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FUNÇÕES ECOSSISTÊMICAS E REDUNDÂNCIA FUNCIONAL DE
VERTEBRADOS MARINHOS RECIFAIS DO OCEANO ATLÂNTICO

Santa Maria, RS

2020

Luiza Waechter Severo

FUNÇÕES ECOSSISTÊMICAS E REDUNDÂNCIA FUNCIONAL DE VERTEBRADOS
MARINHOS RECIFAIS DO OCEANO ATLÂNTICO

Dissertação apresentada ao Curso de Pós-Graduação em Biodiversidade Animal, da Universidade Federal de Santa Maria (UFSM, RS), como requisito parcial para obtenção do título de **Mestre em Ciências Biológicas – Área Biodiversidade Animal**.

Orientadora: Prof^a. Dr^a. Mariana Bender Gomes

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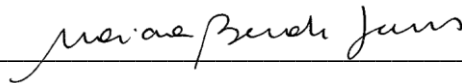
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RESUMO

FUNÇÕES ECOSSISTÊMICAS E REDUNDÂNCIA FUNCIONAL ENTRE VERTEBRADOS MARINHOS RECIFAIS DO OCEANO ATLÂNTICO

AUTORA: Luiza Waechter Severo

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O papel desempenhado por espécies, conhecido como função ecológica, garante o funcionamento de ecossistemas e a provisão de serviços ecossistêmicos. A sobreposição no papel funcional de espécies distintas caracteriza a redundância funcional, uma segurança contra o declínio de populações e extinções locais. Em condições de baixa redundância funcional, o ecossistema se torna mais vulnerável às perdas de biodiversidade e as espécies tendem a ser menos parecidas funcionalmente, ou seja, mais originais. Nos recifes do Oceano Atlântico, vertebrados como tartarugas, mamíferos e peixes (Elasmobranchii e Teleostei) são importantes componentes da fauna e suas funções incluem desde o transporte de carbonato até o controle de teias tróficas. Entretanto, existem lacunas no entendimento das funções ecossistêmicas e no possível grau de redundância funcional entre esses grupos. Neste contexto, os objetivos deste trabalho incluem (i) compilar e categorizar as funções ecossistêmicas de 224 espécies de vertebrados marinhos recifais do Oceano Atlântico, (ii) identificar o grau de redundância funcional entre grupos taxonômicos distintos, (iii) identificar o padrão de riqueza e de originalidade funcional na escala local, e (iv) analisar os efeitos da remoção de espécies ameaçadas nas perdas funcionais nos recifes do Oceano Atlântico. Nós compilamos seis atributos funcionais relacionados com a performance de espécies em funções ecossistêmicas. Sete funções ecossistêmicas foram encontradas na literatura, desde o “Transporte de nutrientes e armazenamento” até a “Regulação trófica”. Nossos resultados revelam que 44,8% do volume funcional dos recifes é ocupado por espécies ameaçadas e “Predadores de topo” têm a maior proporção de espécies ameaçadas (53,8%; n=21). Na escala regional e local, diferentes grupos taxonômicos apresentam sobreposição do espaço funcional (Elasmobranchii e Teleostei). Esta redundância regional se mantém na escala local. Como esperado, por ser considerado o *hotspot* de biodiversidade recifal do Atlântico, o Caribe apresentou maior riqueza taxonômica e funcional (n=134, correspondendo a 79.7% do volume regional). Além disso, os recifes apresentaram um padrão homogêneo de redundância e originalidade funcional. A remoção de espécies mesopredadoras teve o maior efeito sobre a erosão funcional - a remoção de 50% das espécies provoca uma redução de 60% no espaço funcional de vertebrados recifais na costa Brasileira, tornando-se uma grande ameaça para o funcionamento dos recifes.

Palavras-chave: Peixes recifais. Mamíferos marinhos. Tartarugas marinhas. Espaço funcional. Espécies ameaçadas. Caribe.

ABSTRACT

ECOSYSTEM FUNCTIONS AND FUNCTIONAL REDUNDANCY AMONG VERTEBRATES IN ATLANTIC OCEAN REEFS

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The role played by species at the local scale, known as ecological function, ensures ecosystem functioning and the provision of ecosystem services. The overlap ecosystem functions between different species characterizes functional redundancy, an insurance against local extinctions and population declines. Under conditions of low functional redundancy, the ecosystem becomes more vulnerable to biodiversity losses. In Atlantic Ocean reefs, vertebrates such as sea turtles, mammals and fish (Elasmobranchii and Teleostei) are important fauna components and their functions range from the construction of reef structure to trophic regulation. However, there are gaps in the understanding of ecosystem functions and the degree of functional redundancy between these groups. In this context, our project aims to (i) compile and categorize the ecosystem functions of 224 marine reefs species in the Atlantic Ocean, (ii) identify the degree of functional redundancy between species in these four taxonomic groups, (iii) assess species richness and functional originality patterns at the local scale, and (iv) investigate functional loss following the removal of threatened species in Atlantic Ocean reefs. We compiled six functional traits related to the performance of species in ecosystem functions and calculated functional diversity (FRic), functional originality (FUn), functional redundancy (FRed). Further, we estimated the effects of species' loss over functional diversity in reefs. Our results reveal seven ecosystem functions performed by vertebrates in Atlantic reefs. Furthermore, 44.8% of the functional volume is filled by threatened species and "Top predators" have the highest proportion of threatened species (53.8%; n=21). At the regional scale, different taxonomic groups overlap in functional space (mainly between Elasmobranchii and Teleostei), an evidence that considering this set of traits vertebrates of distinct lineages may still be redundant. Regional functional redundancy also holds at the local scale. The Caribbean, a biodiversity hotspot in the Atlantic, showed greater taxonomic and functional richness patterns (n=134; 77.9% of regional functional volume). The removal of mesopredator species had the greatest effect on losses in the functional space, where the removal of 50% of the species will cause approximately 60% of functional loss on the Brazilian coast, for example.

Keywords: Reef fish. Marine mammals. Sea turtles. Functional space. Threatened species. Caribbean.

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INTRODUÇÃO

Os impactos antrópicos nos ecossistemas são geologicamente recentes, embora as alterações na biodiversidade terrestre e marinha já tenham atingido níveis dramáticos (LEWIS e MALSIN, 2015). Apesar de apresentarem um estado incipiente de defaunação comparado aos ecossistemas terrestres, os oceanos exibem efeitos substanciais de ações humanas com um provável cenário futuro de intensificação de declínio de espécies (YOUNG et al., 2016). Nos recifes, a biodiversidade de espécies está relacionada com o funcionamento e estabilidade dos ecossistemas, bem como dos serviços que eles provêm. (HAMMERSCHLAG et al., 2019; VILLÉGER et al., 2017; BELLWOOD et al., 2004). Além disso, estas funções podem estar associadas à recuperação ambiental frente aos próprios distúrbios antrópicos (e.g. resiliência) (BELLWOOD et al., 2004). Dessa forma, a perda de espécies marinhas não apenas prejudica a capacidade dos ecossistemas em prover serviços para a crescente população humana, como também altera seu potencial de recuperação e estabilidade frente às constantes transformações (WORM et al., 2006).

Os impactos associados ao crescimento da população humana por meio da sobrepesca, destruição e/ou alteração de habitat, poluição e as mudanças climáticas, por exemplo, constituem as principais fontes de alteração dos ecossistemas marinhos (HE e SILLIMAN, 2019; WILLIAMS et al., 2019; ESSINGTON, BEAUDREAU e BEAUDREAU, 2006). A pesca tornou-se uma atividade tão comum a ponto de percebermos que seus impactos se estendem muito além das espécies-alvo, afetando a integridade do ecossistema (WILSON et al., 2014; DAYTON et al., 1995). Como consequência, os organismos marinhos são valorizados no sentido econômico, onde suas contribuições para a promoção da biodiversidade são muitas vezes desconsideradas (CISNEROS-MONTEMAYOR, et al., 2013; BELLWOOD et al., 2004; MOBERG e FOLKE, 1999). Entretanto, para promover o manejo adequado das populações marinhas, é fundamental compreender o valor da sua biodiversidade em um sentido mais amplo, incluindo seu valor ecossistêmico, considerando o papel funcional de espécies na estruturação e estabilidade do ecossistema (BELLWOOD et al., 2019; VILLÉGER et al., 2017; FONSECA e GANADE, 2001).

O termo “função ecossistêmica” é definido a partir do movimento e/ou armazenamento de energia e nutrientes dentro de um ecossistema (BELLWOOD et al., 2019; BRANDL et al., 2019). Em ambientes recifais, os peixes herbívoros influenciam a composição de espécies de algas, produtividade primária, fixação de nitrogênio, sucessão, entre outros processos (BRANDL et al., 2019; TÂMEGA et al., 2016; BONALDO, HOEY e BELLWOOD, 2014).

Predadores de topo, como os tubarões, moldam a distribuição de suas presas, sendo peças chave no funcionamento do ecossistema marinho (HAMMERSCHLAG et al., 2019; HEITHAUS et al., 2008). A predação por mamíferos marinhos também tem um papel importante no comportamento de espécies de presas e seus competidores e no armazenamento e ciclagem de nutrientes (BOWEN, 1997). As tartarugas marinhas também auxiliam no fluxo de nutrientes e energia quando saem do mar para desovar e, posteriormente, com o retorno dos filhotes para os oceanos (SCHMITZ, HAWLENA e TRUSSELL, 2010; BOUCHARD e BJORNDAL, 2000). Além disso, esses animais modificam o ecossistema, auxiliam no controle de outras populações, proporcionam a resiliência do recife e, também, controlam o crescimento de algas (CHRISTIANEN et al., 2019; GOATLEY, HOEY e BELLWOOD, 2012; WABNITZ et al., 2010; LEÓN e BJORNDAL, 2002). Os atributos funcionais destas espécies – e.g. tamanho, grupo trófico e mobilidade – são uma ferramenta para o estudo de funções ecossistêmicas em um ambiente muito diverso como os recifes de corais (BELLWOOD et al., 2019).

Tem sido registrado em estudos empíricos que algumas espécies podem desempenhar funções únicas no ecossistema (BELLWOOD, HOEY e CHOAT, 2003), enquanto que outras espécies evolutivamente distintas podem ter papéis funcionais semelhantes, sendo assim redundantes (KELLY et al., 2016; MICHELI e HALPERN, 2005). A redundância funcional é um conceito baseado no pressuposto de que espécies podem desempenhar papéis equivalentes no ecossistema, onde a remoção de espécies não implicaria na perda de funções, proporcionando uma segurança das comunidades frente à distúrbios (FONSECA e GANADE, 2001). Dessa maneira, comunidades com elevada riqueza de espécies tendem a apresentar maior redundância funcional quando comparadas às comunidades empobrecidas (FONSECA e GANADE, 2001; BELLWOOD et al., 2004). Entretanto, uma questão crucial que permanece pouco explorada é se essa vasta biodiversidade é importante para o funcionamento do ecossistema ou se uma porção menor de espécies é suficiente para realizar grande parte das funções (MOUILLOT et al., 2013). Além disso, ainda não se sabe se espécies de grupos taxonômicos distintos são funcionalmente redundantes. Embora a redundância funcional pode produzir efeitos positivos no ecossistema (BELLWOOD et al., 2004; FONSECA e GANADE, 2001), a perda de espécies com funções específicas pode ser a maior ameaça aos serviços ecossistêmicos (BELLWOOD, HOEY e HUGHES, 2011).

O funcionamento e provisão de serviços ecossistêmicos estão associados a funções de espécies (BRANDL et al., 2019). Como isso, a abordagem funcional é uma importante ferramenta para o entendimento e conservação dos ecossistemas (BELLWOOD et al., 2019; LEVINE, 2016). Novas abordagens com foco em processos ecossistêmicos são uma prioridade

para a gestão da resiliência marinha (NYSTRÖM, 2006), principalmente àquelas que focuem em funções desempenhadas por espécies independentemente de afinidades taxonômicas (HUGHES et al., 2005). É preciso identificar quais são as funções que contribuem para o funcionamento do ecossistema marinho, bem como as espécies-chave que não terão seus papéis funcionais reproduzidos de forma similar por espécies de táxons diferentes (HOEY e BELLWOOD, 2009; FONSECA e GANADE, 2001). À vista disso, este trabalho tem como objetivos (i) compilar e categorizar as funções ecossistêmicas de 224 espécies marinhas de tartarugas, mamíferos e peixes recifais – Elasmobranchii e Teleostei – do Oceano Atlântico, (ii) identificar o grau de redundância funcional destes grupos taxonômicos distintos considerando um conjunto de seis atributos funcionais, (iii) identificar o padrão de riqueza de espécies, riqueza funcional e de originalidade na escala recifal e (iv) analisar os efeitos da remoção de espécies ameaçadas segundo o grau de vulnerabilidade, das mais ameaçadas para as menos ameaçadas, em diferentes funções ecossistêmicas de acordo com as perdas no espaço funcional e na diversidade dos recifes do Oceano Atlântico.

Estrutura da Dissertação

Esta dissertação está estruturada em formato *Research Article*, conforme as normas da revista *Functional Ecology*.

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1 ECOSYSTEM FUNCTIONS AND FUNCTIONAL REDUNDANCY
2 AMONG VERTEBRATES IN ATLANTIC OCEAN REEFS

3
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17
18 **Abstract**

19 **1.** Marine vertebrates are essential to reef ecosystem functioning, stability and provision
20 of ecosystem services. However, studies of the functional structure and diversity of
21 vertebrate reef communities are largely focused in fish and rarely investigate the
22 functional similarities among different taxonomic groups at the same time.

23 2. We present the first inventory of ecosystem functions delivered by marine mammals,
24 sea turtles, Elasmobranchii and Teleostei species in Atlantic Ocean reefs. To test the
25 functional redundancy among these distinct groups, we collected six functional traits
26 comparable among marine vertebrate species associated with ecosystem functions at the
27 same time and quantified the effects of removing threatened species on functional
28 diversity losses.

29 3. The greatest overlap among taxonomic groups in the functional space was found
30 between cartilaginous and bony fish species. We found seven ecosystem functions that
31 can be performed by these species from “Bioturbation/bioerosion” to “Trophic
32 regulation” functions. The Caribbean had the greatest functional richness but low
33 species functional uniqueness. The threatened species revealed that more than 44% of
34 the functional volume is threatened by species extinctions. Top predation is the most
35 threatened function (53.8%), mainly performed by sharks and ray species with large
36 body size and high trophic position. However, the mesopredator species removal will
37 have greater effects on Atlantic Ocean reefs losses of functional volume.

38 4. Our study highlights important functional patterns across the Atlantic reefs allowing for
39 a better understanding of their functioning and vulnerabilities. Mesopredators marine
40 vertebrate species have unique functional traits combinations and lower functional
41 redundancy making the “Marine mesopredator” ecosystem function more vulnerable.
42 These considerations for future studies will be essential for the conservation of reef
43 ecosystems around the world.

44
45 **Key-words:** functional originality, functional losses, traits, reef fish, megafauna, threatened
46 species, ecosystem reef dynamics

47

48 **1 | INTRODUCTION**

49 The future of the only place known for the existence of life is being determined by
50 human beings' actions (Lewis & Maslin, 2015). As a result, biodiversity erosion has reached
51 all natural ecosystems on Earth (Steffen, Crutzen, & McNeill, 2007). Marine ecosystems are
52 threatened by the probable acceleration of defaunation in the coming years (Young, McCauley,
53 Galetti, & Dirzo, 2016). Marine biodiversity is associated with the functioning, stability and the
54 supply of ecosystem services as the productivity, nutrient cycling and cultural services
55 themselves (Brandl et al., 2019; Tavares, Mora & Merico, 2019; Villéger, Brosse, Mouchet,
56 Mouillot & Vanni, 2017). In coral reefs, losing species may compromise the functioning,
57 stability and provision of ecosystem services (Bellwood, Hughes, Folke, & Nyström, 2004;
58 David Mouillot, Graham, Villéger, Mason, & Bellwood, 2013; Hammerschlag et al., 2019).
59 The maintenance and sustainability of these ecosystem functions depends on aspects beyond
60 community species richness (Cadotte, Carscadden, & Mirotchnick, 2011). To ensure the
61 ecosystem functioning and services, it is firstly necessary to understand the role of biodiversity
62 in ecosystem functioning (Bellwood, Streit, Brandl, & Tebbett, 2019; Fonseca & Ganade, 2001;
63 Mouillot, Graham, Villéger, Manson & Bellwood, 2013; Larsen, Williams, & Kremen, 2005;
64 Levine, 2016), then know how the loss of species will affect ecosystem functioning.

65 In reefs, fauna species including fish, sharks, rays, sea turtles and mammals have
66 functions that range from regulating primary producers' growth, populations control, top-down
67 effects to reef resilience (Bowen, 1997; Fourqurean, Manuel, Coates, Keenworthy & Smith,
68 2010; Hammerschlag et al., 2019; Heithaus, Frid, Wirsing & Worm, 2008; León & Bjorndal,
69 2002; Wabnitz et al., 2010). These functions are associated with species traits (e.g. maximum
70 size, body mass, trophic group, schooling behaviour, metabolic rate and mobility) (Bellwood
71 et al., 2019; Tavares et al., 2019). Fish species body size, for instance, is related to bioturbation

72 (Bonaldo, Hoey & Bellwood, 2014) and nutrient cycling (Allgeier, Layman, Mumby &
73 Rosemond, 2014). For marine megafauna species, mammals, turtles and sharks, body size is
74 associated to nutrient cycling, trophic regulation and community shaping (Tavares et al., 2019).
75 Yet the diversity of ecosystem functions performed by different taxonomic groups as well as if
76 these functions can be maintained or lost when species are removed remains elusive.

77 Several distinct species may have equivalent functional roles, therefore being redundant
78 (Halpern & Floeter, 2008). Under this rationale, functional redundancy guarantees that no
79 functional loss occurs if a redundant species is removed (Fonseca & Ganade, 2001; Halpern &
80 Floeter, 2008; Pimiento et al., 2020; Rosenfeld, 2002). Yet certain species may play unique
81 roles in the ecosystem (Bellwood, Hoey & Choat, 2003; Mouillot et al., 2013). Reef fish, for
82 instance, one of the most diverse vertebrate assemblages (approximately 6,500 species;
83 Kulbicki et al., 2013), are characterized by high functional redundancy as well as vulnerability
84 of functions (Mouillot et al., 2014). But there are examples of (fish) species that have unique
85 roles in ecosystem functioning, as the *Sparisoma viride* and *S. amplum* in the tropical Atlantic,
86 being the only species acting as excavators because they feed frequently on live scleractinian
87 corals in Caribbean and Brazilian reefs, respectively (Bonaldo et al., 2014; Bruggemann,
88 Kuyper & Beeman, 1994; Ferreira & Gonçalves, 2006). In addition to the potential redundancy
89 of functions (and traits) within a taxonomic group, certain reef functions may be performed by
90 species belonging to distinct taxonomic groups. For instance, certain reef fish and marine turtle
91 species may have similar roles through their diets, being herbivorous, and removing algal cover
92 from coral reefs (Goatley, Hoey, & Bellwood, 2012).

93 The loss of species with certain ecosystem functions and their effects in reef
94 environments are already known (Bonaldo et al., 2014; Bornatowski, Navia, Braga, Abilhoa, &
95 Corrêa, 2014; Ferreira & Gonçalves, 2006; Hammerschlag et al., 2019). The removal of
96 herbivorous reef fish, for instance, can release algal growth that negatively impacts the survival

97 of coral species, thus compromising coral reef resilience (Adam, Burkepile, Ruttenberg &
98 Paddock, 2015; Hughes et al., 2007). The loss of top predators alters the trophic structure of
99 reefs through the release of mesopredators and their effects over primary consumers abundance
100 pattern (Ruppert, Travers, Smith, Fortin & Meekan, 2013). However, it is still unknown for
101 most species whether species from distinct taxonomic groups are functionally redundant is still
102 unknown. Developing new approaches that focus on ecosystem processes is a priority for
103 marine resilience management (Hughes, Bellwood, Folke, Steneck & Wilson, 2005). Although
104 modern functional approaches have the challenge of linking ecosystem function with traits, the
105 protection of species with traits related to critical functions is crucial for reefs' conservation
106 (Bellwood et al., 2019). To which extent would Atlantic Ocean reefs be compromised by the
107 loss of functions performed by threatened species? The answer to this question depends on our
108 knowledge of the functions performed by distinct species, and the level of redundancy or
109 overlap in functions delivered by different taxonomic groups.

110 We investigate the ecosystem functions performed by reef vertebrate species of different
111 taxonomic groups – mammals, sea turtles, Elasmobranchii and Teleostei – in Atlantic Ocean
112 reefs. We provide the first inventory and categorization of ecosystem functions delivered by a
113 set of 224 species in Atlantic reefs. Also, using a trait-based approach (e.g. maximum size (cm),
114 depth category, trophic group (diet category), biomass (g), caudal fin and body shape
115 classifications), we assessed the patterns of functional diversity, functional redundancy and
116 functional originality across reefs in the Atlantic Ocean, from regional to local scales. Finally,
117 we investigated the effect of threatened species removal (%) in different ecosystem functions
118 to losses in the functional space of reefs (% FRic). We predicted that large-bodied species and
119 scrapers, browsers or herbivorous trophic groups would be associated with trophic regulation
120 and nutrient transport/storage functions in reefs. Also, different taxonomic groups as
121 Elasmobranchii and Teleostei would be redundant based on traits similarities in body and

122 caudal fin shape and diet categories. We expected that species richness found in Caribbean reefs
123 will translate into high functional redundancy and originality, as well as buffer functional losses
124 from the loss of species. Finally, we hypothesized that in the Atlantic Ocean, the functional
125 structures of reefs isolated from the Caribbean could be more vulnerable to the loss of
126 vertebrates and their ecosystem functions.

127

128 **2 | MATERIALS AND METHODS**

129 **2.1 | Database**

130 We compiled information for 224 marine vertebrate reef species: four marine mammals,
131 five sea turtles, 88 Elasmobranchii and 127 Teleostei species. The species set considered in this
132 study are those recorded over reef environments (consolidated bottoms, including rhodolith
133 beds, coral, coralline algae and rocky reefs), which can use these habitats for shelter, feeding
134 and/or spawning (Pinheiro et al., 2018). The Teleostei families considered were Acanthuridae,
135 Carangidae, Epinephelidae, Kyphosidae, Lutjanidae and Labridae (subfamily Scarinae), based
136 on the recognized importance of these families as predators/mesopredators or herbivores in
137 reefs (Bonaldo et al., 2014; Longo, Ferreira, & Floeter 2014). The set of reef fish species was
138 obtained combining the Southwestern Atlantic Reef Fish database (Pinheiro et al., 2018), which
139 presents an up-to-date list of the Atlantic Ocean reef fish species (Elasmobranchii and
140 Teleostei), with the global database for Teleostei species of the GASPAR Project (Bender et
141 al., 2017; Kulbicki et al., 2013; Parravicini et al., 2013). For sea turtles and marine mammals,
142 we conducted searches in the available literature to define the set of Atlantic Ocean reef species.

143 The Atlantic reef band was divided in ten provinces (*sensu* to Spalding et al., 2007):
144 Warm Temperate Northwest Atlantic, Tropical Northwestern Atlantic, North Brazil Shelf,
145 Tropical Southwestern Atlantic, Warm Temperate Southwestern Atlantic, St Helena and

146 Ascension Islands, Benguela, Gulf of Guinea, West African Transition and Lusitanian. The
147 provinces approach was chosen because it covers the coastal area of the continents, as well as
148 reefs regions in a regional scale. Shapefiles of species distributions were extract from IUCN
149 (IUCN, 2019), and we obtained presence and absence data for each species in the above-
150 mentioned provinces (See Fig. S1). For a finer detail of the study area (local scale), we built 4
151 x 4-degree grid (for more details about the grid approach, See Section 2.4).

152

153 2.2 | Ecosystem functions and species traits

154 We compiled ecosystem functions associated to each reef vertebrate species through a
155 Google Scholar search combining two keywords: “spp. + ecosystem function” and “spp. +
156 ecosystem functioning”. Ecosystem functions were then organized into categories based on
157 Villéger et al. (2017) and Tavares et al. (2019): “Ecosystem engineering”, “Participating to
158 nutrient cycles” and “Controlling food webs”. The first study presents a classification for the
159 main ecosystem functions associated with bony fish species – food web control, ecosystem
160 engineers and participation in nutrient cycles – and served as the basis for our categorization of
161 ecosystem functions.

162 Trait data were compiled online from FishBase (www.fishbase.org), SeaLifeBase
163 (www.sealifebase.org), IUCN (www.iucnredlist.org) and through literature search. For reef fish
164 Teleostei species, maximum size (cm), depth category and trophic group (diet category) traits
165 were obtained from the GASPAR Project database. For each vertebrate reef species, we
166 compiled the following traits: maximum size (cm), depth category, trophic group (diet
167 category), biomass (g), caudal fin and body shape classifications. The depth categories were
168 “Shallow” (< 30m), to “Mid” (30-50m), “Deep” (50-100m) and “Very deep” (> 100m)
169 following the ascending depth order (Pinheiro et al., 2018). Trophic categories were carnivores,
170 piscivores, planktivores, mobile invertebrate feeders, omnivores, herbivores, scraper

171 herbivores, excavator herbivores, browser herbivores and algal feeders (Bonaldo et al., 2014;
172 Ferreira, Floeter, Gasparini, Ferreira & Joyeux, 2004; Longo et al., 2014). Body mass (**M**) was
173 estimated for each individual species using weight-length relationships: $M = aL^b$, where **L** is
174 the maximum length and **a** and **b** are coefficient estimates for species according FishBase and
175 SeaLifeBase references (Froese & Pauly, 2019; Palomares & Pauly, 2019). When species
176 coefficients were not available, relative's congener species were used. Caudal fin
177 categorizations were: forked, heterocercal, lanceolated, lunated, rounded and truncated
178 (Compagno, Dando & Fowler, 2005; Last et al., 2016). For species without caudal fin, as all
179 turtles and some ray's species, "NA" was inserted for that trait. Body shape categories used
180 were: circular, short deep, wedge shaped, elongated, rhombic, fusiform, oval, lozenge shaped,
181 eel like and shovel shaped (Compagno, Dando & Fowler, 2005; Last et al., 2016).

182 The set of traits used determines the species' performance in reef environments (e.g.
183 food acquisition, nutrient budget, mobility and defense against predation), which represents
184 ecosystem functions delivered by marine vertebrates species such as food chains control
185 (trophic-dynamics regulations), ecosystem engineering (i.e., bioturbation and/or bioerosion)
186 and nutrient cycling (Pimiento et al., 2020; Tavares et al., 2019; Villéger et al, 2017) (for more
187 details about functional traits and ecosystem functions, **See Table S1**).

188 Functional richness values are influenced by variations in the number of traits used,
189 independent of trait values, and by the metric applied (Gower distance in this case). Further,
190 the FRic index decrease with the increasing number of species functional traits after projection
191 in the dimensional space when we use Gower distance, revealing that the number of traits
192 chosen represents satisfactorily the functional diversity of Atlantic Ocean reefs (Legras,
193 Loiseau, Gaertner, Poggiale & Gaertner-Mazouni, 2020).

194

195 2.3 | Functional diversity at the regional scale

196 At the regional scale, we measured the functional richness. First, quantitative traits as
197 the maximum body size (cm) and body mass (g) were standardized to avoid measurement
198 effects of these variables (*scale* function; Package base) (R Core Team, 2018). We then
199 measured the dissimilarity between 224 species considering their six functional traits using the
200 Gower distance (with one ordered, two numerical and three categorical traits) (Gower &
201 Legendre, 1986). On this distance matrix, we conducted a Principal Coordinate Analysis
202 (PCoA) to order species from four different taxonomic groups in the functional space (Villéger,
203 Manson & Mouillot, 2008). This total volume, or functional space, corresponds to the regional
204 functional richness (FRic) – in this case, of the Atlantic Ocean reefs and its provinces. To assess
205 the quality of the functional space, we used the mean squared deviation (mSD) and measured
206 the congruence between the Gower and Euclidian distances (Maire, Grenouillet, Brosse &
207 Villéger, 2015) (**Fig. S2**). The functional volume/space occupied by vertebrate assemblages in
208 each province, and by different taxonomic groups, as well the volume represented by threatened
209 species were calculated using the *convhulln* function (Package geometry) (Habel, Grasman,
210 Gramacy, Stahel & Sterratt, 2015). Species associated with different ecosystem functions and
211 functional traits were mapped in the functional space using the *ordiellipse* function with
212 standard deviations of points (Package vegan) (Oksanen et al., 2018), in order to assess where
213 ecosystem functions centroids are related to ecosystem functions performed by species. Finally,
214 we used a Redundancy Analysis (RDA) (Package vegan) to summarise the variation in the
215 response variables (ecosystem functions) that can be explained by the explanatory variables
216 (species traits) — i.e. which traits are associated with marine vertebrate species ecosystem
217 functions. To teste the RDA significance, we did an Anova analysis (Package stats).

218

219

220 **2.4 | Mapping functional diversity, redundancy and originality in Atlantic Ocean reefs**

221 We measured local species richness and functional diversity patterns by mapping
 222 species distribution and building a 4 x 4-degree grid (~440 km) along the Atlantic Ocean
 223 provinces/reefs. For each grid cell (83 cells in total), we calculated species richness, functional
 224 richness (FRic) (Villéger et al., 2008), functional redundancy (Rao, 1982) and functional
 225 originality (Pimiento et al., 2020). To test if functional richness (FRic) values in local reef
 226 assemblages differs from expected by chance, a null model was built. In this model we
 227 randomized species traits in the database, while controlling for local species richness
 228 (presence/absence data). Thus, communities/grid with their species identity but with random
 229 traits represent what would be expected in a random scenario. In our analyses, the “observed
 230 index” (I_{obs}) corresponds to the raw database. The model simulated the mean of 999 FRic
 231 indices for the simulated Atlantic Ocean reefs communities (I_{sim}), corresponding to “expected
 232 by chance” for each cell. We then calculated the standardized-effect size (SES; Eq. 1) through
 233 the mean standard deviation of the 999 indices from the simulated communities (σ_{sim}) (Gotelli
 234 & McCabe, 2002).

235 **Eq. 1**

$$236 \quad \text{SES} = \frac{(I_{obs} - I_{sim})}{\sigma}$$

237

238 The functional redundancy (FRed) at the local scale (i.e., difference between species
 239 diversity) was calculated using the *rao.diversity* function (FunRedundancy) (Package
 240 SYNCOSA) (Debastini & Pillar, 2012). To determine if functional redundancy in reef
 241 assemblages differs from expected by chance, we applied the same null model approach (Eq.

242 1). The mean standard deviation of 999 functional redundancy indexes was obtained through
243 simulated communities (σ_{sim}) for each cell.

244 Local species' originality was calculated using the mean functional uniqueness (FUn)
245 per cell based on the original Gower's distance matrix. For each species, functional uniqueness
246 was calculated considering the five nearest neighboring species in the functional space built in
247 each grid cell – the local vertebrate assemblage/community. The functional originality values
248 were calculated from the mean functional uniqueness of each grid cell according to species
249 traits combinations (for more details about the functional uniqueness considering the three, ten
250 and fifteen nearest neighboring species, **See Supplementary Material; Fig. S3**). To investigate
251 whether communities' originality differs from expected by chance, we used the same null model
252 applied for functional richness and redundancy (**Eq. 1**), where mean standard deviation of the
253 999 values of functional uniqueness were calculated from the Gower's random distance matrix
254 originated by the simulated communities (σ_{sim}). To test the correlation between the observed
255 functional diversity (FRic), functional redundancy (FRed) and functional uniqueness (FUn)
256 values with the "expected by chance" results, we used a linear regression analysis (Package
257 stats) (R Core Team, 2018).

258

259 **2.5 | Simulating the loss of ecosystem functions in Atlantic Ocean reefs**

260 Different species can overlap in functional space considering its combination of traits.
261 To investigate the importance of threatened species in delivering ecosystem functions in
262 Atlantic reefs, we simulated species' removal according to their threatened status, from
263 Critically Endangered, to Endangered, Vulnerable, and non-threatened species (CR → EN →
264 VU → NT → DD → LC; IUCN, 2019) and measured the loss in functional space when
265 threatened species with different functions are removed. The proportion on functional space

266 loss (% FRic) was estimated from an increasing species' removal (%) in each four ecosystem
267 functions ("Bioturbation/bioerosion", "Herbivory pressure", "Marine top predator" and
268 "Marine mesopredator") along the 83-cell grided map (4° x4°) into three marine regions: the
269 Caribbean, the Southwestern Atlantic and Eastern Atlantic. We used a null model approach to
270 randomly remove species from each community and contrast random species' loss to an ordered
271 removal according to extinction vulnerability (IUCN categories). From one thousand simulated
272 communities and their functional space loss, we extracted the first and fourth quantiles as well
273 as the average null value erosion.

274 To test species removal on an even finer scale and their effect on functional volume
275 loss, we removed the marine mesopredators (n = 114) in each grid cells, representing 83 distinct
276 reef communities. We simulated the removal of these species without considering their threat
277 status and we calculated the proportion of these species removed (%) and the amount of
278 functional volume loss (vol loss) in each Atlantic Ocean provinces/reefs. All analyses were
279 performed using the R software version 3.4.4 (R Core Team, 2018).

280

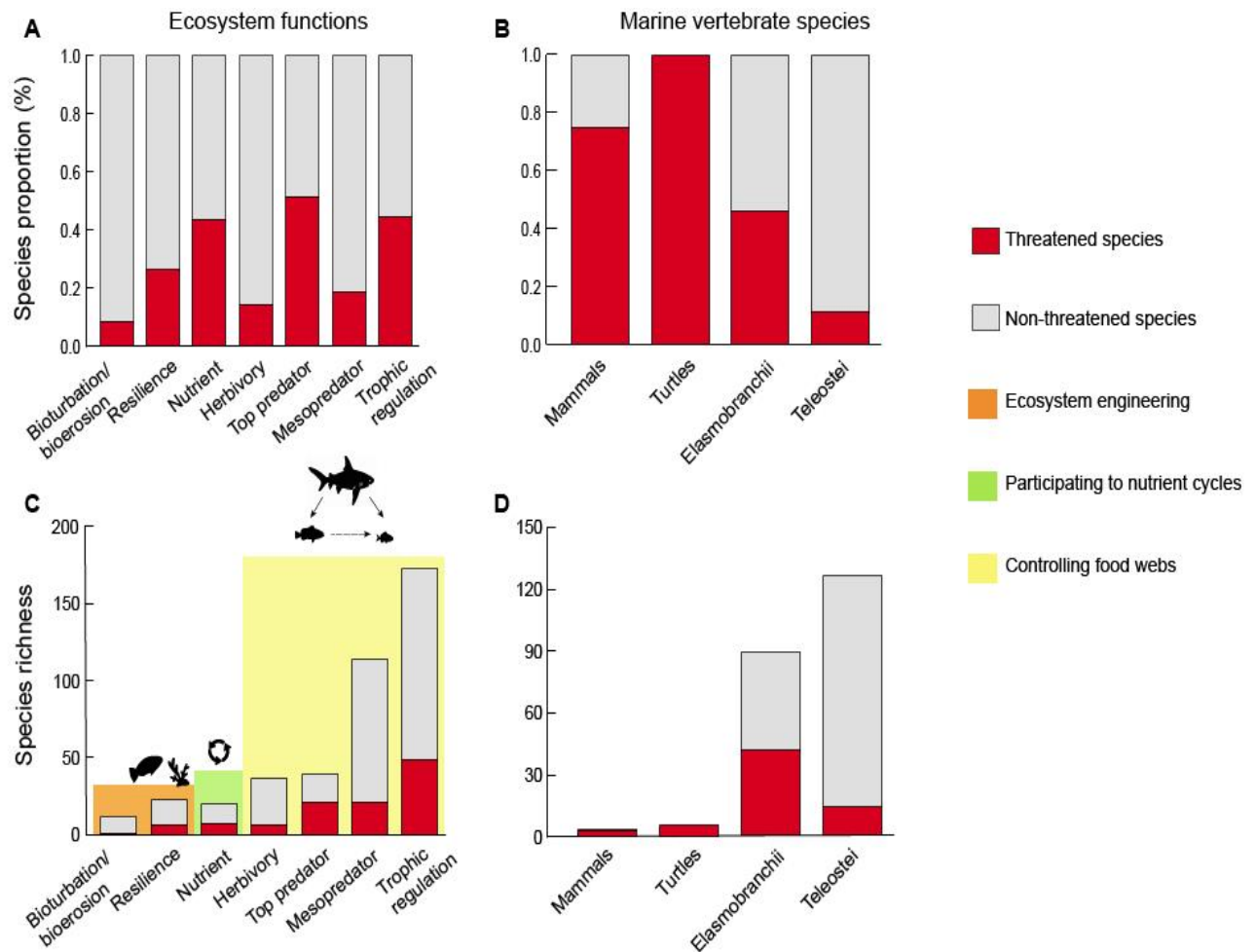
281 **3 | RESULTS**

282 **3.1 | The ecosystem functions of vertebrates in Atlantic Ocean reefs**

283 Our literature search has revealed that Atlantic Ocean reefs' vertebrates contribute to
284 ecosystem functions through "Herbivory pressure", "Nutrient transport and storage", "Coral
285 reef resilience", "Bioturbation/bioerosion", "Trophic regulation", "Marine top predator" and
286 "Marine mesopredator". Despite resilience being considered an emergent ecosystem property
287 (Bellwood et al., 2004), we have compiled species that have been associated to this property in
288 order to assess how resilience relates to traits and how it compromises functional space loss.
289 Out of the 224 species, 201 had at least one function reported in the literature, covering
290 approximately 90% of species in our dataset (See Table S2). Functions with the highest species

291 richness are associated to “Food web control” (Villéger et al., 2017), as “Trophic regulation”
292 (n = 175), followed by “Marine mesopredator” (n = 114), and “Marine top predator” (n = 39)
293 functions (**Fig. 1**). “Bioturbation/bioerosion” had the lower functional redundancy, being
294 represented only by 12 species across Atlantic Ocean reefs. The most redundant function,
295 “Trophic regulation”, also has the greater number of threatened species (n = 50; 28,5%). Yet
296 “Marine top predators” had the greater proportion of threatened species (53.84%), possibly
297 because this group is mostly represented by sharks and rays (**Fig. S4**). Forty-one of
298 Elasmobranchii found in Atlantic Ocean reefs are threatened with extinction (46%) (**Fig. 1**).
299 The most threatened taxonomic group was represented by sea turtles, which had all species
300 threatened with extinction (n = 5; 100%). Besides, marine mammals were the second most
301 threatened group in the Atlantic Ocean reefs (n = 3; 75%).

302



303

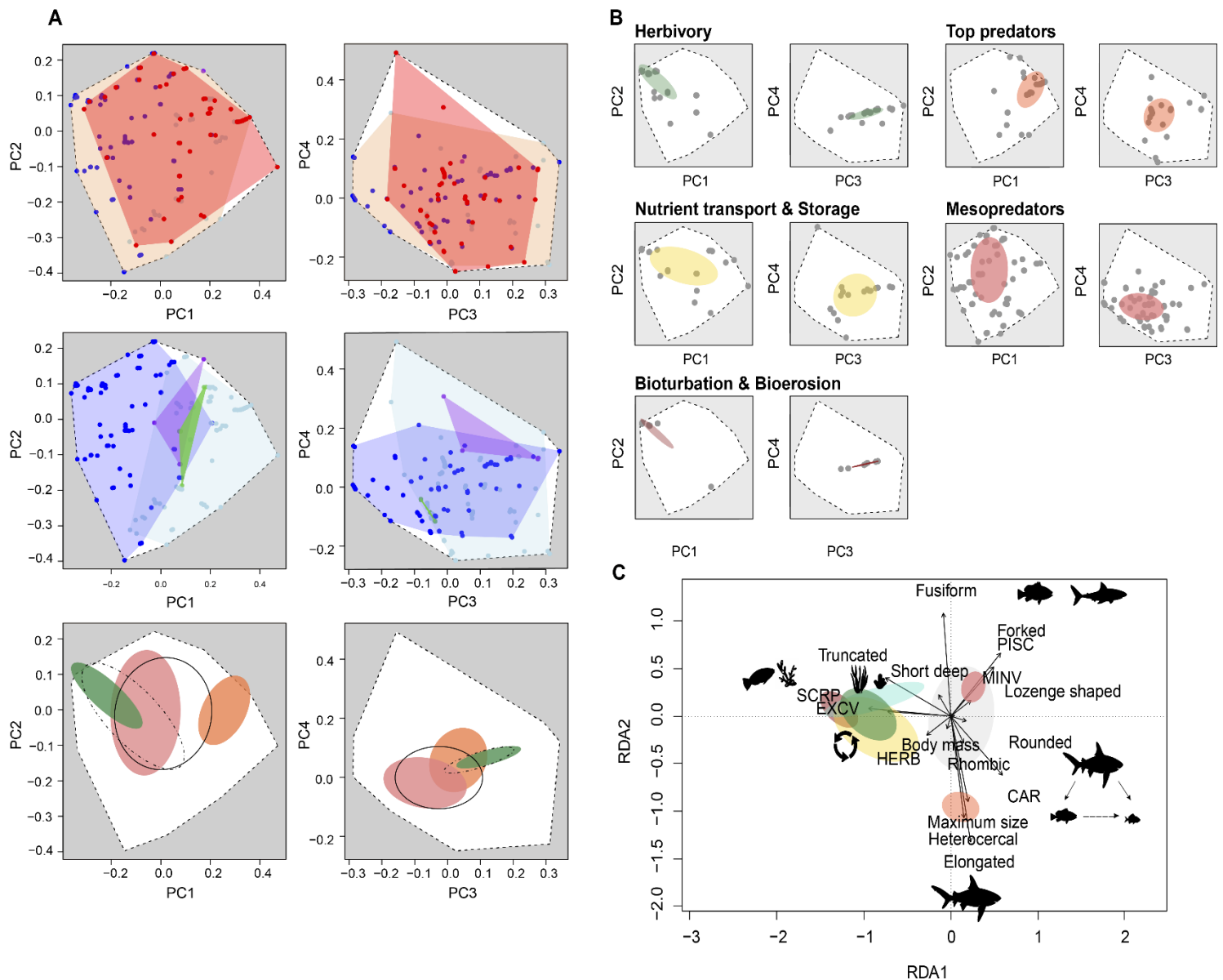
304 **Figure 1.** Ecosystem functions delivered by Atlantic Ocean reef vertebrates and its threatened
 305 status, in red. The proportion of threatened species (CR, EN and VU) in each ecosystem
 306 function (A) and across each taxonomic group (B). The species richness and threatened species
 307 richness found in each ecosystem function (C) and taxonomic group (D).

308

309 3.2 | Atlantic Ocean reefs: linking threatened species, functional traits and ecosystem 310 functions

311 In the Principal Coordinate Analysis (PCoA), the four first axes accounted for 91% of
 312 the variation in the functional space. The Tropical Northwestern Atlantic province, located in
 313 the southern Caribbean, had both the highest species richness (n = 134) and functional diversity.
 314 The functional structure of vertebrates found in this province corresponds to 79.7% of the

315 regional functional space – that of the Atlantic Ocean pool of species. In contrast, Benguela,
316 located in southern Africa, presented the lower species richness ($n = 31$) and functional volume
317 (29.6% of the regional functional space) (See Fig. S5). The distribution of threatened species
318 in functional space ($n = 63$, 44.8% of the regional space) revealed that this set of vertebrates
319 have a varied trait combination, occupying the extremes of the functional space. Yet the overlap
320 in between threatened and non-threatened species and between different taxonomic groups in
321 functional space revealed there is functional redundancy among vertebrates in reefs of the
322 Atlantic Ocean (Fig. 2A). The largest overlap between taxonomic groups was represented by
323 bony and cartilaginous reef fishes, which also filled the largest functional volumes (32.5% and
324 23.4%, respectively). Sea turtles and marine mammals did not show a high overlap in functional
325 space (Fig. 2A). Ecosystem functions may be correlated in functional space: “Trophic
326 regulation” encompasses “Marine top predators” and “Marine mesopredators”. When we
327 consider the first two axes (PC1 and PC2), “Herbivory pressure” function is associated with
328 “Coral reef resilience”, “Trophic regulation” and “Marine mesopredator” functions. When axis
329 PC3 and PC4 are taken into account, this ecosystem function also encompasses top predators’
330 species (Fig. 2A). Despite the functional redundancy identified at the regional scale, when
331 ecosystem functions are mapped into functional space, we found that functions correlated with
332 different areas of the functional space ($p < 0.01$), i.e., are performed by species with a specific
333 set of traits (Fig. 2B). Species with herbivory, scraper and excavator diets were mainly related
334 to “Herbivory pressure”, “Coral reef resilience”, “Nutrient transport and storage” and
335 “Bioturbation/bioerosion” functions. “Marine mesopredator”, “Marine top predator” and
336 “Trophic regulation” were performed mainly by carnivorous with rounded fin, large species
337 with elongated body shape and heterocercal caudal fin and piscivorous with forked caudal fin
338 species, respectively (Fig 2C).



339

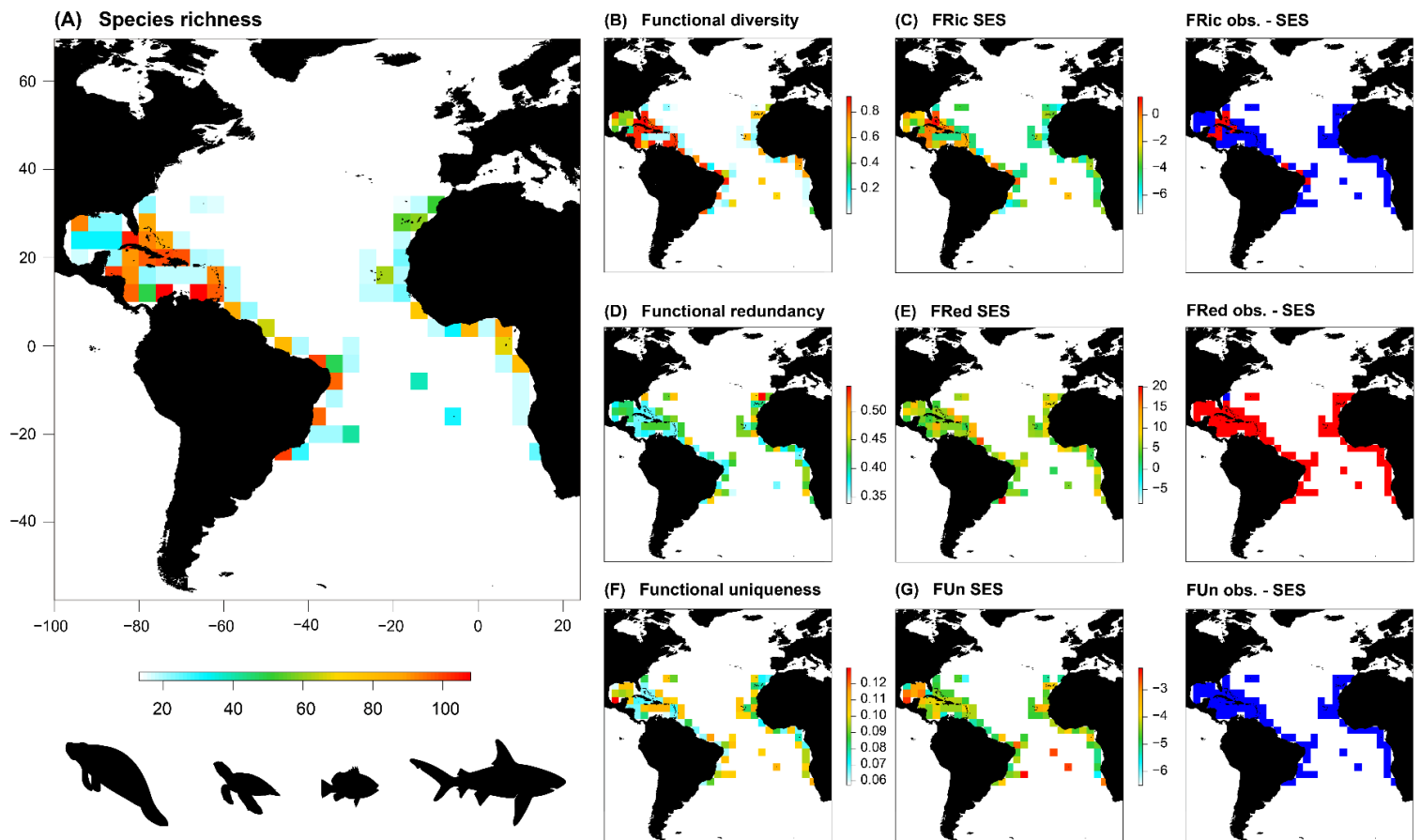
340 **Figure 2.** The functional space (PC1, PC2, PC3 and PC4) occupied by marine vertebrates
 341 across Atlantic Ocean reefs, the mapping of ecosystem functions in the functional space (PC1,
 342 PC2, PC3 and PC4) and the Redundancy Analysis (RDA) for the relationship of attributes and
 343 ecosystem functions. (A) the red polygon represents the volume (43.6%) occupied by
 344 threatened species relative to the regional functional space (dashed line) and the light colour
 345 represents the polygon occupied by non-threatened species; the volume filled by different
 346 taxonomic groups: mammals (purple, four species), sea turtles (green, 0.00003%),
 347 Elasmobranchii (light blue, 23.4%) and Teleostei (dark blue, 32.5%); map of ecosystem

348 functions in the functional space: “Herbivory pressure” (light green), “Marine top predators”
349 (orange) and “Marine mesopredators” (pink). The transparent ellipse with the solid line
350 represents Trophic regulation and encompasses “Marine top predator”, “Marine mesopredator”
351 and “Herbivory pressure”. The dotted circle represents “Coral reef resilience” and encompasses
352 “Herbivory pressure”, “Marine top predator” and “Marine mesopredator”; **(B)** distribution
353 centroid of traits associated to ecosystem functions and species performance in the functional
354 space; coloured circles revealed where the ecosystem function centroid is mapped in the two
355 main axes and the species most correlated; **(C)** the relation between the main functional traits
356 categories related to ecosystem functions performed by 201 Atlantic reef marine vertebrate
357 species.

358

359 **3.3 | Functional diversity across Atlantic Ocean reefs**

360 In the Atlantic, the Caribbean region (Warm Temperate Northwest Atlantic and
361 Tropical Northwestern Atlantic provinces) concentrates the higher richness of vertebrate
362 species associated to reef environments ($n = 230$). The Southwestern Atlantic (Tropical
363 Southwestern Atlantic and Warm Temperate Southwestern Atlantic provinces) also presented
364 high species richness at the grid scale (80 to 100 species). In contrast, Eastern Atlantic reefs
365 had the lowest species richness, where the vast majority of assemblages ranging from 20 to 60
366 species (**Fig. 3A**). Functional richness (FRic) is correlated to species richness (**Fig. 3B**). The
367 null model has revealed that the functional richness observed is higher than “expected by
368 chance” ($p < 0.01$; $R^2 = 0.94$) (**Fig. 3C**). Observed functional redundancy values are similar
369 among assemblages across Atlantic Ocean reefs, being greater in a single grid cell of Lusitanian
370 province (extreme north of Africa continent) (**Fig. 3D**). The observed value does not differ from
371 the “expected by chance” ($p > 0.01$; $R^2 = 0.02$) (**Fig. 3E**). Also, the mean functional uniqueness
372 is similar among reefs assemblages, being greater in a single grid cell of the Caribbean where



373 there are species with unique functional traits combinations (**Fig. 3F**). The functional
 374 uniqueness null model has revealed that the sampled community is more original according to
 375 species functional traits combinations than “expected by chance” ($p < 0.01$; $R^2 = 0.74$) (**Fig. 3G**).
 376 Further, there is a negative correlation between observed functional uniqueness and functional
 377 redundancy values ($p < 0.01$; $R^2 = 0.18$) (for more details about functional diversity indexes
 378 relationship, **See Supplementary Material; Fig. S6**).

379

380 **Figure 3.** Functional diversity of vertebrates in Atlantic Ocean reefs. **(A)** Total species richness
 381 at the grid scale ($n = 224$); **(B)** Functional richness (FRic); **(C)** Standardized-effect size (SES)
 382 of the null model for functional richness (FRic); **(D)** Functional redundancy; **(E)** Standardized-
 383 effect size (SES) of the null model for functional redundancy; **(F)** Functional uniqueness

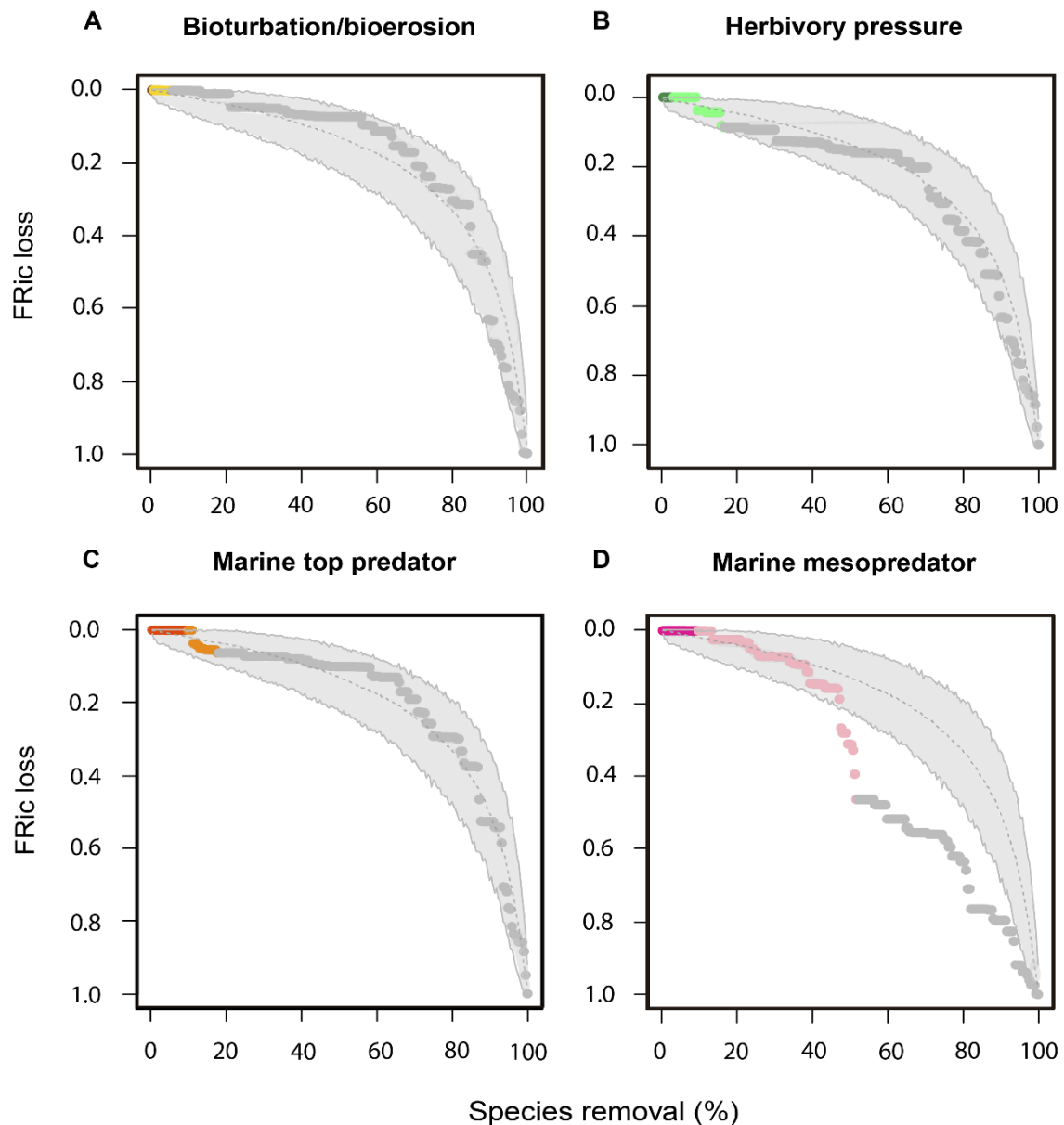
384 considering the five closest species in the functional space in each assemblage; (G)
385 Standardized-effect size (SES) of the null model for functional uniqueness. The color gradient
386 represents the observed and the "expected by chance" values (blue: low values; green to yellow:
387 intermediate values; orange to red: high values). Maps with red grid cells represents where there
388 is greater functional richness, functional redundancy and functional uniqueness than expected
389 by chance ($OBS > SES$). Grid cells where observed indexes were lower than expected by
390 change are coloured blue ($OBS < SES$).

391

392 **3.4 | Threatened species removal and the erosion of ecosystem functions**

393 At the regional scale, the simulated removal of threatened and non-threatened species
394 associated with specific ecosystem functions did not differ from the losses expected under a
395 null model. With the exception of "Marine mesopredators", which removal causes a 40% loss
396 in the functional space at the regional scale (**Fig. 4**). The largest proportion of species removed
397 in reef communities through of mesopredators simulated removal was in the Caribbean (60%),
398 followed by the Brazilian coast and the western region of the African coast (**Fig. 5A**). The
399 greatest losses in functional volume occurred in the southern Caribbean reef communities and
400 the Brazilian coast, followed by the northern region of Africa (vol loss = 0.8) (**Fig. 5B**). Sites
401 with a greater richness of mesopredator species are more redundant – i.e. lower functional
402 losses. The removal of mesopredators also significantly impacts the functional space of the
403 Caribbean and Southwestern Atlantic regions (**Fig. S7J, K**). In the Eastern Atlantic,
404 herbivorous' species removal is compromises almost 20% of the functional volume (**Fig. S7F**).

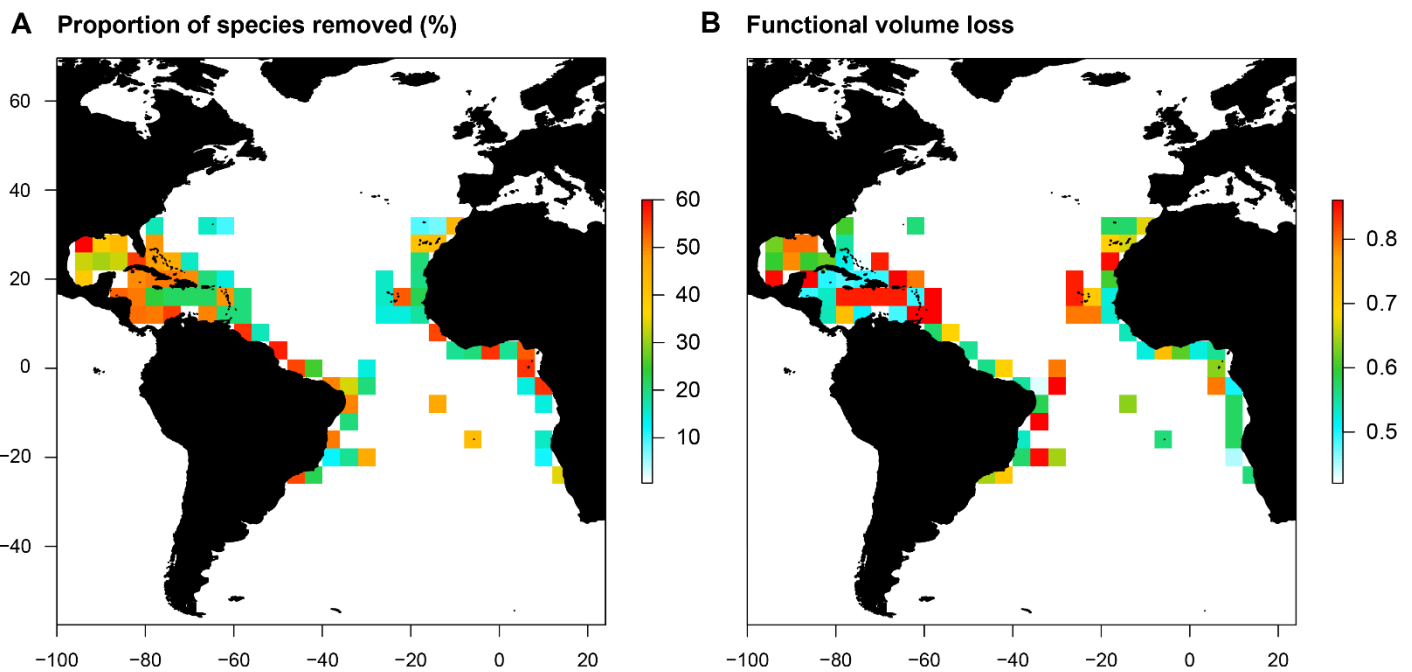
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406

407 **Figure 4.** Functional diversity loss in Atlantic Ocean reefs following the removal of threatened
 408 species within different ecosystem functions: (A) “Bioturbation/bioerosion”; (B) “Herbivory
 409 pressure”; (C) “Marine top predator” and (D) “Marine mesopredator”. Each colored dot
 410 represents a single species that performs these functions; with darker colors depicting the
 411 removal of threatened species and lighter tones the removal of non-threatened species. Gray
 412 points represent other species that do not perform these ecosystem functions in particular. Grey
 413 lines represent the 95% CI of the null model distribution, where species are removed randomly.

414



415 **Figure 5.** The effects of marine vertebrate mesopredator species removal in (A) the proportion
 416 of species removed and, as a consequence, (B) the functional volume loss in each grid cell (i.e.
 417 each Atlantic Ocean reef communities). The color gradient represents the proportion (%) and
 418 the volume loss values (blue: low values; green to yellow: intermediate values; orange to red:
 419 high values).

420

421 **4 | DISCUSSION**

422 We have identified seven ecosystem functions delivered by this set of 224 marine
 423 vertebrate species in Atlantic Ocean reefs, including mammals, sea turtles, Elasmobranchii and
 424 Teleostei taxa. The importance of these taxonomic groups and their functions in reef ecosystems
 425 have been reported and categorized yet (Brandl et al., 2019; Hammerschlag et al., 2019;
 426 Pimiento et al., 2020; Tavares et al., 2019; Villéger et al., 2017), but there have been few
 427 attempts to identify similarities in functions delivered by species belonging to distant lineages.
 428 Marine megafauna species (i.e., large fishes, sea turtles and marine mammals) may share

429 comparable functional traits associated to specific ecosystem functions found in the oceans
430 (Pimiento et al., 2020; Tavares et al., 2019). However, the ecosystem functions delivered by
431 different marine taxa is a novel approach for reef species.

432 The set of species and traits used in this study revealed that there is functional overlap
433 (certain functional redundancy degree) between mammals, sea turtles and fish species in
434 Atlantic reefs, whereas small sharks and large Teleostei species caused the greatest functional
435 loss by acting as marine mesopredators. The functional uniqueness approach also showed a
436 homogeneous distribution pattern along the Atlantic Ocean, but some reef communities had
437 higher FUn values. Moreover, the functional trait set used is adequate to promote functional
438 diversity analysis according to taxonomic groups biological specifications. Pimiento et al.
439 (2020) revealed that for marine megafauna, there is a compartmentalization in the functional
440 space between Elasmobranchii, Teleostei and mammals. In addition, sharks were responsible
441 for the greatest losses of functional richness according to their attributes, being the most
442 threatened taxonomic group due to vulnerability to extinctions. As a consequence, these species
443 will also have a higher uniqueness value, along with bone fish species (Pimiento et al., 2020).
444 Despite the similarities, our study approached the functional indexes in a large cross taxa group
445 of reef species not limited to the marine megafauna. Still, we related the importance of
446 functional attributes in the performance of species in ecosystem functions.

447 The seven ecosystem functions represented by these species are associated with reef
448 dynamics and functioning – from nutrient cycling, organism distribution to control of prey
449 populations by top predators – and are critical to reef resilience (Tavares et al., 2019; Villéger
450 et al., 2017). In coral reefs, the bioerosion caused mainly by parrotfishes (subfamily Scarinae)
451 is important for the three-dimensional physical reef structure because the sediments rework and
452 transport (e.g. CaCO₃ removal from living organisms) (Bonaldo et al., 2014; Bruggemann,

453 Kessel, Rooij & Breeman, 1996; Lellys, Moura, Bonaldo, Francini-Filho & Gibran, 2019).
454 Similarly, the herbivory pressure exerted by grazing reef fish and sea turtles (e.g. *Scarus*
455 *trispinosus*, *Scarus iseri*, *Acanthurus chirurgus* and *Chelonia mydas* species) controls algal and
456 seagrass growth, influencing coral settlement and survivorship, and therefore shaping the
457 structure and dynamics of reefs (Bonaldo et al., 2014; Burkepile & Hay, 2008; Christianen et
458 al., 2019; Goatley et al., 2012; Suchley & Alvarez-Filip, 2017). Further, top and mesopredators
459 may trigger cascading effects, altering prey populations' size and behaviour (Heithaus et al.,
460 2008; Myers, Baum, Shepherd, Powers & Peterson, 2007).

461 Despite differences in the distribution of taxonomic groups in the regional functional
462 space, traits were effectively associated with ecosystem functions when mapped in the
463 functional space. Rounded fin species, and carnivore diet were related to trophic regulation.
464 Forked fin, lozenge shaped species (e.g. manta rays), piscivore and mobile invertivore diets
465 were related to marine mesopredator function. Besides, marine top predator species were
466 mainly associated with maximum size, heterocercal fin and elongated body shape traits. Body
467 length and body mass are correlated, being considered a key functional trait, influencing dietary
468 preferences and metabolic rates, which are correlated with organisms' trophic position (Tavares
469 et al., 2019). All functions that are examples of trophic control have been associated in
470 functional space. Reef resilience, for instance, is associated with herbivory pressure on reef
471 environments (Adam et al., 2015; Green, Bellwood, & International Union for Conservation of
472 Nature, 2009; Hughes et al., 2007). Our results have revealed that herbivory is mainly
473 performed by bony fish, where 27% of species are browsers, excavators, scrapers, or feed on
474 microalgae, therefore potentially removing amounts of plant material from the substrate when
475 feeding (Ferreira & Gonçalves, 2006; Francini-Filho, Ferreira, Coni, De Moura, & Kaufman
476 2010; Mantyka & Bellwood, 2007). While the herbivory pressure exerted by *Chelonia mydas*
477 individuals equals many reef fish (Goatley et al., 2012), in Hawaiian Archipelago (Central

478 Pacific Ocean) and Fernando de Noronha (Western Atlantic Ocean) reefs, green turtles have a
479 major contribution of total herbivore biomass only in sheltered sites (with low rugosity, low
480 coral cover and high algal cover), highlighting that different vertebrate herbivory species may
481 target distinct algal resources, where the functional complementarity is needed to maintain the
482 coral reefs ecosystem functioning (Cardona, Campos & Velásquez-Vacca , 2020).

483 The potential loss of threatened species ($n = 63$) may compromise a large proportion of
484 the regional functional space (44.8%) and its ecosystem functions. These species mostly share
485 a macrocarnivore diet and large body size, which have been investigated in previous studies as
486 good predictors of extinction risk for fish and marine mammal species (Bender et al., 2013;
487 Ceretta et al., 2020; Dulvy & Reynolds, 2002; Dulvy, Sadovy & Reynolds, 2003). Sharks and
488 rays are the majority of top predator species in Atlantic Ocean reefs (89.7%) and are largely
489 threatened (46%). The majority of top predator species are large-bodied mammals, sharks and
490 rays, most being targeted by fisheries around the world, as well as in the Atlantic Ocean (Fenner,
491 2014; Giglio, Luiz, & Gerhardinger, 2015; Lewison et al., 2014; Morais, Ferreira, & Floeter,
492 2017). In the Atlantic, Elasmobranchii species suffers from bycatch due to pelagic longline
493 fisheries, leading to changes in population dynamics (Oliver, Braccini, Newman & Harvey,
494 2015). These species share life-history traits – e.g. slow growth and late maturity – making their
495 stocks more fragile and harder to recover, increasing their vulnerability (Dulvy et al., 2014;
496 Stevens, Bonfil, Dulvy & Walker, 2000). Despite the functional role of sharks having important
497 effects on reefs trophic cascades, the functional redundancy among apex predators is
498 questionable since most of shark’s species are no longer considered top predators but
499 mesopredators as a consequence of reduction of their size and biomass, reinforcing threats to
500 marine mesopredators ecosystem function (Roff et al., 2016).

501 Although not being the most threatened group (18.4%; 21 spp. threatened with
502 extinction), the simulated removal of mesopredator species (i.e. Elasmobranchii and large
503 Teleostei species) might compromise the functional structure of Atlantic Ocean reefs, at the
504 province, regional and local spatial scale. These species have distinct traits, which imply a wide
505 distribution in the functional space, high functional richness and greater losses in functional
506 space when removed. For marine ecosystems, the importance of mesopredators for the reef
507 functioning is already known. As a consequence, their removal from reef ecosystems might
508 compromise the nutrient cycling between adjacent pelagic and reef habitats and may also
509 modify the behaviour of herbivorous reef fish (McMaculey et al., 2012; Rizzari, Frisch, Hoey
510 & McCormick, 2014). Moreover, this species loss will affect one of the last resources of reefs,
511 since top predator populations stocks have already been greatly depleted (Worm et al., 2013).
512 Furthermore, there is evidence for limited redundancy between small sharks and teleosts
513 according to maximum prey size and gap width analysis, suggesting that these reef shark
514 species have singular effect in the food web as mesopredators (Barley, Clark & Meeuwig,
515 2019). In the Caribbean, changes in reef environments have been associated to the absence of
516 mesopredator species as groupers and sharks, caused by anthropogenic effects such fishing
517 pressure, habitat degradation and pollution (Cheung et al., 2010; Ward-Paige et al., 2010). In
518 the Southwestern Atlantic coast, species as groupers have suffered marked population declines
519 in recent decades (Bender et al., 2014; Zapelini, Bender, Giglio & Schiavetti, 2019). Overall,
520 the rarity and limited distribution of sharks and large bodied groupers to few reefs, suggests
521 that their ecological function may be compromised in the Brazilian province (Morais, Ferreira
522 & Floeter, 2017).

523 As expected, being the center of marine biodiversity in the Atlantic Ocean (Bellwood et
524 al., 2004; Floeter et al., 2008), the Caribbean had the highest species richness and functional
525 richness at the local (grid) scale. Such species richness pattern has been observed for several

526 (different) marine taxonomic groups' in the Atlantic Ocean (McWilliam et al., 2018;
527 Miloslavich et al., 2010; Mouillot et al., 2014; Roberts, 2002; Tittensor et al., 2010). Also, as
528 the second center of diversity in the Atlantic Ocean – being considered a regional hotspot
529 responsible for 94% of the Southwestern Atlantic reef fish species endemism (Moura, 2002;
530 Pinheiro et al., 2018) – the Brazilian coast presented a high species richness. The values
531 exhibited for the Brazilian coast reef fauna are slightly lower when compared to the Caribbean,
532 but greater than that of the African coast.

533 The high functional richness identified for assemblages in the Caribbean and along the
534 Brazilian coast (Tropical Northwestern Atlantic, Tropical Southwestern Atlantic and Warm
535 Temperate Southwestern Atlantic provinces) is possibly and outcome of the taxonomic
536 diversity found in these assemblages. While species richness means redundancy (Fonseca and
537 Ganade, 2001; Halpern & Floeter 2008), it also means that functional vulnerability of
538 uniqueness (Mouillot et al., 2014) could characterize these assemblages. There are different
539 taxonomic groups, with a diversity of trait combinations, and also lower redundancy. The
540 observed functional redundancy values have revealed a homogeneous distribution pattern at the
541 local and regional scales. Such redundancy and lower than expected functional richness could
542 be the result of functional traits chosen (maximum size, depth category, trophic group, biomass,
543 caudal fin and body shape) and the presence of species with a broad geographical distribution
544 (e.g. marine mammals, sea turtles and sharks), covering several Atlantic Ocean reefs regions.
545 However, the standardize effect-size might suggest that there is no type of selection acting on
546 functional redundancy across these reefs. For the set of 224 Atlantic marine vertebrate species,
547 the functional redundancy highlighted that functional traits approach is more limited when
548 comparing distinct taxonomic groups, since compiling commensurate traits between these
549 lineages and, at the same time, associated with functional performance of species is an arduous
550 task. Similarly, the functional uniqueness identified homogeneous ecosystem functions

551 distribution pattern if considering the five nearest neighboring species in each grid cell (e.g. ten
552 and fifteen closest species presented regions with higher functional originality clustering). This
553 may be an outcome of species uniqueness not being associated with species richness and
554 functional diversity patterns around Atlantic reefs. Further, the standardized-effect size
555 indicates that the observed species originality is also higher than the expected by chance. This
556 result is probable caused by different marine vertebrate groups which are expected to be more
557 distinct physically and functionally (Hammerschlag et al., 2019).

558 Despite reef ecosystems are home to a fascinating diversity of species, described in
559 heterogeneous and admirable forms of life, we do not know enough about the ecosystem
560 functions delivered by distinct reef species. These habitats host approximately one quarter to
561 one third of all marine life, whereas one third of reef-building coral species are facing great
562 extinction risk from anthropogenic local impacts and climate change (Carpenter et al., 2008;
563 Fisher et al., 2015), compromising the ecosystem functioning. The link between functional
564 traits and ecosystem functions is essential to the management and conservation of reef species
565 (Bellwood et al., 2019; Fonseca & Ganade, 2001; Villéger et al., 2017; Pimiento et al., 2020).
566 Our results highlight the relationship between species' functional traits and ecosystem functions
567 and indicate that the functional overlap between different taxonomic groups may be limited
568 according to the set of traits used. The mesopredators removal had the greatest effect on the
569 erosion of the functional space, which could severely compromise the structure and functioning
570 of all Atlantic reefs, reinforcing that these species deserve attention in conservation planning.
571 As demonstrated in our analysis, studies on ecosystem functions of marine species can be
572 excellent conceptual frameworks to understand how to contribute to save reefs from future
573 degradation. (Bellwood et al., 2019).

574

575

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581

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867 **SUPPORTING INFORMATION**

868 **Table S1:** Functional traits and their relationship with ecosystem functions performed by 201
 869 marine vertebrate species of distinct taxonomic groups in Atlantic Ocean reefs. The set of traits
 870 used was based in Pimiento et al. (2020), Tavares et al. (2019) and Villéger et al. (2017).

Functional trait	Ecosystem function
Maximum body size	Food acquisition; nutrient transport and storage; capacity to connect and disparate ecosystems
Body mass	Metabolic demand; food acquisition; nutrient transport and storage; per capita excretion rates
Maximum depth	Habitat use; location of ecosystem contributions; nutrient transport and storage; trophic-dynamics regulation
Trophic group	Controlling food webs; nutrient transport and storage; capacity to partition the niche; capacity to provide trophic functional redundancy
Caudal fin	Mobility within/between habitat(s)
Body shape	Mobility within/between habitat(s); social interactions

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873 **Table S2:** List of 201 Atlantic Ocean reef marine vertebrate species and their ecosystem
 874 functions reported in literature.

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Species	Taxonomic group	IUCN	IUCN Trend	HP	NTS	BB	CRR	MTP	MS	TR
		Status 2019								
<i>Acanthurus bahianus</i>	Osteichthyes	LC	Stable	1	1	0	1	0	0	1
<i>Acanthurus chirurgus</i>	Osteichthyes	LC	Stable	1	1	0	1	0	0	0
<i>Acanthurus coeruleus</i>	Osteichthyes	LC	Stable	1	1	0	0	0	0	0
<i>Acanthurus monroviae</i>	Osteichthyes	LC	Unknown	1	0	0	0	0	0	0
<i>Acroteriobatus annulatus</i>	Osteichthyes	LC	Unknown	0	0	0	1	0	1	1
<i>Acroteriobatus blochii</i>	Chondrichthyes	LC	Unknown	0	0	0	1	0	1	1
<i>Aetobatus narinari</i>	Chondrichthyes	NT	Decreasing	0	0	0	0	0	1	1
<i>Alectis alexandrina</i>	Osteichthyes	LC	Stable	0	0	0	0	0	1	1
<i>Alectis ciliaris</i>	Osteichthyes	LC	Unknown	0	0	0	0	0	1	1
<i>Alopias superciliosus</i>	Chondrichthyes	VU	Decreasing	0	0	0	0	1	0	1
<i>Alopias vulpinus</i>	Chondrichthyes	VU	Decreasing	0	0	0	0	1	0	1
<i>Apsilus dentatus</i>	Osteichthyes	LC	Unknown	0	0	0	0	0	1	1
<i>Apsilus fuscus</i>	Osteichthyes	LC	Unknown	0	0	0	0	0	1	1
<i>Atlantoraja castelnaui</i>	Chondrichthyes	EN	Decreasing	0	0	0	0	0	0	1
<i>Atlantoraja cyclophora</i>	Chondrichthyes	VU	Decreasing	0	0	0	0	0	0	1
<i>Atlantoraja platana</i>	Chondrichthyes	VU	Decreasing	0	0	0	0	0	0	1
<i>Campogramma glaycos</i>	Osteichthyes	LC	Stable	0	0	0	0	0	1	1
<i>Caranx bartholomaei</i>	Osteichthyes	LC	Stable	0	0	0	0	0	1	1
<i>Caranx crysos</i>	Osteichthyes	LC	Unknown	0	0	0	0	0	1	1
<i>Caranx fischeri</i>	Osteichthyes	LC	Stable	0	0	0	0	0	1	1
<i>Caranx hippos</i>	Osteichthyes	LC	Stable	0	0	0	0	0	1	1
<i>Caranx latus</i>	Osteichthyes	LC	Stable	0	0	0	0	0	1	1
<i>Caranx lugubris</i>	Osteichthyes	LC	Stable	0	0	0	0	0	1	1
<i>Caranx rhonchus</i>	Osteichthyes	LC	Stable	0	0	0	0	0	1	1
<i>Caranx ruber</i>	Osteichthyes	LC	Unknown	0	0	0	0	0	1	1
<i>Caranx senegallus</i>	Osteichthyes	LC	Stable	0	0	0	0	0	1	1
<i>Carcharhinus amboinensis</i>	Chondrichthyes	DD	Unknown	0	0	0	0	1	0	1
<i>Carcharhinus brachyurus</i>	Chondrichthyes	NT	Unknown	0	0	0	0	1	0	1
<i>Carcharhinus falciformis</i>	Chondrichthyes	VU	Decreasing	0	0	0	0	1	0	1
<i>Carcharhinus galapagensis</i>	Chondrichthyes	NT	Unknown	0	0	0	0	1	0	1

<i>Carcharhinus leucasá</i>	Chondrichthyes	NT	Unknown	0	0	0	0	1	0	1
<i>Carcharhinus limbatus</i>	Chondrichthyes	NT	Unknown	0	0	0	0	1	0	1
<i>Carcharhinus obscurus</i>	Chondrichthyes	VU	Decreasing	0	0	0	0	1	1	1
<i>Carcharhinus perezi</i>	Chondrichthyes	NT	Decreasing	0	0	0	0	1	0	1
<i>Carcharhinus porosus</i>	Chondrichthyes	DD	Unknown	0	0	0	0	1	0	1
<i>Carcharhinus signatus</i>	Chondrichthyes	VU	Decreasing	0	0	0	0	1	0	1
<i>Carcharias taurus</i>	Chondrichthyes	VU	Unknown	0	0	0	0	1	0	1
<i>Carcharodon carcharias</i>	Chondrichthyes	VU	Unknown	0	0	0	0	1	0	1
<i>Caretta caretta</i>	Reptile	VU	Decreasing	0	1	0	0	0	0	0
<i>Cephalopholis cruentata</i>	Osteichthyes	LC	Stable	0	0	0	0	0	1	1
<i>Cephalopholis fulva</i>	Osteichthyes	LC	Decreasing	0	0	0	0	0	1	1
<i>Cephalopholis nigri</i>	Osteichthyes	LC	Unknown	0	0	0	0	0	1	1
<i>Cephalopholis taeniops</i>	Osteichthyes	LC	Stable	0	0	0	0	0	1	1
<i>Chelonia mydas</i>	Reptile	EN	Decreasing	1	1	0	1	0	0	1
<i>Chloroscombrus chrysurus</i>	Osteichthyes	LC	Stable	0	0	0	0	0	1	1
<i>Cryptotomus roseus</i>	Osteichthyes	LC	Unknown	1	0	0	0	0	0	0
<i>Dasyatis hypostigma</i>	Chondrichthyes	DD	Unknown	0	0	0	0	0	1	1
<i>Decapterus macarellus</i>	Osteichthyes	LC	Unknown	0	0	0	0	0	1	1
<i>Decapterus muroadsi</i>	Osteichthyes	LC	Unknown	0	0	0	0	0	1	1
<i>Dermochelys coriacea</i>	Reptile	VU	Decreasing	0	0	0	0	0	0	1
<i>Epinephelus adscensionis</i>	Osteichthyes	LC	Stable	0	0	0	0	0	1	1
<i>Epinephelus aeneus</i>	Osteichthyes	NT	Decreasing	0	0	0	0	0	1	1
<i>Epinephelus caninus</i>	Osteichthyes	DD	Unknown	0	0	0	0	0	1	1
<i>Epinephelus costae</i>	Osteichthyes	DD	Unknown	0	0	0	0	0	1	1
<i>Epinephelus drummondhayi</i>	Osteichthyes	DD	Decreasing	0	0	0	0	0	1	1
<i>Epinephelus flavolimbatus</i>	Osteichthyes	VU	Decreasing	0	0	0	0	0	1	1
<i>Epinephelus goreensis</i>	Osteichthyes	NT	Decreasing	0	0	0	0	0	1	1
<i>Epinephelus guttatus</i>	Osteichthyes	LC	Unknown	0	0	0	0	0	1	1
<i>Epinephelus itajara</i>	Osteichthyes	VU	Decreasing	0	0	0	0	0	1	1
<i>Epinephelus marginatus</i>	Osteichthyes	VU	Decreasing	0	0	0	0	0	1	1
<i>Epinephelus morio</i>	Osteichthyes	VU	Decreasing	0	0	0	0	0	1	1
<i>Epinephelus striatus</i>	Osteichthyes	CR	Decreasing	0	0	0	0	0	1	1
<i>Eretmochelys imbricata</i>	Reptile	CR	Decreasing	1	1	0	1	0	0	1

<i>Etelis oculatus</i>	Osteichthyes	DD	Unknown	0	0	0	0	0	1	1
<i>Galeocerdo cuvier</i>	Chondrichthyes	NT	Decreasing	0	1	0	0	1	0	1
<i>Galeorhinus galeus</i>	Chondrichthyes	VU	Decreasing	0	0	0	0	1	0	1
<i>Girella zonata</i>	Osteichthyes	VU	Unknown	1	0	0	0	0	0	0
<i>Gymnura altavela</i>	Chondrichthyes	VU	Decreasing	0	0	0	0	1	1	1
<i>Gymnura micrura</i>	Chondrichthyes	DD	Unknown	0	0	0	0	0	0	1
<i>Hemicaranx amblyrhynchus</i>	Osteichthyes	LC	Unknown	0	0	0	0	0	1	1
<i>Hemicaranx bicolor</i>	Osteichthyes	LC	Stable	0	0	0	0	0	1	1
<i>Hexanchus griseus</i>	Chondrichthyes	NT	Unknown	0	0	0	0	1	0	1
<i>Hypanus americanus</i>	Chondrichthyes	DD	Unknown	0	0	0	0	0	0	1
<i>Hypanus marianae</i>	Chondrichthyes	DD	Unknown	0	0	0	0	0	0	1
<i>Hyporthodus haifensis</i>	Osteichthyes	LC	Unknown	0	0	0	0	0	1	1
<i>Hyporthodus mystacinus</i>	Osteichthyes	LC	Unknown	0	0	0	0	0	1	1
<i>Hyporthodus nigritus</i>	Osteichthyes	NT	Unknown	0	0	0	0	0	1	1
<i>Hyporthodus niveatus</i>	Osteichthyes	VU	Decreasing	0	0	0	0	0	1	1
<i>Isistius brasiliensis</i>	Chondrichthyes	LC	Unknown	0	0	0	0	0	0	1
<i>Isurus oxyrinchus</i>	Chondrichthyes	EN	Decreasing	0	0	0	0	1	0	1
<i>Isurus paucus</i>	Chondrichthyes	EN	Decreasing	0	0	0	0	1	0	1
<i>Kyphosus bigibbus</i>	Osteichthyes	LC	Unknown	1	0	0	0	0	0	0
<i>Lepidochelys olivacea</i>	Reptile	VU	Decreasing	0	1	0	0	0	0	0
<i>Leucoraja circularis</i>	Chondrichthyes	EN	Decreasing	0	0	0	0	1	0	1
<i>Leucoraja fullonica</i>	Chondrichthyes	VU	Decreasing	0	0	0	0	1	0	1
<i>Lichia amia</i>	Osteichthyes	LC	Unknown	0	0	0	0	0	1	1
<i>Lutjanus agennes</i>	Osteichthyes	DD	Unknown	0	0	0	0	0	1	1
<i>Lutjanus analis</i>	Osteichthyes	NT	Decreasing	0	0	0	0	0	1	1
<i>Lutjanus apodus</i>	Osteichthyes	LC	Decreasing	0	0	0	0	0	1	1
<i>Lutjanus buccanella</i>	Osteichthyes	DD	Unknown	0	0	0	0	0	1	1
<i>Lutjanus campechanus</i>	Osteichthyes	VU	Decreasing	0	0	0	0	0	1	1
<i>Lutjanus cyanopterus</i>	Osteichthyes	VU	Decreasing	0	0	0	0	0	1	1
<i>Lutjanus dentatus</i>	Osteichthyes	DD	Unknown	0	0	0	0	0	1	1
<i>Lutjanus endecacanthus</i>	Osteichthyes	DD	Unknown	0	0	0	0	0	1	1
<i>Lutjanus fulgens</i>	Osteichthyes	LC	Unknown	0	0	0	0	0	1	1
<i>Lutjanus goreensis</i>	Osteichthyes	DD	Unknown	0	0	0	0	0	1	1

<i>Lutjanus griseus</i>	Osteichthyes	LC	Unknown	0	0	0	0	0	1	1
<i>Lutjanus jocu</i>	Osteichthyes	DD	Decreasing	0	0	0	0	0	1	1
<i>Lutjanus mahogoni</i>	Osteichthyes	LC	Unknown	0	0	0	0	0	1	1
<i>Lutjanus synagris</i>	Osteichthyes	NT	Decreasing	0	0	0	0	0	1	1
<i>Lutjanus vivanus</i>	Osteichthyes	LC	Decreasing	0	0	0	0	0	1	1
<i>Mobula alfredi</i>	Chondrichthyes	VU	Decreasing	0	0	0	0	0	0	1
<i>Mobula birostris</i>	Chondrichthyes	VU	Decreasing	0	0	0	0	0	1	1
<i>Mobula hypostoma</i>	Chondrichthyes	DD	Unknown	0	0	0	0	0	0	1
<i>Mobula japanica</i>	Chondrichthyes	NT	Unknown	0	0	0	0	0	0	1
<i>Mobula tarapacana</i>	Chondrichthyes	VU	Decreasing	0	0	0	0	0	0	1
<i>Mobula thurstoni</i>	Chondrichthyes	NT	Decreasing	0	0	0	0	0	0	1
<i>Mustelus canis</i>	Chondrichthyes	NT	Unknown	0	0	0	0	1	0	1
<i>Mycteroperca acutirostris</i>	Osteichthyes	LC	Stable	0	0	0	0	0	1	1
<i>Mycteroperca bonaci</i>	Osteichthyes	NT	Decreasing	0	0	0	0	0	1	1
<i>Mycteroperca cidi</i>	Osteichthyes	DD	Unknown	0	0	0	0	0	1	1
<i>Mycteroperca fusca</i>	Osteichthyes	VU	Decreasing	0	0	0	0	0	1	1
<i>Mycteroperca interstitialis</i>	Osteichthyes	VU	Decreasing	0	0	0	0	0	1	1
<i>Mycteroperca microlepis</i>	Osteichthyes	VU	Decreasing	0	0	0	0	0	1	1
<i>Mycteroperca phenax</i>	Osteichthyes	DD	Stable	0	0	0	0	0	1	1
<i>Mycteroperca rubra</i>	Osteichthyes	LC	Unknown	0	0	0	0	0	1	1
<i>Mycteroperca tigris</i>	Osteichthyes	DD	Decreasing	0	0	0	0	0	1	1
<i>Mycteroperca venenosa</i>	Osteichthyes	NT	Decreasing	0	0	0	0	0	1	1
<i>Myliobatis goodei</i>	Chondrichthyes	DD	Unknown	0	1	0	0	0	1	1
<i>Narcine brasiliensis</i>	Chondrichthyes	DD	Unknown	0	1	0	0	0	0	0
<i>Negaprion brevirostris</i>	Chondrichthyes	NT	Unknown	0	0	0	0	1	0	1
<i>Nicholsina collettei</i>	Osteichthyes	LC	Unknown	1	0	0	0	0	0	0
<i>Ocyurus chrysurus</i>	Osteichthyes	DD	Decreasing	0	0	0	0	0	1	1
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<i>Oligoplites palometa</i>	Osteichthyes	LC	Stable	0	0	0	0	0	1	1
<i>Oligoplites saliens</i>	Osteichthyes	LC	Stable	0	0	0	0	0	1	1
<i>Oligoplites saurus</i>	Osteichthyes	LC	Unknown	0	0	0	0	0	1	1
<i>Paranthias furcifer</i>	Osteichthyes	LC	Stable	0	0	0	0	0	1	1
<i>Prionace glauca</i>	Chondrichthyes	NT	Unknown	0	0	0	0	1	0	1

<i>Prionurus biafraensis</i>	Osteichthyes	LC	Stable	1	0	0	0	0	0	0
<i>Pristipomoides aquilonaris</i>	Osteichthyes	LC	Unknown	0	0	0	0	0	1	1
<i>Pristipomoides freemani</i>	Osteichthyes	LC	Unknown	0	0	0	0	0	1	1
<i>Pristipomoides macrophthalmus</i>	Osteichthyes	LC	Unknown	0	0	0	0	0	1	1
<i>Pseudobatos horkelii</i>	Chondrichthyes	CR	Decreasing	0	0	0	1	0	1	1
<i>Pseudobatos lentiginosus</i>	Chondrichthyes	NT	Unknown	0	0	0	1	0	1	1
<i>Pseudobatos percellens</i>	Chondrichthyes	NT	Unknown	0	0	0	1	0	1	1
<i>Pseudocaranx dentex</i>	Osteichthyes	LC	Unknown	0	0	0	0	0	1	1
<i>Pteroplatytrygon violacea</i>	Chondrichthyes	LC	Unknown	0	0	0	0	1	0	1
<i>Rhincodon typus</i>	Chondrichthyes	EN	Decreasing	0	1	0	0	0	0	1
<i>Rhinobatos rhinobatos</i>	Chondrichthyes	EN	Decreasing	0	0	0	1	0	1	1
<i>Rhinoptera bonasus</i>	Chondrichthyes	NT	Unknown	1	1	1	0	1	1	1
<i>Rhinoptera brasiliensis</i>	Chondrichthyes	EN	Decreasing	0	0	0	0	0	1	1
<i>Rhizoprionodon lalandii</i>	Chondrichthyes	DD	Unknown	0	0	0	0	1	1	1
<i>Rhizoprionodon porosus</i>	Chondrichthyes	LC	Stable	0	1	0	0	0	0	1
<i>Rhomboplites aurorubens</i>	Osteichthyes	VU	Decreasing	0	0	0	0	0	1	1
<i>Rioraja agassizi</i>	Chondrichthyes	VU	Unknown	0	0	0	0	0	1	1
<i>Scarus coelestinus</i>	Osteichthyes	DD	Unknown	1	1	1	1	0	0	1
<i>Scarus coeruleus</i>	Osteichthyes	LC	Unknown	1	0	0	0	0	0	0
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<i>Scarus hoefleri</i>	Osteichthyes	LC	Unknown	1	0	0	0	0	0	0
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<i>Schroederichthys saurisqualus</i>	Chondrichthyes	VU	Unknown	0	0	0	1	0	1	1
<i>Scyliorhinus stellaris</i>	Chondrichthyes	NT	Unknown	0	0	0	0	0	1	1
<i>Selar crumenophthalmus</i>	Osteichthyes	LC	Stable	0	0	0	0	0	1	1
<i>Selene brownii</i>	Osteichthyes	LC	Unknown	0	0	0	0	0	1	1
<i>Selene dorsalis</i>	Osteichthyes	LC	Stable	0	0	0	0	0	1	1
<i>Selene setapinnis</i>	Osteichthyes	LC	Stable	0	0	0	0	0	1	1
<i>Selene vomer</i>	Osteichthyes	LC	Stable	0	0	0	0	0	1	1

<i>Seriola carpenteri</i>	Osteichthyes	LC	Unknown	0	0	0	0	0	1	1
<i>Seriola dumerili</i>	Osteichthyes	LC	Unknown	0	0	0	0	0	1	1
<i>Seriola fasciata</i>	Osteichthyes	LC	Unknown	0	0	0	0	0	1	1
<i>Seriola lalandi</i>	Osteichthyes	LC	Stable	0	0	0	0	0	1	1
<i>Seriola zonata</i>	Osteichthyes	LC	Stable	0	0	0	0	0	1	1
<i>Sousa teuszii</i>	Mammal	CR	Decreasing	0	0	0	0	1	0	1
<i>Sparisoma amplum</i>	Osteichthyes	LC	Unknown	1	0	1	1	0	0	0
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<i>Sparisoma chrysopterum</i>	Osteichthyes	LC	Unknown	1	0	1	0	0	0	0
<i>Sparisoma cretense</i>	Osteichthyes	LC	Unknown	1	0	0	0	0	0	0
<i>Sparisoma frondosum</i>	Osteichthyes	DD	Unknown	1	0	0	1	0	0	0
<i>Sparisoma griseorubrum</i>	Osteichthyes	DD	Unknown	1	0	0	0	0	0	0
<i>Sparisoma radians</i>	Osteichthyes	LC	Unknown	1	0	0	0	0	0	0
<i>Sparisoma rubripinne</i>	Osteichthyes	LC	Unknown	1	0	1	0	0	0	0
<i>Sparisoma strigatum</i>	Osteichthyes	LC	Unknown	1	0	0	0	0	0	0
<i>Sparisoma tuiupiranga</i>	Osteichthyes	LC	Stable	1	1	0	0	0	0	0
<i>Sparisoma viride</i>	Osteichthyes	LC	Unknown	1	1	1	1	0	0	1
<i>Sphyrna lewini</i>	Chondrichthyes	EN	Unknown	0	0	0	0	1	0	1
<i>Sphyrna mokarran</i>	Chondrichthyes	EN	Decreasing	0	0	0	0	1	0	1
<i>Sphyrna tiburo</i>	Chondrichthyes	LC	Stable	0	0	0	0	1	0	1
<i>Sphyrna zygaena</i>	Chondrichthyes	VU	Decreasing	0	0	0	0	1	0	1
<i>Squatina guggenheim</i>	Chondrichthyes	EN	Decreasing	0	0	0	0	1	0	1
<i>Stenella longirostris</i>	Mammal	LC	Unknown	0	0	0	0	1	0	1
<i>Torpedo marmorata</i>	Chondrichthyes	DD	Unknown	0	0	0	0	1	0	1
<i>Trachinotus carolinus</i>	Osteichthyes	LC	Unknown	0	0	0	0	0	1	1
<i>Trachinotus cayennensis</i>	Osteichthyes	LC	Stable	0	0	0	0	0	1	1
<i>Trachinotus falcatus</i>	Osteichthyes	LC	Stable	0	0	0	0	0	1	1
<i>Trachinotus goodei</i>	Osteichthyes	LC	Unknown	0	0	0	0	0	1	1
<i>Trachinotus goreensis</i>	Osteichthyes	LC	Unknown	0	0	0	0	0	1	1
<i>Trachinotus marginatus</i>	Osteichthyes	LC	Unknown	0	0	0	0	0	1	1
<i>Trachinotus maxillosus</i>	Osteichthyes	LC	Unknown	0	0	0	0	0	1	1

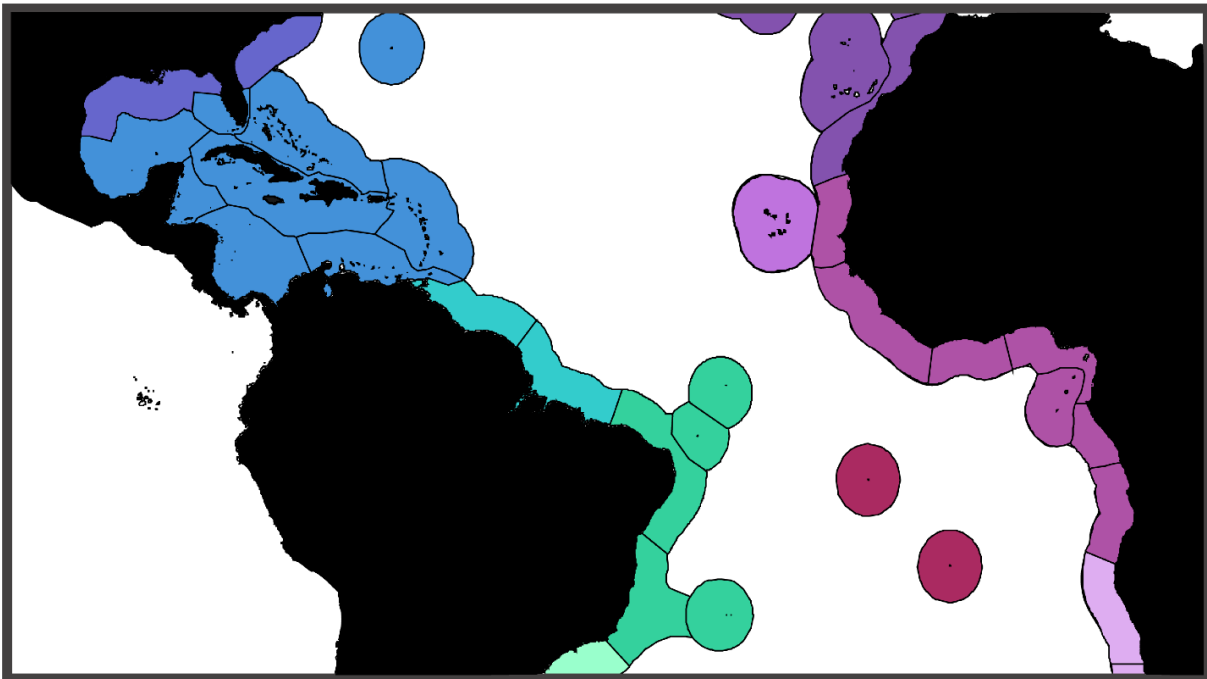
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<i>Trichechus manatus</i>	Mammal	VU	Decreasing	1	1	0	0	1	0	1
<i>Trichechus senegalensis</i>	Mammal	VU	Unknown	1	0	0	0	1	0	1
<i>Urotrygon microphthalmum</i>	Chondrichthyes	LC	Unknown	0	0	0	0	0	0	1
<i>Zapteryx brevirostris</i>	Chondrichthyes	VU	Decreasing	0	0	0	0	0	1	1

876 Legend: “Herbivory pressure” (HP); “Nutrient transport and storage” (NTS);

877 “Bioturbation/bioerosion” (BB); “Coral reef resilience (CRR); “Marine top predator” (MTP);

878 “Marine mesopredator” (MS) and “Trophic regulation” (TR).

879



880

881 **Figure S1:** Map of the marine provinces considered in our study (modified from Spalding et

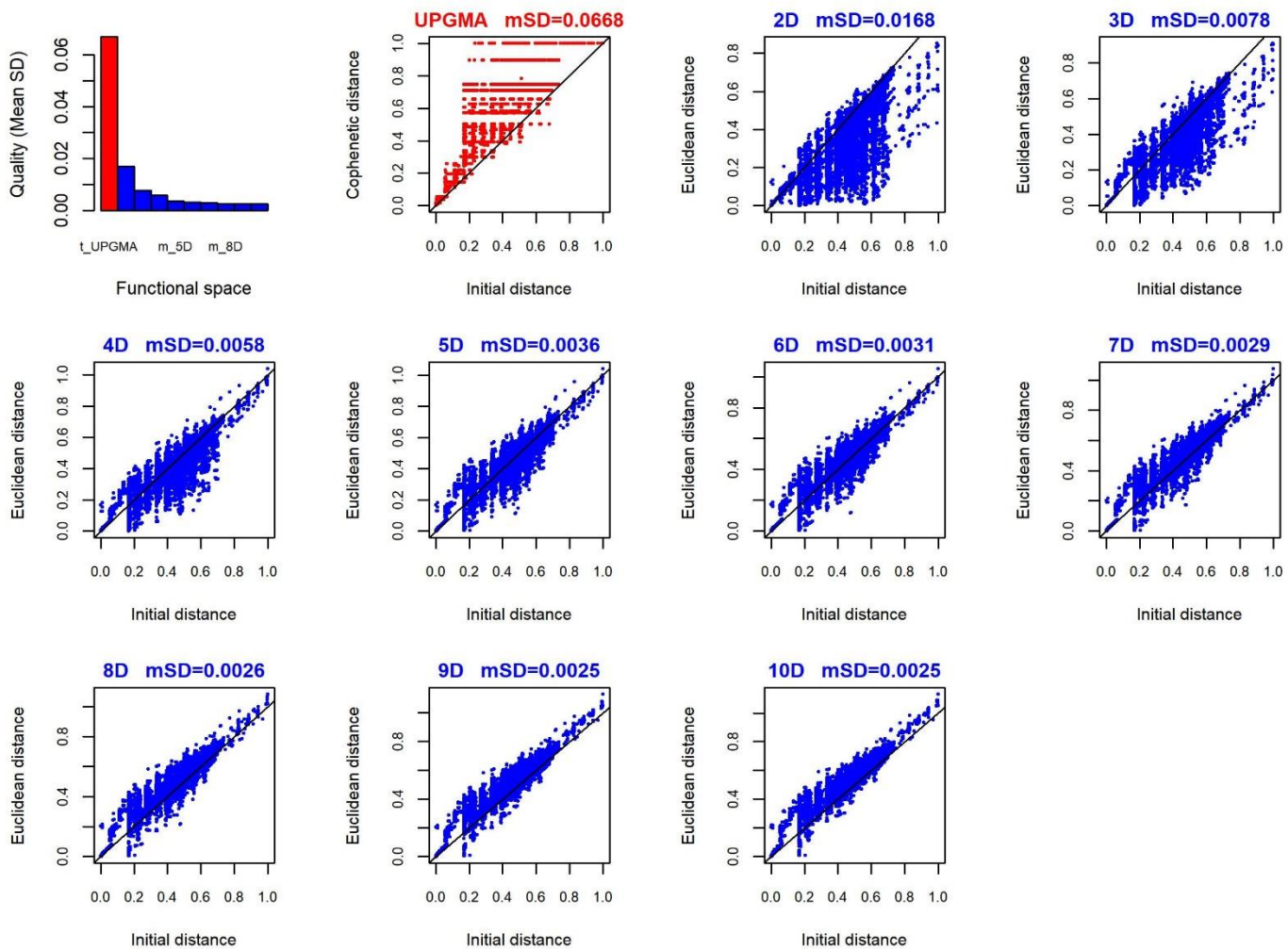
882 al., 2007): Warm Temperate Northwest Atlantic (■), Tropical Northwestern Atlantic (■),

883 North Brazil Shelf (■), Tropical Southwestern Atlantic (■), Warm Temperate Southwestern

884 Atlantic (■), St Helena and Ascension Islands (■), Benguela (■), Gulf of Guinea (■), West

885 African Transition (■) and Lusitanian (■).

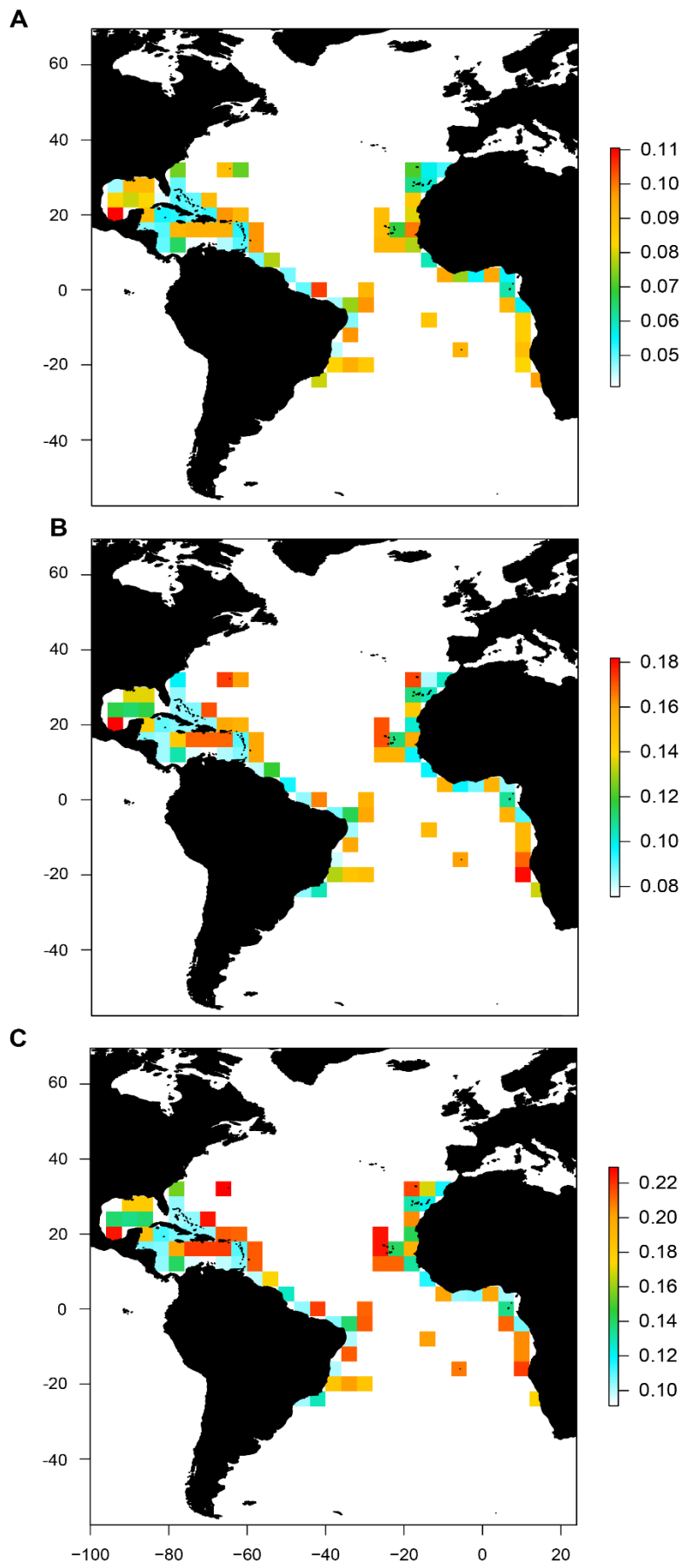
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888 **Figure S2:** Functional space quality. The top-left bar chart represents (mean squared deviation,
 889 mSD) the quality of ten PCoA axis for the estimation of functional space. Functional space
 890 occupied by 224 marine vertebrate species in Atlantic Ocean reefs was described with six
 891 functional traits (one ordinal, two continuous and three categorical). The other panels represent
 892 the correlation between the Gower distance according to species traits (initial distance) and the
 893 Euclidian distance. Each blue point represents a pair of species. From this analysis we have
 894 chosen to maintain 5 PCoA axis to the calculation of functional indexes.

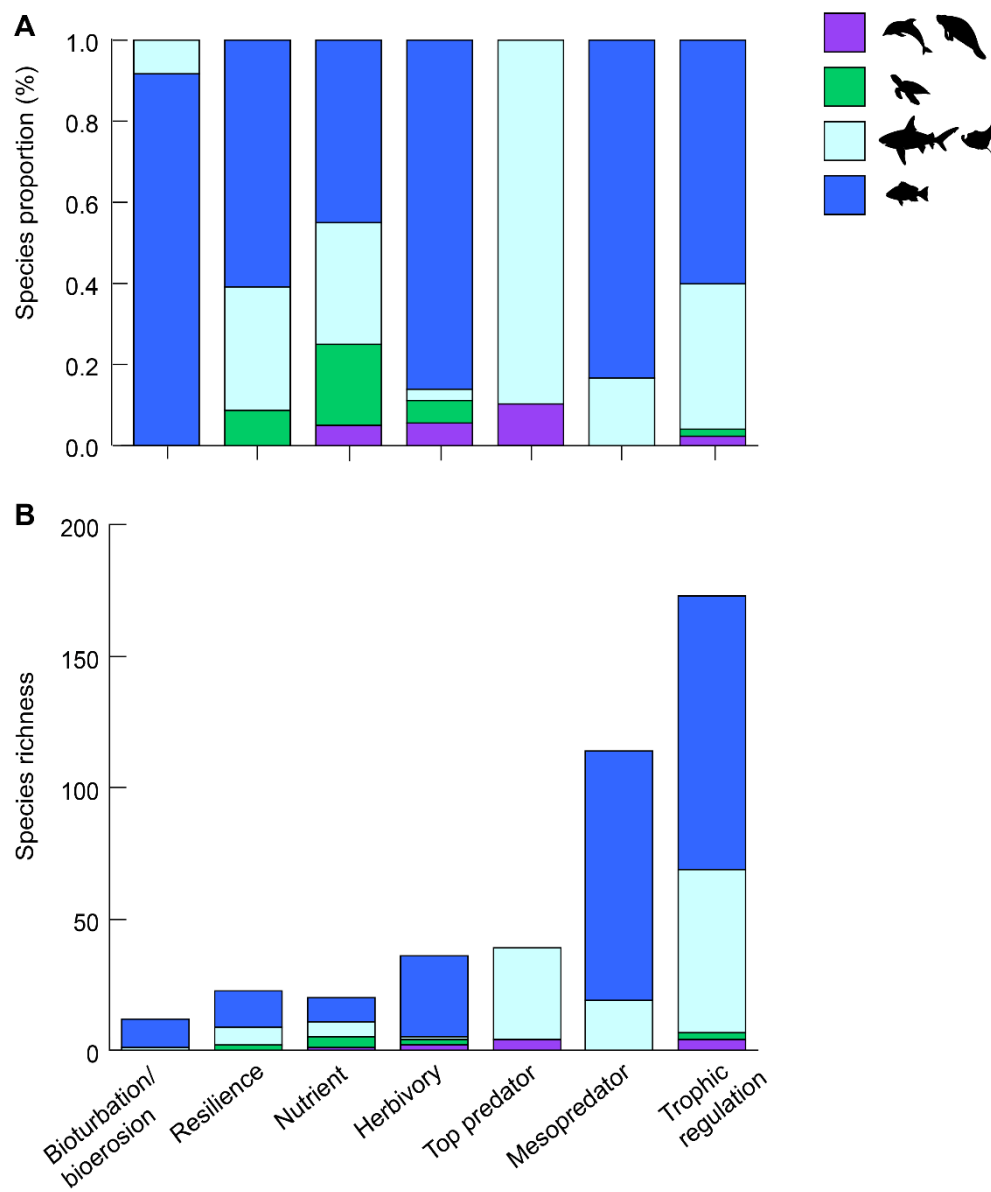
895



897 **Figure S3:** Functional uniqueness (species originality) considering the **(A)** three, **(B)** ten and
 898 **(C)** fifteen closest species in the functional space in each reef assemblage (grid scale). The color
 899 gradient represents the observed and the "expected by chance" values (blue: low values; green
 900 to yellow: intermediate values; orange to red: high values).

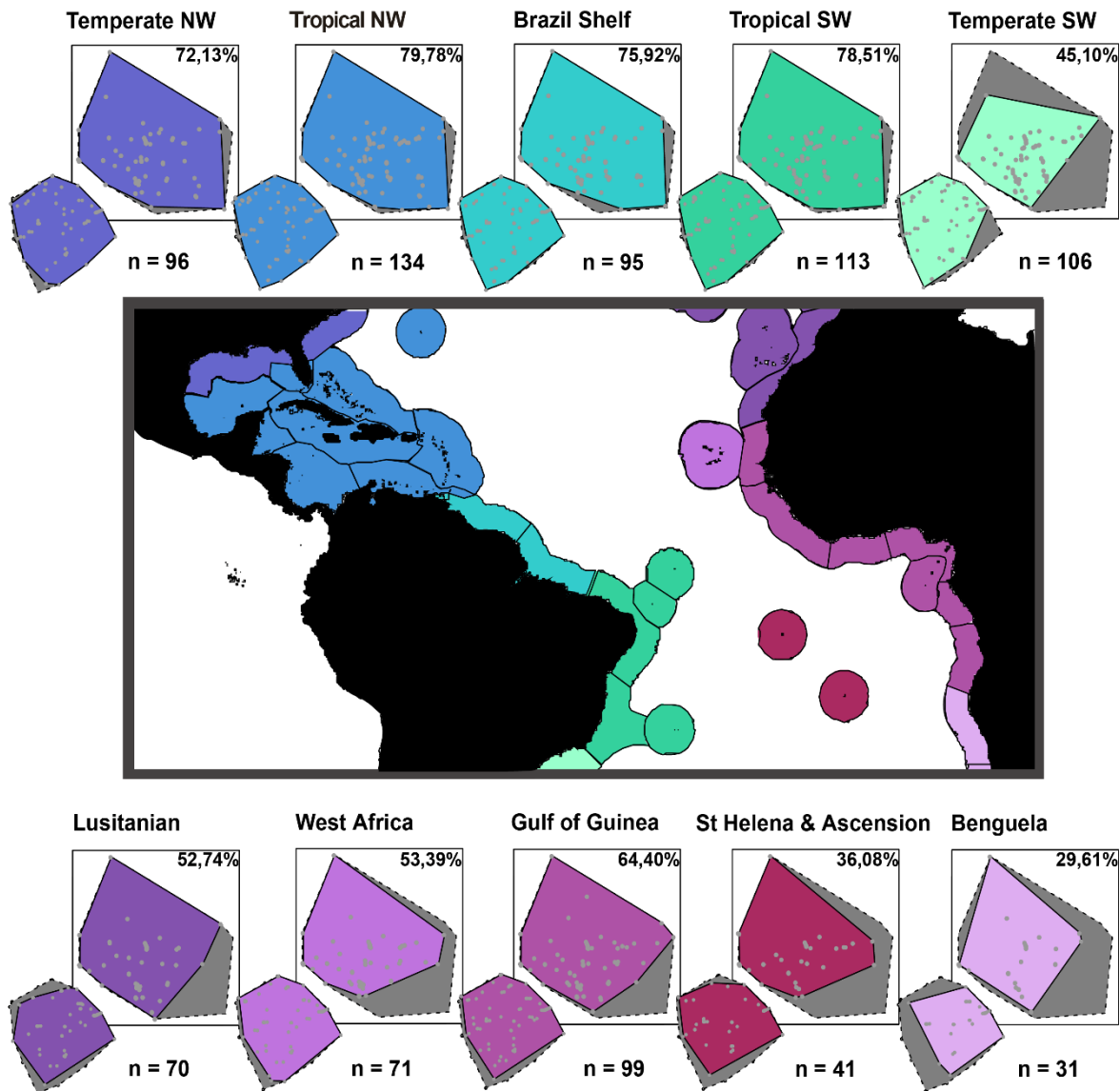
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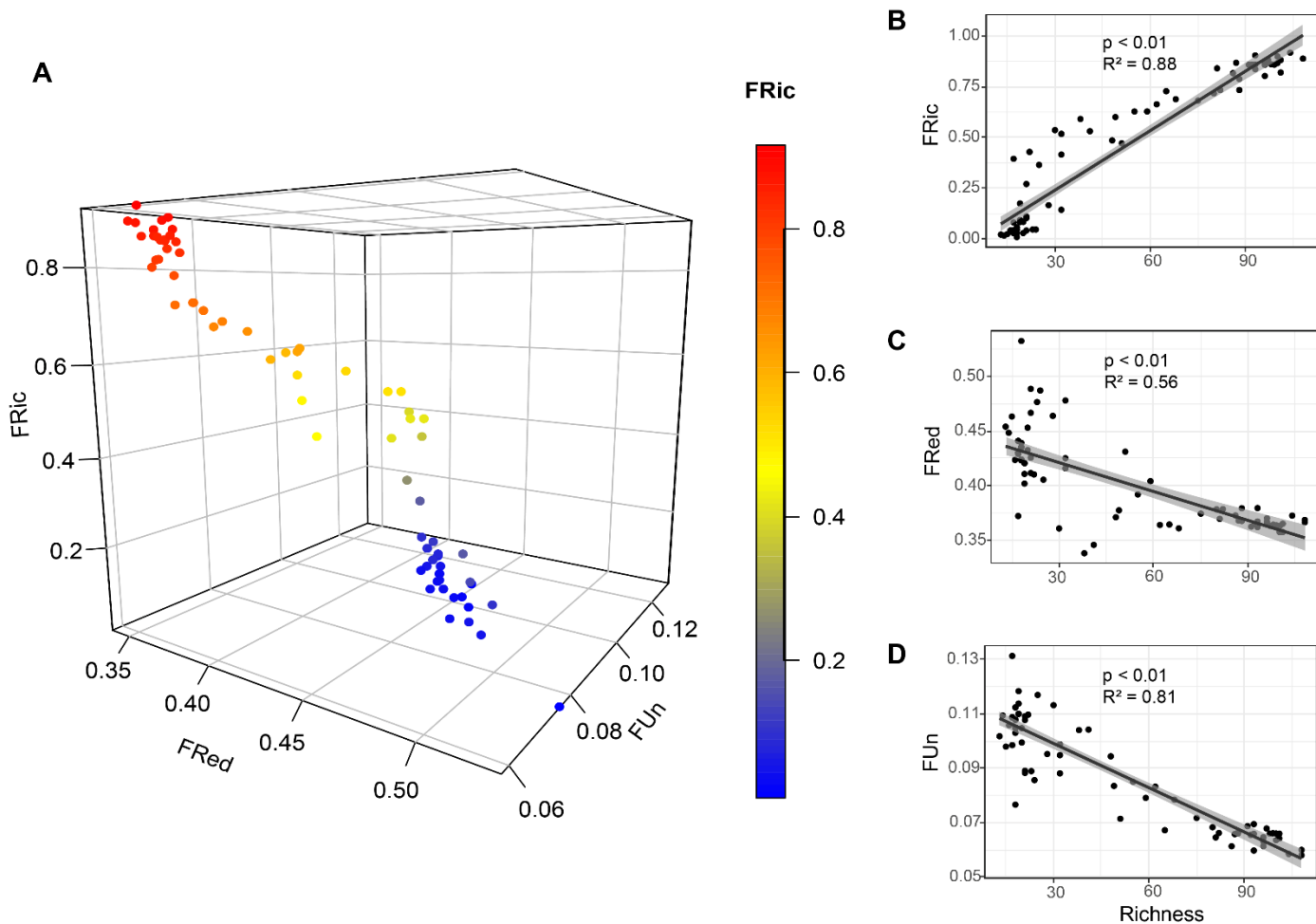
904 **Figure S4:** The contribution of taxonomic groups to the ecosystem functions identified for
 905 Atlantic Ocean reefs. (A) Species richness in each ecosystem function and the (B) proportion
 906 of taxonomic groups delivering such ecosystem functions. Marine mammals (purple), sea
 907 turtles (green), Elasmobranchii (light blue) and Teleostei (dark blue).
 908



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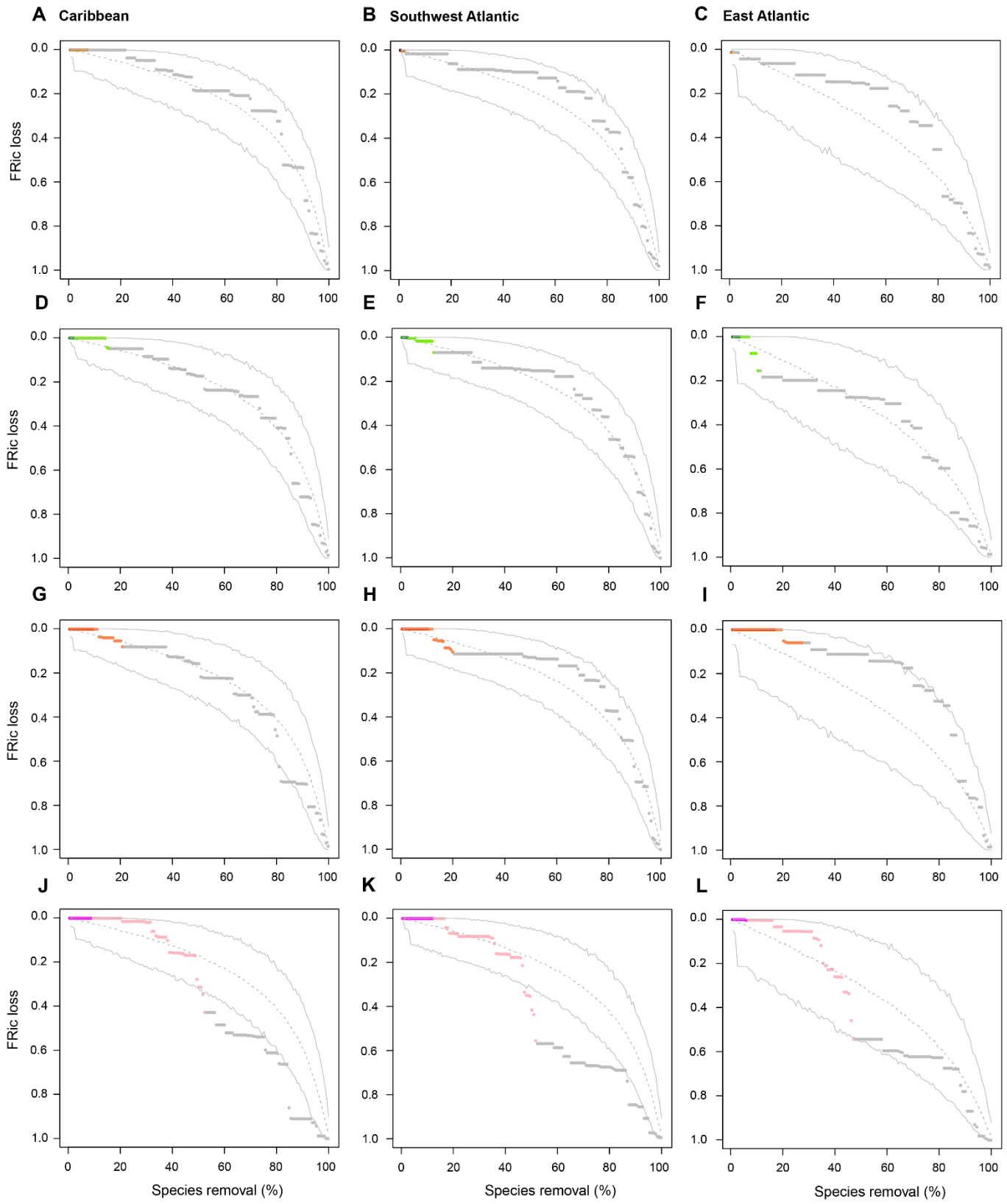
910 **Figure S5:** Marine vertebrates' functional space across ten Atlantic Ocean provinces. Each
 911 province is represented by a color on the map and functional space polygons. The small

912 polygons on the left represent PC1 and PC2, while larger polygons represent the PC3 and PC4
 913 axes. The regional volume (Atlantic) is represented in gray. The colored dots represent the
 914 position of the taxa in each province. In the upper left corner of each plot, the percentage
 915 represents the volume of the functional space occupied by each province. Below each plot n
 916 represents species richness in each province.



917 **Figure S6:** Observed functional diversity values for Atlantic Ocean reefs at grid scale (**A**)
 918 Functional richness (FRic), functional redundancy (FRed) and functional uniqueness (FUn)
 919 relationship. Notice that maximum functional redundancy is associated with lower functional
 920 uniqueness values; (**B-D**) Relationship between functional diversity indices and local species
 921 richness.

922



923

924 **Figure S7:** The erosion of functional diversity and ecosystem functions in reef assemblages
925 across the Atlantic Ocean: Caribbean (**A, D, G, J**), Southwestern Atlantic (**B, E, H, K**) and
926 Eastern Atlantic (**C, F, I, L**). Each colored dot represents species distributed in
927 “Bioturbation/bioerosion”, “Herbivory pressure”, “Marine top predator” and “Marine
928 mesopredator” ecosystem functions. Darker tones depict the removal of threatened species and
929 lighter tones the removal of non-threatened species. Gray points represent other species that do
930 not perform these ecosystem functions in particular. Grey lines represent the 95% CI of the null
931 model distribution, where species are removed randomly.