0	57
Carangidae	*Selene vomer*	4	0	0
Lutjanidae	*Lutjanus alexandrei*	9	20	90
Lutjanidae	*Lutjanus analis*	2	0	0
Lutjanidae	*Lutjanus jocu*	4	5	40
Lutjanidae	*Lutjanus synagris*	17	0	5
Lutjanidae	*Ocyurus chrysurus*	9	0	63
Haemulidae	*Anisotremus moricandi*	0	5	0
Haemulidae	*Anisotremus surinamensis*	11	0	7
Haemulidae	*Anisotremus virginicus*	47	15	26
Haemulidae	*Haemulon aurolineatum*	443	46	73
Haemulidae	*Haemulon parra*	119	3	14
Haemulidae	*Haemulon plumierii*	261	6	21
Haemulidae	*Haemulon squamipinna*	786	337	560
Haemulidae	*Haemulon steindachneri*	180	0	0
Haemulidae	*Orthopristis ruber*	87	0	0
Sparidae	*Calamus pennatula*	0	0	1
Sciaenidae	*Equetus lanceolatus*	0	0	1
Sciaenidae	*Odontoscion dentex*	25	3	9
Sciaenidae	*Pareques acuminatus*	9	4	68
Mullidae	*Mulloidichthys martinicus*	455	2	682
Mullidae	*Pseudupeneus maculatus*	26	5	43
Pempheridae	*Pempheris schomburgkii*	491	14	0
Chaetodontidae	*Chaetodon ocellatus*	1	0	7
Chaetodontidae	*Chaetodon striatus*	4	5	5
Pomacanthidae	*Holacanthus ciliaris*	3	5	13

			Recifes Naturais	
Família	**Espécie**	**Recifes Artificiais**	**Rasos (<30 m)**	**Profundos (>30 m)**
Pomacanthidae	*Holacanthus tricolor*	2	1	23
Pomacanthidae	*Pomacanthus paru*	2	3	10
Kyphosidae	*Kyphosus incisor*	1	0	229
Cirrhitidae	*Amblycirrhitus pinos*	4	1	6
Pomacentridae	*Abudefduf saxatilis*	38	15	47
Pomacentridae	*Chromis multilineata*	32	8	27
Pomacentridae	*Stegastes fuscus*	9	12	0
Pomacentridae	*Stegastes pictus*	0	0	25
Pomacentridae	*Stegastes variabilis*	1	2	0
Sphyraenidae	*Sphyraena barracuda*	37	0	16
Sphyraenidae	*Sphyraena guachancho*	1	0	0
Sphyraenidae	*Sphyraena picudilla*	21	0	0
Labridae	*Bodianus rufus*	13	7	38
Labridae	*Clepticus brasiliensis*	0	0	6
Labridae	*Halichoeres brasiliensis*	11	5	4
Labridae	*Halichoeres dimidiatus*	2	3	21
Labridae	*Halichoeres penrosei*	7	1	0
Labridae	*Halichoeres poeyi*	23	9	14
Labridae	*Thalassoma noronhanum*	5	1	47
Labridae	*Xyrichtys martinicensis*	0	5	0
Labridae:Scarinae	*Cryptotomus roseus*	0	1	0
Labridae:Scarinae	*Scarus trispinosus*	1	1	5
Labridae:Scarinae	*Scarus zelindae*	4	1	7
Labridae:Scarinae	*Sparisoma amplum*	0	0	1
Labridae:Scarinae	*Sparisoma axillare*	14	24	20
Labridae:Scarinae	*Sparisoma frondosum*	6	5	10
Labridae:Scarinae	*Sparisoma radians*	2	0	0
Opistognathidae	*Opistognathus* sp	6	0	2
Labrisomidae	*Labrisomus nuchipinnis*	0	3	0
Blenniidae	*Ophioblennius trinitatis*	0	2	0
Gobiidae	*Elacatinus figaro*	0	6	16
Microdesmidae	*Ptereleotris randalli*	0	2	0
Ephippidae	*Chaetodipterus faber*	83	0	0
Paralichthyidae	*Paralichthys brasiliensis*	1	0	0
Acanthuridae	*Acanthurus bahianus*	10	27	16
Acanthuridae	*Acanthurus chirurgus*	39	42	93
Acanthuridae	*Acanthurus coeruleus*	47	11	40
Scombridae	*Scomberomorus regalis*	0	0	1
Balistidae	*Balistes vetula*	0	1	0
Monacanthidae	*Cantherhines macrocerus*	0	0	11

			Recifes Naturais	
Família	**Espécie**	**Recifes Artificiais**	**Rasos (<30 m)**	**Profundos (>30 m)**
Monacanthidae	*Cantherhines pullus*	3	0	4
Ostraciidae	*Acanthostracion polygonius*	1	1	0
Tetraodontidae	*Canthigaster figueiredoi*	0	0	4
Tetraodontidae	*Sphoeroides spengleri*	0	1	1

O Capítulo I evidencia que embora o conceito de diversidade biológica seja antigo (Hill, 1973; Molles, 1978; Rao, 1982; Simpson, 1949), ele tem sido utilizado com diferentes interpretações (Magurran, 2004). O que é chamado de diversidade no estudo de peixes recifais, muitas vezes remete à contagem de indivíduos, espécies, funções ou linhagens, ou à medidas de entropia e equitabilidade (Pielou, 1966; Shannon, 1948). Métricas de entropia geralmente não permitem comparação acurada por não cumprirem o princípio da replicação (Chao, Chiu e Jost, 2014). Dessa forma, muitas informações sobre a diversidade verdadeira de uma área podem estar mascaradas (Jost, 2006). Além das métricas de diversidade propriamente ditas, as demais dimensões funcional e filogenética têm tido pouco destaque no estudo de peixes recifais. Do ponto de vista funcional, é importante entender o papel que cada espécie desempenha no ecossistema (Villéger *et al.*, 2017). Medidas de redundância funcional (Mouillot *et al.*, 2014), média dos valores dos atributos ponderada pela abundância (CWM em inglês) (Lavorel *et al.*, 2008) ou até diversidade funcional propriamente dita (Chiu e Chao, 2014) permitem uma comparação mais acurada entre áreas e uma interpretação melhor de como a comunidade se comporta ao longo de gradientes ambientais (Mason *et al.*, 2013; Mouchet *et al.*, 2010; Mouillot *et al.*, 2013).

Estudos de diversidade filogenética são essenciais para entender processos evolutivos que deram forma às comunidades e identificar centros de diversificação (Véron *et al.*, 2019). Do ponto de vista aplicado, entender como a diversidade filogenética e funcional se distribui em uma região permite elencar áreas prioritárias para a conservação (Giglio *et al.*, 2018; Tkachenko e Soong, 2010). Vale chamar atenção também para a pouca quantidade de estudos de diversidade de peixes recifais em áreas mesofóticas (30-150 m de profundidade). Recifes mesofóticos podem funcionar como refúgio para algumas espécies (Bongaerts *et al.*, 2010; Pereira *et al.*, 2018), bem como podem abrigar atributos funcionais e linhagens evolutivas diferentes das encontradas nos recifes rasos (Soares *et al.*, 2020). O papel de áreas mesofóticas como refúgio para a comunidade de peixes recifais foi tratado no Capítulo II.

No capítulo II testei a hipótese de refúgio dos recifes profundos (HRRP) utilizando a diversidade de peixes recifais registradas nos recifes rasos e profundos da Paraíba. A composição de espécies foi diferente entre os recifes rasos e os profundos. Das 85 espécies registradas no estudo, 15 foram exclusivas dos recifes rasos, indicando que os recifes profundos não teriam como exportar essas espécies para os recifes rasos caso elas fossem extintas localmente. Essa diferença na composição de espécies ficou evidenciada pelos padrões de diversidade alfa, que foram significativamente maiores nos recifes profundos para espécies raras (^{0}D) nas três dimensões da diversidade (taxonômica, funcional e filogenética). No entanto, os padrões de diversidade beta indicaram uma alta taxa de substituição de espécies não só entre os recifes rasos e profundos, mas também dentro dos recifes rasos e dentro dos recifes profundos. Embora os valores de diversidade alfa tenham sido significativamente maiores nos recifes profundos, os resultados da diversidade beta indicaram que os recifes rasos não são um subconjunto dos recifes profundos. Além disso, tanta as áreas recifais rasas quanto as profundas são mais heterogêneas entre si. Juntos, esses resultados indicam que os recifes profundos da Paraíba não funcionam como refúgio para a comunidade de peixes, tendo em vista que cada área recifal rasa e profunda contribui para a diversidade regional. No entanto, como observado em corais (Morais e Santos, 2018), espécies generalistas de profundidade (i.e. encontradas nos recifes rasos e profundos) podem utilizar as áreas profundas como refúgio.

O Atlântico Sul é considerado como uma das áreas com maior concentração de ecossistemas mesofóticos do mundo (Soares, Tavares e Carneiro, 2018). Embora haja um crescente número de estudos nas regiões mais profundas (Laverick *et al.*, 2016), ainda há pouca ou nenhuma informação sobre a diversidade de peixes (Araújo *et al.*, 2020; Laverick *et al.*, 2018). Estudos de comunidade de peixes nas áreas profundas podem funcionar como base para o entendimento de mecanismos que moldam a diversidade de peixes e seus padrões de distribuição espacial e temporal (Leibold *et al.*, 2004). Do ponto de vista da conservação, é importante que áreas de proteção marinha abarquem um gradiente de profundidade a fim de preservar a diversidade beta (Appolloni *et al.*, 2017), manter espécies exclusivas de áreas rasas e profundas (Rocha *et al.*, 2018; Soares *et al.*, 2020), e manter corredores ecológicos de espécies que utilizam tanto áreas rasas quanto áreas profundas em diferentes estágios de seu desenvolvimento (Abesamis *et al.*, 2018; Asher, Williams e Harvey, 2017).

No Capítulo III, comparei a diversidade de peixes entre recifes artificiais (i.e. naufrágios centenários) e naturais presentes na costa da Paraíba a fim de entender o papel das estruturas artificiais na manutenção da diversidade regional. Recifes artificiais e naturais apresentaram composição de espécies diferentes, com 21 das 88 espécies de peixes exclusivas dos recifes artificiais. Essas 21 espécies são comuns em recifes naturais da região (Feitoza, Rosa e Rocha, 2005; Freitas e Lotufo, 2015; Honório, Ramos e Feitoza, 2010; Medeiros *et al.*, 2021; Pinheiro *et al.*, 2018; Soares *et al.*, 2016), porém estão ausentes precisamente nos recifes próximos aos naufrágios, o que sugere que foram “roubadas” pelas embarcações desde o momento em que afundaram (1873-1926). A diversidade gama taxonômica, funcional e filogenética foi maior nos recifes artificiais, o que também sustenta o papel degradador dos naufrágios em escala regional, já que todas as espécies são nativas e oriundas da região. Além disso, a diversidade beta regional foi maior nos recifes naturais nas dimensões taxonômicas e funcional, indicando que as embarcações naufragadas são mais homogêneas biologicamente do que os ambientes naturais. Entretanto, a diversidade alfa significativamente maior nos recifes artificias para espécies raras (^0D) nas três dimensões da diversidade (taxonômica, funcional e filogenética) indica a influência positiva das estruturas artificiais sobre a diversidade em escala local, tipicamente descrita na literatura (Consoli *et al.*, 2015; Tews *et al.*, 2004; Zhang *et al.*, 2021). Nesse sentido, os recifes artificiais estudados parecem atrair mais espécies de peixes via mecanismos de seleção de habitat e recrutamento de larvas (Leibold *et al.*, 2004; Mercader *et al.*, 2019; Nicholls e Racey, 2006), o que pode ter causado o empobrecimento biológico dos recifes naturais adjacentes.

Recentemente, o governo brasileiro demonstrou interesse em afundar mais de 70 embarcações, aviões e estruturas semelhantes ao longo do litoral brasileiro (Estadão, 2020), o que torna urgente a necessidade de desenvolver mais trabalhos que avaliem o papel dessas estruturas para a manutenção da diversidade de peixes. Estruturas artificiais também têm sido apontadas como facilitadoras da dispersão de espécies invasoras (Soares *et al.*, 2020). As principais justificativas para o uso de estruturas artificiais como os naufrágios são o aumento na produção de estoques pesqueiros e áreas de pesca, e uso turístico como áreas de mergulho e contemplação (Bohnsack, 1989; Carr e Hixon, 1997; Shani, Polak e Shashar, 2012). No entanto, os recifes artificiais poderiam atuar não como áreas de produção de estoques pesqueiros, e sim como áreas de atração de espécies, facilitando a sobre-exploração porque os estoques estariam concentrados nos recifes artificiais (Burt *et al.*, 2009; Grossman, Jones e Seaman, 1997; Rilov e Benayahu, 2000). A partir dos resultados obtidos no capítulo III, os recifes artificiais da Paraíba parecem atuar na atração de espécies e não no aumento da produção (Wilson *et al.*, 2001). Mas também vale destacar que os padrões de diversidade beta demonstram que tanto os recifes artificiais quanto os naturais contribuem, de maneira significativa, para a diversidade regional. Por causa disso, as quatro embarcações naufragadas devem ser incluídas em planos de conservação e manejo das áreas recifais da Paraíba (Morais e Santos, 2018; Paraíba, 2018). Afundamentos futuros devem ser realizados com extrema cautela e seguir critérios rígidos de proteção dos recifes naturais existentes na região, detalhados no Capítulo III desta tese.

Finalmente, destaco as principais conclusões dos três capítulos:

- Estudos de diversidade de peixes recifais devem incluir métricas que cumpram o princípio da replicação e que expressem o número efetivo de entidades biológicas (i.e. espécies, funções, linhagens), como os números de Hill, pois permitem comparações mais fidedignas entre as comunidades;
- As dimensões funcional e filogenética da diversidade e o componente espacial beta são escassos na literatura de peixes recifais, e, portanto, representam campos promissores para a investigação científica do grupo;
- Os recifes naturais profundos da Paraíba podem funcionar como refúgio apenas para poucas espécies generalistas de profundidade, mas não para toda a comunidade de peixes recifais;
- Recifes naturais rasos e profundos da Paraíba apresentam conjuntos particulares de espécies, funções e linhagens, devendo ser tratados como ecossistemas distintos, complementares e igualmente importantes para o manejo e conservação em escala regional;
- As embarcações que naufragaram na costa paraibana entre 1873 e 1926 favorecem o acúmulo de espécies de peixes em escala local, porém, em escala regional, devem estar envolvidas na degradação gradativa dos recifes naturais adjacentes;

- O afundamento de estruturas artificiais na plataforma continental da Paraíba deve ser realizado com extrema cautela e seguindo um rigoroso protocolo de implementação e monitoramento, caso contrário resultarão na degradação dos recifes naturais da região.

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