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VICTOR EMMANUEL LOPES DA SILVA

ESPÉCIES RARAS E SEU PAPEL NA ESTRUTURAÇÃO FUNCIONAL DE ASSEMBLEIAS DE PEIXES ESTUARINOS TROPICAIS

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

Orientador(a): Prof(a). Dr.(a) Nidia Noemi Fabré

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DEDICATÓRIA

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“If you love something – and there are many things that I love – you do want more and more and more of it… but that’s not the way to produce good work.”

J.K. Rowling

RESUMO

A raridade de espécies em estuários é geralmente relacionada com a falta de características distintas que permitem que espécies abundantes explorem o ecossistema estuarino apesar das constantes mudanças em seus parâmetros físico-quimicos que ocorrem durante sua dinâmica. Neste contexto, é esperado que espécies raras apresentariam traços diferentes daqueles encontrados em espécies abundantes. Contudo, pouco é conhecido sobre o papel funcional que tais espécies desempenham nestas áreas. Usando dois diferentes cenários de perda de espécies (remoções ocorrendo aleatoriamente e da espécie mais rara até a mais comum), nos avaliamos a contribuição de espécies raras para a estrutura funcional de assembleias de peixes estuarinos em uma região tropical. Nossos resultados mostram que embora espécies raras desempenhem funções redundantes no estuário estudado, estas espécies tem um papel crucial na diferenciação de nicho em grupos funcionais, aumentando a diversidade resposta dentro destes grupos e, portanto, garantido que funções chaves sejam mantidas.

Palavras-chave: Biodiversidade. Funcionalidade ecossistêmica. Raridade. Perda de espécies.

ABSTRACT

Species rarity in estuaries is often related to the lack of distinct features that allow abundant species to explore the estuarine ecosystem despite its constant shifts in physical-chemical parameters throughout its dynamics. In this respect, it is expected that rare species would present different traits in comparison to abundant species. However, little is known about the functional role played by these species in these areas. Using two different scenarios of species loss (removal happening at random and from rarest to the most common species), we evaluated the contribution of rare species to the functional structure of estuarine fish assemblages in a tropical region. Our results show that although rare species play redundant functions in estuaries, these species have a crucial role in increasing niche differentiation within functional groups, enhancing response diversity inside groups and, hence, keeping key functions.

Key-word: Biodiversity. Ecosystem functioning. Rarity. Species loss.

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1 APRESENTAÇÃO

Mais do que nunca ecólogos têm direcionado seus esforços para a compreensão da relação entre biodiversidade e funções ecossistêmicas (KANG et al., 2015; WANG; BROSE, 2018). Tal fato resulta do crescente número de espécies em extinções que vem ocorrendo em grande parte das comunidades naturais, afetando principalmente as espécies raras que tendem a ser altamente sensíveis a distúrbios naturais e antropogênicos (LYONS et al., 2005). Contudo, pouco é conhecido sobre como a perda dessas espécies pode estar afetando os ecossistemas, incluindo aqueles altamente produtivos, como os estuários. Para tanto, uma compreensão mais profunda do papel funcional dessas espécies no ecossistema se faz necessária.

Este trabalho de dissertação é dividido em dois capítulos. No primeiro capítulo, encontra-se uma revisão da literatura onde são abordados os avanços e desafios que tem emergido no campo da diversidade funcional, focando-se principalmente nos conceitos e teorias que relacionam a diversidade de espécies e a funcionalidade e estabilidade ecossistêmica. Este capitulo também contém uma seção que aborda a relação entre a teoria de redundância funcional e a raridade de espécies, dois tópicos que têm chamado a atenção da comunidade científica na última década.

O segundo capítulo é o artigo principal da dissertação, que tem como objetivo principal definir o papel das espécies raras na estrutura funcional de assembleias ictiícas estuarinas. Especificamente, este trabalho conjuga de diversas métricas de diversidade funcional com simulações de perda de espécies para avaliar como as espécies menos abundantes contribuem para a funcionalidade do ecossistema estuarino estudado.

2 REVISÃO DA LITERATURA

2.1 Biodiversidade e funcionalidade ecossistêmica: teorias e avanços

As mudanças que os sistemas naturais têm sofrido nos últimos anos por pressões naturais ou ações antropogênicas têm levado os ecólogos a direcionar cada vez mais seus esforços para compreender a funcionalidade dos processos ecossistêmicos e identificar como estas mudanças podem estar afetando tais processos (KANG et al., 2015; TILMAN, 1999, 2001; WANG; BROSE, 2018). Para tanto, o conceito de diversidade funcional emergiu como instrumento principal de diversos estudos ecológicos, uma vez que a diversidade de funções exercidas pelos organismos é tida como componente chave da estabilidade ecossistêmica, sendo de importância não apenas para a compreensão das relações entre biodiversidade e serviços ecossistêmicos, como também dos mecanismos de coexistência de espécies (DIAZ; CABIDO, 2001; TILMAN, 2000).

Historicamente, diversas hipóteses foram formuladas na tentativa de se compreender como a diversidade de espécies afeta o funcionamento de um determinado ecossistema (KANG et al., 2015). Tais hipóteses, usualmente, são relacionadas principalmente com a participação das espécies na cadeia trófica (KANG et al., 2015; WANG; BROSE, 2018), uma vez que a transferência de energia é um componente chave da funcionalidade ecossistêmica. Por exemplo, uma das teorias mais conhecidas e estudadas é da hipótese da diversidade-estabilidade postulada por MacArthur (MACARTHUR, 1955) que relaciona alta diversidade de espécies com máxima estabilidade ecossistêmica. Para MacArthur (1955), a estabilidade de sistemas naturais é alcançada pelo aumento no número de espécies, uma vez que tal incremento faz com que um maior número de nichos tróficos disponíveis no ecossistema sejam ocupados.

Embora muitos estudos tenham mostrado uma relação positiva entre a riqueza de espécies e a diversidade de funções (DIMITRIADIS; KOUTSOUBAS, 2011), um debate acerca das similares entre diferentes espécies emergiu nos anos 90, fazendo com que novas perspectivas nascessem dentro do estudo das relações entre espécies e funções. A hipótese da redundância ecológica (WALKER, 1992), por exemplo, vai de encontro a teoria da diversidade-estabilidade, assumindo que algumas funções-chave de ecossistemas podem ser desempenhadas por diversas espécies. Ou seja, ao contrário do que MacArthur acreditava, o incremento de novas espécies, nem sempre garantiria o preenchimento de um nicho desocupado. Como exemplo podemos destacar o papel da herbivoria em recifes de corais. Embora o grupo de peixes herbívoros apresente diferentes estratégias para obtenção de alimentos e diferenças comportamentais, todos são responsáveis pelo controle de crescimento de algas (NYSTRÖM, 2006), que é uma das funções cruciais para a estabilidade do ecossistema. De fato, a retirada de herbívoros é relacionada com a fragilização do ambiente estuarino (NYSTRÖM, 2006), fazendo com que a redundância seja um componente importante destes ecossistemas, garantindo resiliência.

2.2 Redundância funcional

Segundo Walker (1992), algumas espécies tendem a serem ecologicamente similares, desempenhando funções iguais no ecossistema. Em teoria, tendo diversas espécies desempenhando a mesma função, o ecossistema se manteria estável, mesmo diante de distúrbios (ELMQVIST et al., 2003; NYSTRÖM, 2006). Contudo, diversas discussões têm sido conduzidas acerca de tal pressuposto. Por exemplo, alguns autores afirmam que mesmo dentro de um grupo funcional, ou seja, um grupo de espécies que desempenham uma mesma função, espécies podem desempenhar as funções de forma diferentes, muitas vezes apresentando certo grau de complementariedade por trás de uma redundância aparente (BLÜTHGEN; KLEIN, 2011; VALONE; BARBER, 2008). De fato, Elmqvist et al. (2003) propuseram o conceito de “diversidade resposta”, que seria a habilidade que espécies de um mesmo grupo funcional têm de desempenharem uma determinada função de forma diferente frente a distúrbios naturais e antropogênicos. Para os autores, estas diferenças podem ser o mecanismo chave por trás da resiliência e estabilidade ecossistêmica, uma vez que tal variabilidade de respostas permite a continuidade das funções do ecossistema e, consequentemente, sua reorganização e reestruturação após a ocorrência de um distúrbio (MORI; FURUKAWA; SASAKI, 2013).

Por exemplo, o estudo de (JONSSON et al., 2002) mostrou que crustáceos e plecópteros apesar de desempenharem funções similares em riachos, apresentam respostas diferentes frente a distúrbios antropogênicos, fazendo com que a diversidade resposta contribua para o mantimento das funções desempenhadas. Particularmente, os autores observaram que embora a ocorrência e abundância de crustáceos sejam afetadas durante processos de acidificação e de incremento de poluição por matéria orgânica, a função ecossistêmica não é perdida, uma vez que os plecópteros se mostram mais resistentes e continuam a desempenharem tal função mesmo após a ocorrência do distúrbio. No entanto, poucos estudos têm se proposto investigar a relação entre diversidade resposta e a resiliência ecológica de ecossistemas, fazendo com que tal mecanismo seja pouco compreendido (CARIVEAU et al., 2013; CHILLO; ANAND; OJEDA, 2011).

Além disso, outros questionamentos são bastantes pertinentes tratando-se da relação entre biodiversidade e funções ecossistêmicas. Em muitos estudos, um acréscimo de espécies usualmente gera um aumento na diversidade funcional das comunidades (HALPERN; FLOETER, 2008; MAYFIELD et al., 2010). Se espécies tendem a serem redundantes, por que não ocorre uma estabilidade da diversidade funcional? Tal pergunta tem regido diversos novos estudos, e embora a maioria dos resultados ainda sejam inconclusivos e muitas vezes contraditórios, alguns avanços foram feitos. Por exemplo, alguns autores têm discutidos que esse acrescimento na diversidade funcional geralmente é ocasionado pela inclusão de espécies raras (LYONS et al., 2005; MOUILLOT et al., 2013), uma vez que o aumento do esforço amostral tende a aumentar as chances de incluir tais espécies nas amostras (MAGURRAN, 1989).

2.3 O papel das espécies raras nos ecossistemas

De uma forma simplória, espécies raras podem ser definidas como aquelas espécies que apresentam tamanho populacional pequeno (HARNIK; SIMPSON; PAYNE, 2012). Contudo, o conceito de raridade é bem mais complexo e amplo, e pode estar relacionado não apenas com questões ligadas a abundância das espécies, mas também com diferentes escalas (espaciais e temporais) e com a função desempenhada pela espécie no ecossistema, uma vez que espécies podem ser caracterizadas como funcionalmente raras – desempenhando funções distintas – (VIOLLE et al., 2017). O debate acerca do papel de espécies consideradas raras quanto a sua abundância e ocorrência em ecossistemas tem se intensificado na última década (MOUILLOT et al., 2013; LEITÃO et al., 2016), principalmente por causa do pressuposto de que tais espécies tendem a serem ecologicamente diferentes daquelas que são abundantes, uma vez que a raridade de espécies em muitos ambientes é relacionada com a presença de filtros ambientais (DE ANDRADE et al., 2015). Ou seja, a baixa abundância dessas espécies muitas vezes ocorre devido à ausência de características morfológicas e fisiológicas distintas que são necessárias para que elas sejam abundantes em um determinado ambiente (MATTHEWS et al., 2010). Sendo assim, tais espécies tendem a apresentar traços distintos, que permitem que elas desenvolvam funções diferentes nas comunidades (LEITÃO et al., 2016). Contudo, a falta de conhecimento sobre a relação entre raridade de espécies e funcionalidade ecossistêmica resulta em diversas questões ainda não compreendidas, tais como o qual impactante a perda de tais espécies pode ser para o ecossistema e o quão importante essas espécies são.

Uma boa parte dessa falta de conhecimento tem raízes em um contexto histórico, onde as espécies raras foram, por muito tempo, negligenciadas em muitos estudos ecológicos (LYONS et al., 2005), uma vez que a maior parte da biomassa total e uso de energia na comunidade resulta da contribuição das espécies mais comuns e abundantes (GRIME, 1998). Por exemplo, em ambientes altamente produtivos, tais como estuários, o papel funcional desempenhado por espécies menos abundantes é pouco conhecido. A raridade de espécies em áreas estuarinas resulta principalmente da própria dinâmica ecossistêmica, que é marcada por grandes alterações dos parâmetros químico-físicos da água, que limitam a abundância e ocorrência de muitas espécies (MATTHEWS et al., 2010). Tais mudanças fazem com que a maior parte das espécies que utilizam essas áreas sejam transitórias e ocorram em baixa abundância (ELLIOTT et al., 2007), fazendo com que a estrutura das assembleias e distribuição de traços funcionais sejam constantemente alterados. Portanto, a inclusão de espécies raras em estudos futuros se faz necessária para uma melhor compreensão dos processos ecossistêmicos, e planejamento adequado de planos de manejo e conservação para tais espécies e ecossistemas.

Contudo, a inclusão das espécies raras em estudos é apenas um dos desafios que ainda temos que superar. De fato, existem muitas outras questões que devem ser levadas em consideração na tentativa de definir relações concretas entre a diversidade de espécies e funções ecossistêmicas (VITULE et al., 2017). Entre as diversas problemáticas existentes podemos destacar a análise de contribuição individual de espécies para o funcionamento ecossistêmico (variabilidade funcional intraespecífica), ameaças locais e regionais a biodiversidade e até mesmo o desenvolvimento de novas metodologias.

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3 SPECIES RARITY AND THE FUNCTIONAL STRUCTURE OF ESTUARINE FISH ASSEMBLAGES: ARE LESS ABUNDANT SPECIES REDUDANT?

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Abstract

Species rarity in estuaries is often related to the lack of distinct features that allow abundant species to explore the estuarine ecosystem despite its constant shifts in physical-chemical parameters throughout its dynamics. In this respect, it is expected that rare species would present different traits in comparison to abundant species. However, little is known about the functional role played by these species in these areas. Using two different scenarios of species loss (removal happening at random and from rarest to the most common species), we evaluated the contribution of rare species to the functional structure of estuarine fish assemblages in a tropical region. Our results show that although rare species play redundant functions in estuaries, these species have a crucial role in increasing niche differentiation within functional groups, enhancing response diversity inside groups and, hence, keeping key functions.

Key-word: Biodiversity. Ecosystem functioning. Rarity. Species loss.

3.1 Introduction

In many studies rare species are often neglected, as common taxa typically contribute the most for overall biomass and energy use in assemblages (Cao et al. 1998; Grime 1998; Lyons et al. 2005; Leitão et al. 2016). That is especially the case in functional ecology studies, where the potential contribution of less abundant species is underestimated (Lyons and Schwartz 2001). However, recent works have recognized that these species may play crucial roles in high-diversity environments (Leitão et al. 2016; Umaña et al. 2017), presenting distinct combinations of traits that allow them to perform unique functions in ecosystems (Mouillot et al. 2013). The main problem relies on the fact that rare species are characterized by small population size and narrow habitat tolerance, features that increase their risk of extinction, making them highly sensitive to disturbances (Harnik et al. 2012). In fact, it is well accepted among the scientific community that rare species are the taxa most affected by natural and anthropogenic changes that have been occurring in many ecosystems worldwide (Davies et al. 2004). Yet, the functional consequences of their extirpation are still largely unknown.

In estuaries, for example, the number of studies that have evaluated the functional structure of these areas is very low (Silva-Júnior et al. 2016), and less is known about the functional role played by rare species. Estuarine systems are transition zones between freshwater and marine environments that are characterized by constant changes in their chemical, physical and biological components (Bianchi 2007). These constant shifts in their structure limit not only the number of species occurring in these habitats but also their abundance (Magurran and Henderson 2003), as common species tend to present morphological and physiological features that allow them to tolerate these conditions (Matthews et al. 2010; Andrade et al. 2015). In estuarine fish assemblages, for instance, abundant species typically present distinct adaptations, intraspecific variability in fish behavior (Bourke et al. 1997; Silva-Falcão et al. 2012) and greater functional specialization and originality (Sales et al. 2016). Consequently, species rarity in estuaries is rather related to environmental filtering (i.e. temperature, salinity, turbidity, rainfall) than biotic interactions (i.e. competition) (Quinlan and Phlips 2007; Arrieira et al. 2015).

Under this latter assumption, we could assume that rare species should be ecologically different from common species, presenting distinct sets of traits and, therefore, performing unique functions. However, controversies surrounding this topic rely on the fact that estuaries tend to present high levels of functional redundancy (Dolbeth, Vendel, Baeta, et al. 2016), with many species performing similar functions throughout its dynamics – which is characterized by constants shifts in their chemical, physical and biological structure. Indeed, functional redundancy among species has been pointed out as the key element providing stability in these ecosystems (Baptista et al. 2015), which could indicate that less abundant species are either redundant or do not contribute significantly to the total functional structure of these areas. Thereby, identifying whether rare species detain different traits in comparison to common taxa within the community is not enough, being necessary to understand whether or not these functions are unique and, hence, vulnerable.

In this respect, this study aims to provide some insights into the relationship between species rarity and ecosystem functioning in estuaries by testing whether rare species contribute disproportionately to functional diversity of tropical estuarine fish assemblages. Specifically, we simulated two scenarios of species loss (losing species at random and losing species from the rarest to the most common) and compared how the removal of species would affect the functional structure of assemblages. We hypothesized that the extirpation of rare species would negatively affect functional diversity components, assuming that such species might present distinct traits in comparison to those which are typically abundant and, thereby, performing unique functions.

3.2 Materials and Methods

3.2.1 Study area and fish sampling

The study was carried out in a tropical semi-humid region of the southwestern Atlantic, characterized by two well-defined seasons (a dry and a reaniy season). The Mundaú lagoon estuary (9°38’15”S ; 35°46’20”W) is one of the largest and most productive estuarine systems in the northeastern Brazil, providing multiple services of ecological, economic and social values for local communities. Six sampling sites were established along the estuarine lagoon, and each site was monthly sampled from November 2013 to October 2014 (a total of 72 samples) using a block net (1000 m long and 3 m high with mesh size of 35 mm). After sampling, all collected fishes were immediately stored in ice to aid preservation until further analyses. In laboratory, individuals were identified at species level, weighed in *g* (*Ww*), and the following morphological measurements were recorded: standard length (*SL*), body height (*Bh*), body width (*Bw*), head hight (*Hh*), caudal fin height (*CFh*), caudal peduncle length (*CPl*), caudal peduncle height (*CPh*), eye diameter (*Ed*), mouth height (*Mh*) and mouth width (*Mw*). All measures were taken using a numeric vernier caliper with precision of 0.1 mm. Although we did not fix a maximum sample size for measurement per species, a sub-sample of 10 individuals per 1 cm interval was randomly chosen whenever species presented high capture rates (n>100 individuals per haul). Morphometric measures were registered for 1488 fishes.

3.2.2 Functional traits

Twelve functional traits related to food acquisition and locomotion were estimated using the morphological measurements mentioned above (Table 1). Traits were selected for presenting a strong relationship with fish performance, such as the detection and capture of food resources (Karpouzi and Stergiou 2003), swimming efficiency (Sibbing and Nagelkerke 2001) and metabolic allocation of energy in the body (Villéger et al.

2012). As samples were mainly comprised of juveniles and sub-adults (85.6% of total abundance), ontogenic changes were not considered.

Table 1. List of traits used to calculate functional diversity of fish species from the studied estuary: weighed in *g* (*Ww*), standard length (*SL*), body height (*Bh*), body width (*Bw*), head hight (*Hh*), caudal fin height (*CFh*), caudal peduncle length (*CPl*), caudal peduncle height (*CPh*), eye diameter (*Ed*), mouth height (*Mh*) and mouth width (*Mw*).

Functional trait		**Formula**	**Reference**
Swimming	Body transversal shape (BTS)	$\frac{Bh}{Bw}$	(Sibbing and Nagelkerke 2001)
	Body transversal surface (BTSu)	$\frac{\ln\left(\left(\frac{\pi}{4} \times Bw \times Bd\right)+1\right)}{\ln(Ww+1)}$	(Villéger et al. 2010)
	Caudal peduncle throttling (CPT)	$\frac{CFh}{CPh}$	(Webb 1984)
	Relative height (RH)	$\frac{Bh}{SL}$	(Gatz 1979)
	Relative peduncle length (RPL)	$\frac{CPl}{SL}$	(Watson and Balon 1984)
Feeding	Eye size (ES)	$\frac{Ed}{Hh}$	(Boyle and Horn 2006)
	Oral gape shape (OGS)	$\frac{Mh}{Mw}$	(Karpouzi and Stergiou 2003)
	Oral gape surface (OGSu)	$\frac{Mw \times Mh}{Bw \times Bh}$	(Karpouzi and Stergiou 2003)

Table 1. List of traits used to calculate functional diversity of fish species from the studied estuary: weighed in *g* (*Ww*), standard length (*SL*), body height (*Bh*), body width (*Bw*), head hight (*Hh*), caudal fin height (*CFh*), caudal peduncle length (*CPl*), caudal peduncle height (*CPh*), eye diameter (*Ed*), mouth height (*Mh*) and mouth width (*Mw*).

Functional trait	**Formula**	**Reference**
Relative head length (RHL)	$\frac{Hl}{SL}$	(Watson and Balon 1984)
Relative mouth height (RMH)	$\frac{Mh}{SL}$	(Gatz 1979)
Relative mouth width (RMW)	$\frac{Mw}{SL}$	(Gatz 1979)
Size (S)	$\log_{10}(Ww+1)$	(Villéger et al. 2012)

3.2.3 Functional diversity measures

To evaluate the functional structure of assemblages, two different approaches were used. First, as suggested by Mason et al. (2005), we computed the different facets of functional diversity with dissimilarity indices: (1) functional richness (FRic) which represents the amount of functional space filled by species, (2) functional evenness (FEve) that evaluates how the biomass of a community is distributed in the niche space, and (3) functional divergence (FDiv) which indicates the degree of niche differentiation among species. These indices were measured to obtain a better picture of how much of the niche space is being occupied by species and how different functions are being performed (Mason et al. 2005; Villéger et al. 2008). We standardized FRic to constrain values between 0 and 1, and forced values to zero when samples presented less than three species to avoid misinterpretations in our results (Villéger et al. 2008; Dolbeth, Vendel, Pessanha, et al. 2016).

Second, we analyzed functional diversity through Rao's quadratic entropy (RaoQ), which incorporates the relative abundance of species and the functional pairwise distances between them (Pavoine 2012). This index results from the mean functional distance between two randomly chosen individuals in an assemblage and it is affected by the distribution of traits in the samples, as well as by the covariance between them (Botta-Dukát 2005; Rao 2010). Additionally, we performed a principal coordination analysis (PCoA) using the Gower distance species-trait matrix to provide a functional typology of fish assemblages (Weithoff 2003). The PCoA creates a multidimensional functional space and estimates the functional dissimilarity among species. Before plotting PCoA results, the mean squared-deviation index was applied to evaluate the extent to which the functional space accurately represented the functional distance between species pairs (Maire et al. 2015). The mSD analysis showed that a six-dimensional space would accurately represent the functional distance between species pairs. Therefore, we plotted the six first PCoA axis to get a better visualization of species distribution in niche space.

As proposed by Bello et al. (2007), functional redundancy (FR) was described as the difference between species diversity and functional diversity: FR = SD – FD. This method assumes that functional redundancy is the part of species diversity that has not been explained by functional diversity, which means that when all species in the community are functionally different the redundancy is zero (Dolbeth, Vendel, Pessanha, et al. 2016). Species diversity was described by the Shannon index (D), as it illustrates the complexity of communities and it is more sensitive to the number of rare species (Magurran 1989).

3.2.4 Species loss simulation

To test how potential species losses may affect the functional structure of assemblages, two different scenarios were simulated: (1) species loss occurring from the rarest to the most common species, and (2) species loss occurring at random. For both scenarios, we followed the steps described by (Leitão et al. 2016), sequentially removing species using nine degrees of loss (from 10% to 90%) and measuring functional indexes of samples after each removal. In the first scenario, we started by computing the rarity index for each species using the approach described by Chu et al. (2003). Species were ranked, and removals were made from the rarest to the most common. In the random loss scenario, prior removal, the order of species was shuffled 1000 times keeping their trait values constant. At last, statistical differences between both scenarios were tested using a Mann-Whitney test.

3.2.5 Functional vulnerability

To assess vulnerability of functional diversity to the loss of rare species, we used an adapted version of the richness-independent vulnerability index (RIV) proposed by Carmona et al. (2017): RIV = P_R – P. In the original logistic behind the calculation of this index, vulnerability is expressed as the ratio between P_R and P, which represent the percentage of removed species that is necessary to decrease functional diversity to a given value (typically 25% of its total) under the most plausible order of species loss (P) and under random extinctions (P_R). However, in our study we estimated P_R and P for assemblages after each species extirpation as the percentage of the original RaoQ value. If functional diversity is more affected by extinctions following the most plausible order – P – (from the rarest to the most common) than what should be expected under random extinctions – P_R –, P_R will be greater than P, therefore RIV would be a positive value (Carmona et al. 2017).

All analyzes were carried out in the R statistics software. Functional diversity measures were performed using the FD package (Laliberté et al. 2015).

3.3 Results

3.3.1 Fish assemblages’ structure

A total of 8448 individuals, belonging to 39 species and 16 families were collected during the studied period (Table S1). As expected, samples were mainly comprised of a few abundant taxa and many rare species. For instance, *Cathorops spixii* (Agassiz, 1829) and *Mugil curema* Valenciennes, 1836 were collected all year round and contributed with 76% of overall abundance. Functionally, most species were redundant, including some rare species, and only a few taxa were placed far from the center of the functional space (Figure 1 and S1). Those species were mostly represented by marine straggler fishes, especially by carnivorous carangids such as *Carangoides bartholomaei* (Cuvier, 1833), *Selene vomer* (Linnaeus, 1758), *Trachinotus falcatus* (Linnaeus, 1758) and *T. goodei* Jordan & Evermann, 1896.

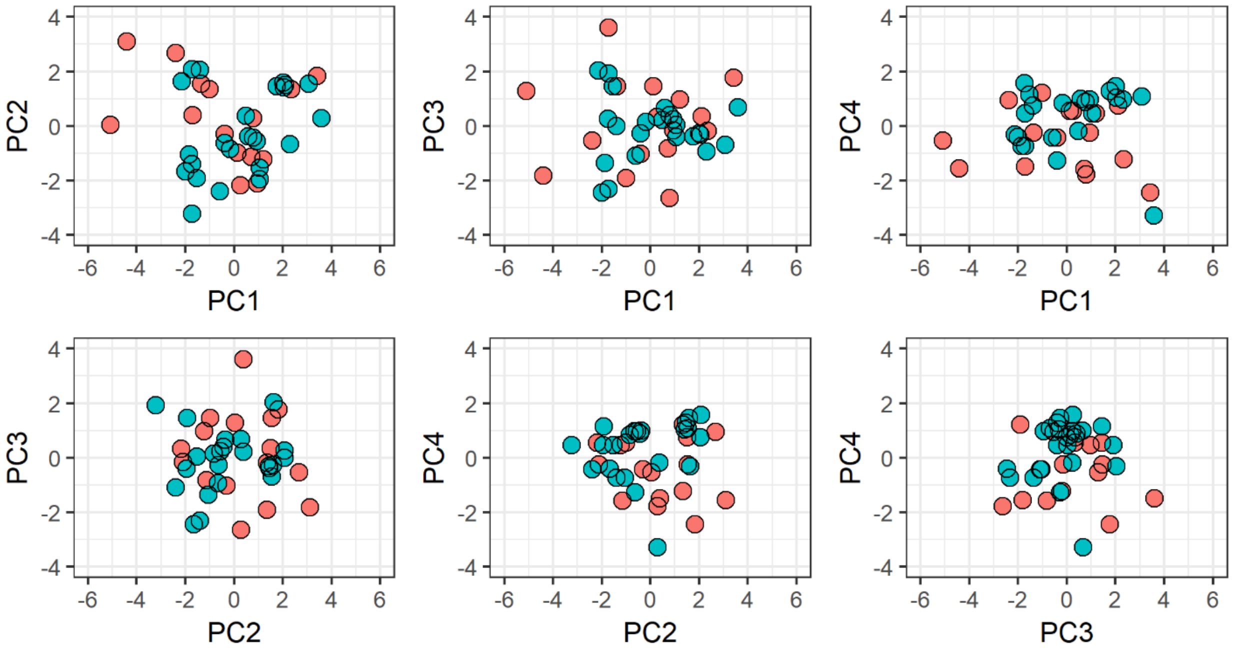

Figure 1. First four-dimensional functional space of the fish species pool (39 species) from the Mundaú lagoon estuary. Each plot represents two axes of the principal

coordinate analysis (PCoA) carried out using the Gower distance species-trait matrix. Species (circles) are plotted according to their traits (rare species are represented by red circles, while blue circles represent the common species). To see the full six-dimensional functional spaces see Figure S1 in the supplementary material.

3.3.2 Consequences of species loss and functional vulnerability

Simulations showed distinct patterns for each measured functional index (Figure 2). As expected, in both scenarios species removal caused functional richness (FRic) and functional diversity (RaoQ) to decrease, however there was no significant difference between both scenarios ($p>0.05$). That was also the case for FEve and functional redundancy (FR), which did not show any significant difference between both scenarios ($p>0.05$). On the other hand, functional divergence (FDiv) showed an interesting pattern with FDiv decreasing as rare species were removed and increasing in the random loss scenario ($p<0.05$), indicating that rare species are responsible to enhance niche differentiation among estuarine fish assemblages. However, these species did not contribute disproportionally to the functional structure of studied assemblages, with RIV values staying negative until the removal of 50% of these species (Figure 3).

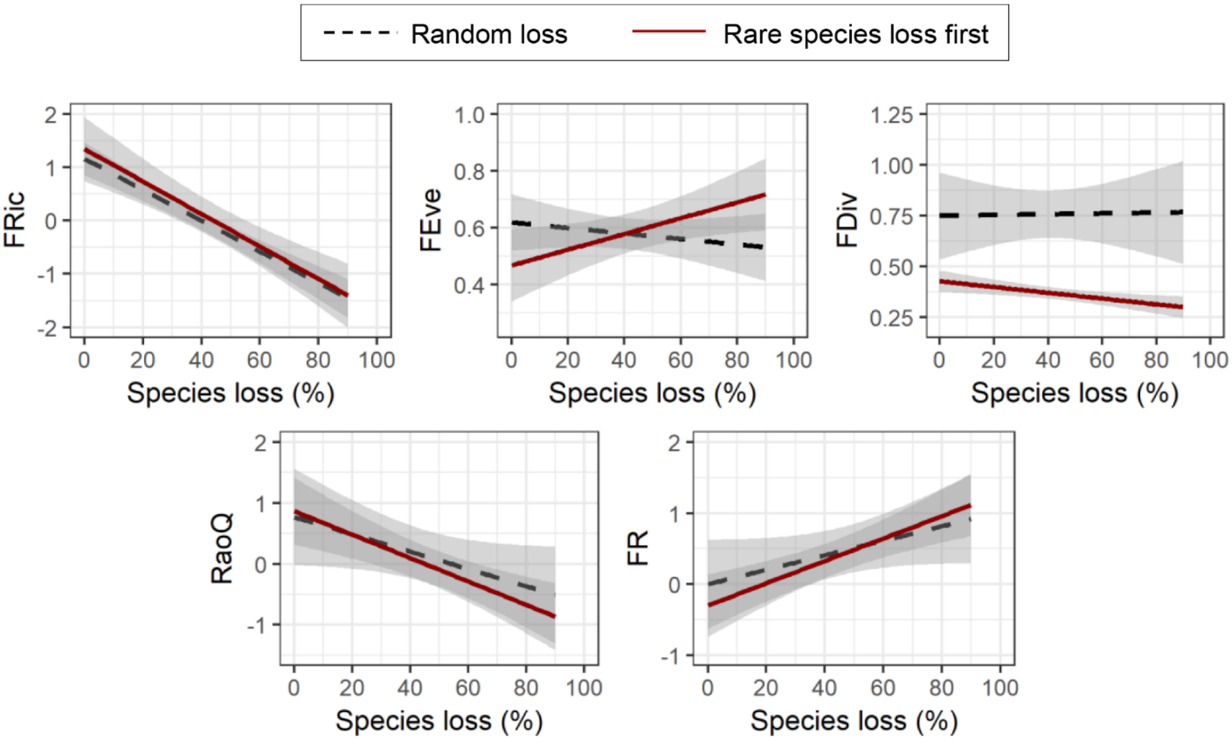

Figure 2. Simulation of the impact of species loss in the functional components of fish assemblages from the Mundaú lagoon estuary. Shaded areas indicate the 95% confidence interval. (FRich: functional richness; FEve: functional eveness; FDiv: functional divergence; RaoQ: functional diversity index; FR: functional redundancy).

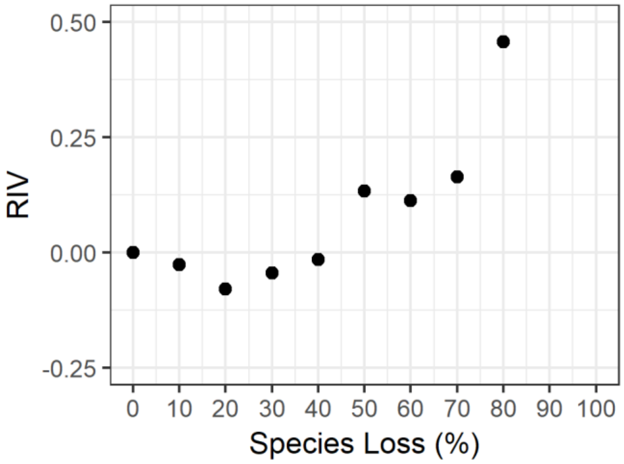

Figure 3. Relationship between species loss and richness-independent vulnerability (RIV) in the Mundaú lagoon estuary.

3.4 Discussion

Our study shows that even though some rare species present different traits and enhance niche differentiation among species, their contribution to the total functional structure of assemblages is not disproportional in comparison to common taxa, indicating that these species might be performing redundant functions in the estuary. In general, estuarine fish assemblages tend to have high levels of functional redundancy (Baptista et al. 2015; Dolbeth, Vendel, Baeta, et al. 2016), which is a feature usually related to the stability of ecosystems, as stated by Walker's redundancy hypothesis (Walker 1992). At the heart of the concept, species in the same functional group (a group of species that perform a similar "job") may extend their ecosystem function once neighboring species go extinct (Walker 1992), which in theory, would allow ecosystems to remain stable, maintaining their structure and functions even in face of disturbances (Elmqvist, Folke, Nyström, et al. 2003; Kang et al. 2015; Santoro et al. 2015). Nevertheless, many authors have addressed some important issues related to this hypothesis. For instance, there has been an ongoing discussion on whether species are indeed equally functional in ecosystems (Loreau 2004). Specifically, it has been shown that even within functional groups, species may differ in the way they perform a particular role (Elmqvist, Folke, Nyström, et al. 2003; Nyström 2006; Laliberté et al. 2010), indicating a subtle level of complementarity hidden behind an apparent redundancy (Blüthgen and Klein 2011).

For example, in our study the loss of species from the rarest to the most common taxa caused functional divergence (FDiv) to decrease, showing that rare species enhance the level of niche differentiation among species. However, their extirpation did not impact differently the functional structure of assemblages in comparison to the random loss of species, suggesting that these species play redundant functions. High niche differentiation is often related to the ability to perform different functions, hence, increasing functional diversity (Mason et al. 2005). Nevertheless, functional divergence may also occur inside functional groups, allowing species to explore the same resource in different ways, minimizing competition and facilitating the coexistence of similar species (Nyström 2006; Mori et al. 2013). In functional ecology, this is called “response diversity”, which is defined as the diversity of differences among species that contribute to the same ecosystem function (Elmqvist, Folke, Nystrom, et al. 2003). More precisely, response diversity occurs when species within a single functional group present different morphological and physiological features, high behavior plasticity and distinct life history strategies, resulting a wider range of traits that is used to perform a particular function in different ways (Nyström 2006). These differences among species are believed to be strongly related to resilience, as species would respond differently in the face of disturbance, providing ecological insurance to ecosystem functioning (Bellwood et al. 2003; Bellwood et al. 2004; Mori et al. 2013), making the presence of rare species in the studied ecosystem a key element to its stability.

In studied assemblages, rare species appears to enhance niche differentiation inside the group of carnivorous, as species that were placed far from the center of the functional species were all from this guild. In estuaries, food items available to be explored by this group may be influenced by many factors, but especially by seasonality, freshwater flow and tidal regime (Oliveira and Kjerfve 1993). High rainfall rates or low freshwater flow, for instance, has been pointed out as the main drivers of assemblages structuring in mobile estuarine invertebrates (Attrill and Thomas 1996; González-Ortegón et al. 2015), altering their abundance and occurrence throughout estuarine dynamics. These shifts in resources availability make the existence of different feeding strategies inside the carnivorous guild necessary to maintain ecosystem functioning.

Moreover, response diversity may also be influenced by species and traits distribution (Nyström 2006). According to Peterson et al. (1997), species within functional groups may operate at different scales of space and time to minimize competition and reinforce the maintaining of ecosystem functions. In the Mundaú lagoon estuary, rare species were mainly characterized by marine straggler fishes which have their distribution and occurrence limited by environmental gradients (Elliott et al. 2007; Harrison and Whitfield 2008). These species often occur in small numbers and just for a short amount of time within estuaries since a combination of optimum salinity and temperature conditions is needed (Morgan et al. 2006). Hence, the estuarine dynamics itself appears to play a crucial role in the functional structuring of assemblages by filtering the presence of distinct species and traits (Passos et al. 2016).

The information provided herein is, however, concerning as rare species are extremely sensitive to disturbances and human-induced impacts due to their small population size and narrow habitat tolerance (Harnik et al. 2012). These species have been the group most affected by current impacts worldwide, especially in estuaries (Barletta et al. 2010), and thereby, their continuing loss may lead ecosystems to collapse, as unique traits would be lost, and response diversity would decrease. Low response diversity may lead functional groups to extinction or make ecosystems functionally insignificant as key functions may be lost (Elmqvist, Folke, Nystrom, et al. 2003; Graham et al. 2011; Senapathi et al. 2015). In this respect, studies at larger scales of space and time that link response diversity to species rarity in estuaries are needed to comprehend the implications of species loss in the face of the current changes that natural communities have undergone, especially in tropical regions where these environments are suffering unprecedent levels of anthropogenic pressures (Blaber and Barletta 2016).

In conclusion, we rejected our hypothesis that rare species perform distinct functions in the studied estuary, however, the results provided herein show that rare species play indeed an important role in the functional structuring of fish assemblages by increasing response diversity within functional groups, ensuring the maintaining of key functions for the ecosystem. Therefore, we highly recommend that for the proper management of tropical estuaries, rare species should be treated as important as the most common and abundant species in future studies. Specifically, a closer examination of functional traits that these species have and how they respond to natural and anthropogenic changes in these environments is in order to avoid the loss of important functions, which may jeopardize that ecosystem as a whole. We also highlight the importance of estuarine dynamics in the selection of traits and species, which faced with the current scenario of global warming is an important issue to be taken in consideration.

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3.6 Supplementary material

Table S1. List of species captured in the Mundaú lagoon estuary and their respective traits values: OGS = oral gape shape; RHL = relative head length; CPT = caudal peduncle throttling; BTS = body transversal shape; RMH = relative mouth height; OGSH = oral gape shape; ES = eye size; BTSU = body transversal surface; S = size; RH = relative height; RPL = relative peduncle length; RMW = relative mouth width.

Species	**Functional traits**											
	OGS	**RHL**	**CPT**	**BTS**	**RMH**	**OGSH**	**ES**	**BTSU**	**S**	**RH**	**RPL**	**RMW**
Albula Vulpes	0.32	0.15	3.97	1.64	0.09	0.94	0.38	1.28	2.55	0.22	0.10	0.10
Anchovia clupeoides	2.46	0.19	2.85	3.68	0.20	1.18	0.20	1.74	1.34	0.24	0.10	0.18
Archosargus rhomboidalis	0.25	0.33	3.33	3.29	0.15	1.60	0.29	1.65	1.64	0.44	0.11	0.10
Bairdiella ronchus	0.79	0.23	2.93	2.15	0.18	1.01	0.23	1.52	1.92	0.29	0.12	0.17
Caranx bartholomaei	0.52	0.24	8.54	2.61	0.12	0.77	0.40	1.30	2.58	0.32	0.08	0.16
Caranx crysos	0.81	0.30	8.20	2.93	0.19	0.97	0.30	1.61	1.69	0.36	0.08	0.19
Caranx hippos	0.86	0.29	10.22	2.92	0.19	0.93	0.30	1.56	1.89	0.37	0.09	0.21
Caranx latus	0.96	0.29	10.68	3.17	0.20	0.93	0.31	1.58	1.83	0.39	0.11	0.22
Cathorops spixii	0.79	0.14	4.25	1.17	0.12	0.82	0.22	1.75	1.49	0.16	0.12	0.14
Centropomus ensiferus	0.85	0.20	2.85	2.13	0.16	1.05	0.31	1.42	2.10	0.25	0.17	0.16
Centropomus parallelus	0.84	0.20	2.70	2.07	0.17	1.06	0.29	1.38	2.26	0.27	0.16	0.16
Centropomus undecimalis	1.22	0.18	2.76	2.02	0.18	1.00	0.31	1.34	2.27	0.24	0.14	0.18
Cetengraulis edentulus	1.41	0.22	2.56	3.05	0.20	1.18	0.18	1.72	1.44	0.29	0.12	0.18
Citharichthys arenaceus	1.20	0.31	1.32	10.83	0.16	1.03	0.26	2.01	1.11	0.49	0.04	0.16
Cynoscion acoupa	1.38	0.17	3.23	2.07	0.17	0.89	0.27	1.34	2.25	0.22	0.13	0.19
Cynoscion jamaicensis	1.24	0.19	2.57	1.81	0.21	1.05	0.24	1.44	2.07	0.24	0.12	0.19

Table S1. List of species captured in the Mundaú lagoon estuary and their respective traits values: OGS = oral gape shape; RHL = relative head length; CPT = caudal peduncle throttling; BTS = body transversal shape; RMH = relative mouth height; OGSH = oral gape shape; ES = eye size; BTSU = body transversal surface; S = size; RH = relative height; RPL = relative peduncle length; RMW = relative mouth width.

Species	**Functional traits**											
	OGS	**RHL**	**CPT**	**BTS**	**RMH**	**OGSH**	**ES**	**BTSU**	**S**	**RH**	**RPL**	**RMW**
Cynoscion microlepidatus	0.80	0.18	2.00	2.70	0.15	1.50	0.45	2.03	1.15	0.23	0.10	0.10
Diapterus auratus	0.23	0.32	4.21	3.82	0.10	0.94	0.25	1.71	1.59	0.43	0.12	0.11
Diapterus rhombeus	0.24	0.32	4.11	3.90	0.10	0.94	0.18	1.81	1.42	0.43	0.13	0.11
Elops saurus	1.90	0.13	5.97	2.46	0.16	0.97	0.30	1.40	2.14	0.19	0.13	0.17
Eucinostomus argenteus	0.37	0.25	3.43	2.82	0.11	1.02	0.37	1.96	1.31	0.32	0.11	0.11
Gobioides broussonnetii	1.16	0.08	1.88	1.58	0.08	0.91	0.53	1.12	2.74	0.10	0.06	0.09
Lutjanus analis	0.65	0.28	5.15	2.41	0.17	0.88	0.51	1.53	2.01	0.35	0.15	0.19
Macrodon ancylodon	1.43	0.17	2.20	1.85	0.16	1.03	0.33	1.39	1.99	0.18	0.16	0.15
Micropogonias furnieri	0.57	0.23	3.04	2.21	0.13	0.98	0.32	1.46	2.02	0.27	0.11	0.14
Mugil curema	0.30	0.18	3.58	1.91	0.09	0.87	0.23	1.33	2.34	0.25	0.15	0.10
Mugil curvidens	0.32	0.19	3.76	2.31	0.09	0.85	0.23	1.35	2.23	0.27	0.16	0.11
Mugil incilis	0.28	0.18	2.33	1.64	0.09	0.90	0.24	1.35	2.22	0.22	0.14	0.09
Mugil liza	0.27	0.15	3.55	1.79	0.08	0.82	0.17	1.20	2.74	0.21	0.14	0.09
Mugil rubrioculus	0.25	0.18	3.31	1.84	0.09	0.86	0.21	1.36	2.32	0.26	0.16	0.10
Oligoplites palometa	1.61	0.19	7.40	3.47	0.18	0.99	0.15	1.40	2.07	0.28	0.06	0.19
Oligoplites saurus	0.99	0.19	6.66	3.49	0.16	1.11	0.28	1.44	2.01	0.29	0.07	0.14
Polydactylus virginicus	1.36	0.19	2.55	2.15	0.16	1.15	0.25	1.51	1.69	0.23	0.13	0.14
Sciades herzbergii	0.83	0.13	4.95	0.97	0.12	0.74	0.24	1.34	2.28	0.16	0.15	0.16

Table S1. List of species captured in the Mundaú lagoon estuary and their respective traits values: OGS = oral gape shape; RHL = relative head length; CPT = caudal peduncle throttling; BTS = body transversal shape; RMH = relative mouth height; OGSH = oral gape shape; ES = eye size; BTSU = body transversal surface; S = size; RH = relative height; RPL = relative peduncle length; RMW = relative mouth width.

Species	**Functional traits**											
	OGS	**RHL**	**CPT**	**BTS**	**RMH**	**OGSH**	**ES**	**BTSU**	**S**	**RH**	**RPL**	**RMW**
Scomberomorus cavalla	1.30	0.15	6.89	2.88	0.13	0.88	0.28	1.33	2.07	0.21	0.05	0.15
Selene vomer	0.23	0.60	8.83	6.75	0.13	1.14	0.44	1.65	1.75	0.63	0.10	0.11
Strongylura marina	0.41	0.06	3.67	1.11	0.05	1.27	0.38	1.22	2.53	0.07	0.08	0.04
Trachinotus falcatus	0.17	0.31	5.63	5.75	0.10	1.00	0.28	1.72	1.63	0.60	0.15	0.10
Trachinotus goodei	0.28	0.26	7.61	4.43	0.12	0.91	0.16	1.48	2.11	0.52	0.13	0.14

Table S2. Ecological characteristics of species captured in the Mundaú lagoon estuary (EUFG: estuarine-use functional group; Diet: feeding behavior based mainly on juveniles' food items).

Species	**EUFG**	**Diet**
Albula Vulpes	Marine migrant	Carnivorous
Anchovia clupeoides	Estuarine migrant	Planktivorous
Archosargus rhomboidalis	Estuarine migrant	Omnivorous
Bairdiella ronchus	Marine stragglers	Carnivorous
Caranx bartholomaei	Marine stragglers	Carnivorous
Caranx crysos	Marine stragglers	Piscivorous
Caranx hippos	Marine stragglers	Carnivorous
Caranx latus	Marine stragglers	Carnivorous
Cathorops spixii	Estuarine resident	Omnivorous
Centropomus ensiferus	Marine migrant	Carnivorous
Centropomus parallelus	Marine migrant	Carnivorous
Centropomus undecimalis	Marine migrant	Carnivorous
Cetengraulis edentulus	Estuarine migrant	Planktivorous
Citharichthys arenaceus	Estuarine resident	Carnivorous
Cynoscion acoupa	Marine migrant	Carnivorous
Cynoscion jamaicensis	Marine migrant	Carnivorous
Cynoscion microlepidatus	Marine migrant	Carnivorous
Diapterus auratus	Estuarine migrant	Carnivorous
Diapterus rhombeus	Estuarine migrant	Carnivorous
Elops saurus	Marine migrant	Carnivorous
Eucinostomus argenteus	Marine migrant	Omnivorous
Gobioides broussonnetii	Estuarine migrant	Detritivores
Lutjanus analis	Marine migrant	Carnivorous
Macrodon ancylodon	Marine migrant	Carnivorous
Micropogonias furnieri	Marine migrant	Carnivorous
Mugil curema	Marine migrant	Detritivores
Mugil curvidens	Marine migrant	Detritivores
Mugil incilis	Marine migrant	Detritivores
Mugil liza	Marine migrant	Detritivores
Mugil rubrioculus	Marine migrant	Detritivores
Oligoplites palometa	Marine stragglers	Carnivorous
Oligoplites saurus	Marine stragglers	Carnivorous
Polydactylus virginicus	Estuarine resident	Omnivorous

Table S2. Ecological characteristics of species captured in the Mundaú lagoon estuary (EUFG: estuarine-use functional group; Diet: feeding behavior based mainly on juveniles' food items).

Species	**EUFG**	**Diet**
Sciades herzbergii	Estuarine resident	Omnivorous
Scomberomorus cavalla	Marine stragglers	Piscivorous
Selene vomer	Marine stragglers	Carnivorous
Strongylura marina	Marine stragglers	Piscivorous
Trachinotus falcatus	Marine stragglers	Carnivorous
Trachinotus goodei	Marine stragglers	Carnivorous

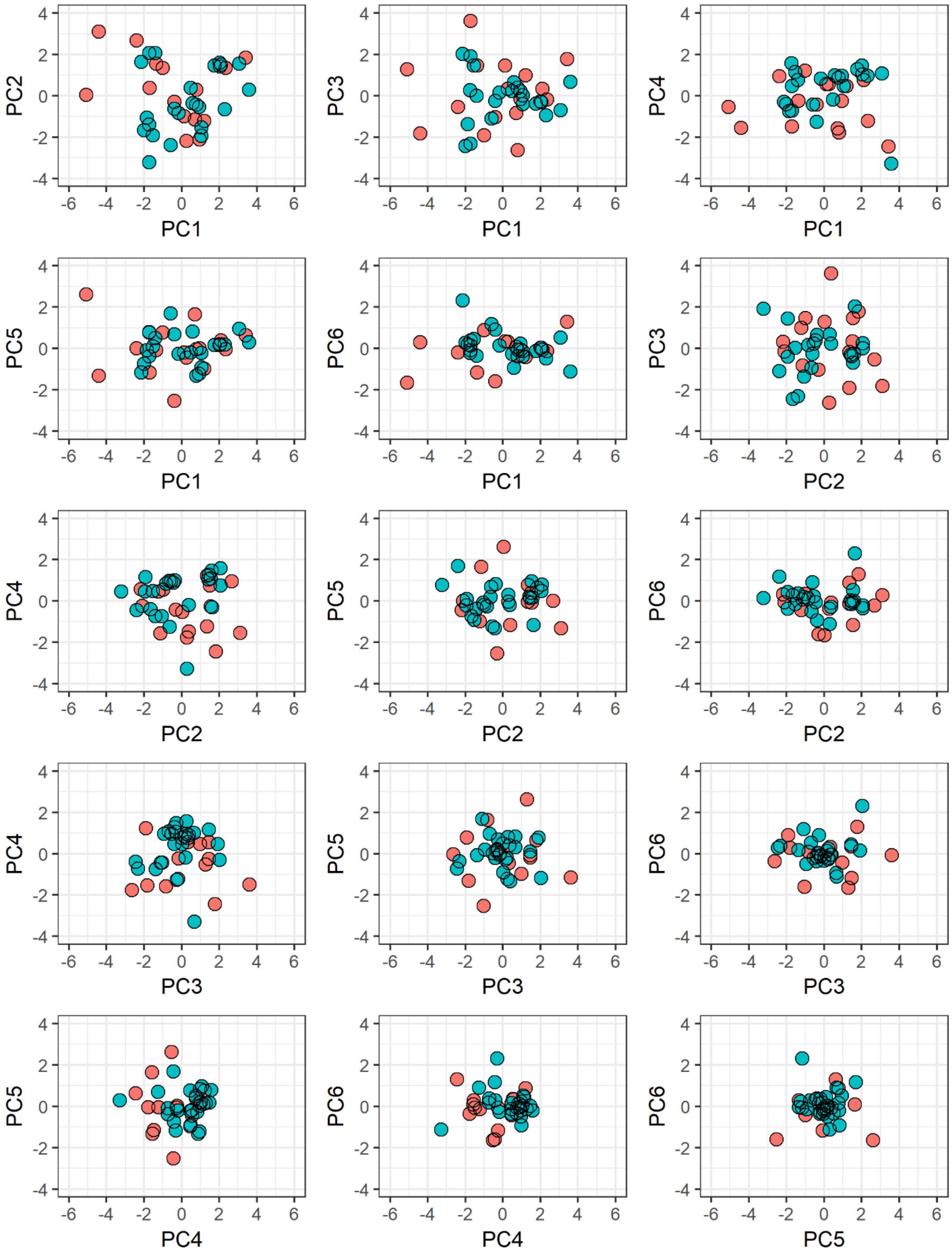

Figure S1. Six-dimensional functional space of the fish species pool (39 species) from the studied estuary. Each plot represents two axes of the principal coordinate analysis

(PCoA) carried out using the Gower distance species-trait matrix. Species (red and blue circles) are plotted according to their traits (rare species are represented by red circles, while blue circles represents the common species).

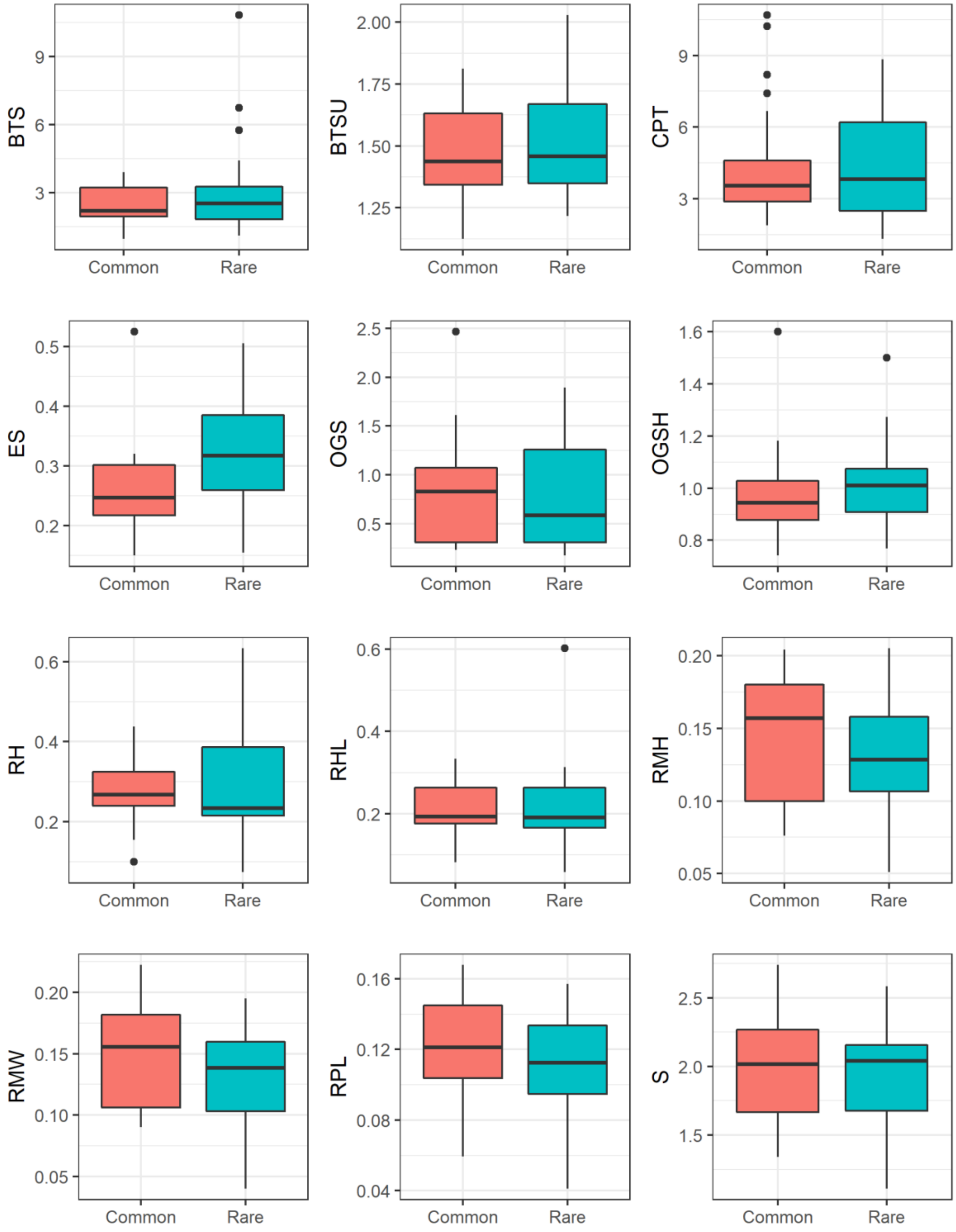

Figure S2. Variability in traits values of common and rare species collected in the Mundaú estuarine lagoon: OGS = oral gape shape; RHL = relative head length; CPT =

caudal peduncle throttling; BTS = body transversal shape; RMH = relative mouth height; OGSH = oral gape shape; ES = eye size; BTSU = body transversal surface; S = size; RH = relative height; RPL = relative peduncle length; RMW = relative mouth width.

4 CONCLUSÃO

Os resultados obtidos mostram que espécies raras desempenham um papel crucial na estruturação funcional de comunidades ictiícas em ambientes estuarinos. Ao contrário do esperado, nossos resultados indicam que tais espécies não desempenham funções distintas, porém estas espécies são responsáveis por incrementarem a diferenciação de nicho entre as espécies dentro de grupos funcionais (especificamente o grupo dos carnívoros), aumentando a diversidade resposta e permitindo que espécies utilizem recursos de formas diferenciadas. Tal diferenciação não apenas reduz a competição interespecífica por presas, mas também garante a continuidade das funções desempenhadas por este grupo mesmo frente as mudanças que ocorrem durante a dinâmica estuariana.

Além disso, nosso estudo também destaca a importância da própria dinâmica estuarina na filtragem de espécies e traços. Especificamente, foi possível observar que as constantes mudanças nos parâmetros físico-quimicos da água – características dos ambientes estuarinos –, tem um papel determinante na ocorrência de espécies raras, que por sua vez incrementam a diversidade de respostas dentro de grupos funcionais que desempenham funções chaves no estuário. Tal processo garante estabilidade ao ecossistema, permitindo que as funções desempenhadas pelas espécies ictiícas sejam mantidas apesar de mudanças na composição biológica, e na disponibilidade de presas e recursos.