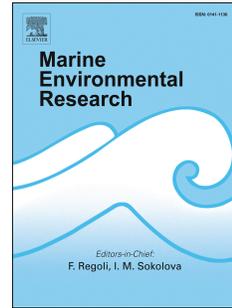


Journal Pre-proof

Diversity patterns of reef fish along the Brazilian tropical coast

Maria Elisabeth de Araújo, Felipe Monteiro Gomes de Mattos, Felipe Pimentel Lopes de Melo, Lais de Carvalho Teixeira Chaves, Caroline Vieira Feitosa, Daniel Lino Lippi, Fabiana Cézar Félix Hackradt, Carlos Werner Hackradt, Jorge Luiz Silva Nunes, Zelinda Margarida de Andrade Nery Leão, Ruy Kenji Papa de Kikuchi, Antonio Vicente Ferreira Junior, Pedro Henrique Cipresso Pereira, Cláudio Henrique Rodrigues Macedo, Cláudio Luis Santos Sampaio, João Lucas Leão Feitosa



PII: S0141-1136(20)30117-3

DOI: <https://doi.org/10.1016/j.marenvres.2020.105038>

Reference: MERE 105038

To appear in: *Marine Environmental Research*

Received Date: 7 February 2020

Revised Date: 26 May 2020

Accepted Date: 1 June 2020

Please cite this article as: de Araújo, M.E., de Mattos, F.M.G., de Melo, F.P.L., de Carvalho Teixeira Chaves, L., Feitosa, C.V., Lippi, D.L., Félix Hackradt, Fabiana.Cé., Hackradt, C.W., Nunes, J.L.S., de Andrade Nery Leão, Z.M., de Kikuchi, R.K.P., Ferreira Junior, A.V., Pereira, P.H.C., Rodrigues Macedo, Clá.Henrique., Sampaio, Clá.Luis.Santos., Feitosa, Joã.Lucas.Leã., Diversity patterns of reef fish along the Brazilian tropical coast, *Marine Environmental Research* (2020), doi: <https://doi.org/10.1016/j.marenvres.2020.105038>.

This is a PDF file of an article that has undergone enhancements after acceptance, such as the addition of a cover page and metadata, and formatting for readability, but it is not yet the definitive version of record. This version will undergo additional copyediting, typesetting and review before it is published in its final form, but we are providing this version to give early visibility of the article. Please note that, during the production process, errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

© 2020 Published by Elsevier Ltd.

Author contributions:

M.E.A. Project administration. M.E.A. and J.L.L.F. Conceptualization; Data curation; Supervision; J.L.L.F., F.M.G.M., F.P.L.M. and L.C.T.C. Writing – original draft; J.L.L.F. and F.P.L.M. Methodology; Visualization; M.E.A., J.L.L.F., L.C.T.C., C.V.F., D.L.L., F.C.F.H., C.W.H., J.L.S.N., Z.M.A.N.L., R.K.P.K., A.V.F.Jr., P.H.C.P., C.H.R.M. and C.L.S.S. Investigation; All coauthors: Writing – review & editing.

Journal Pre-proof

Title Page**1. Title**

Diversity patterns of reef fish along the Brazilian tropical coast

2. Full names of the authors

Maria Elisabeth de Araújo^{a,b}, Felipe Monteiro Gomes de Mattos^{b,c}, Felipe Pimentel Lopes de Melo^d, Lais de Carvalho Teixeira Chaves^{b,e}, Caroline Vieira Feitosa^{b,f}, Daniel Lino Lippi^{a,b}, Fabiana César Félix Hackrad^g, Carlos Werner Hackrad^g, Jorge Luiz Silva Nunes^{b,h}, Zelinda Margarida de Andrade Nery Leãoⁱ, Ruy Kenji Papa de Kikuchi^j, Antonio Vicente Ferreira Junior^a, Pedro Henrique Cipresso Pereira^b, Cláudio Henrique Rodrigues Macedo^b, Cláudio Luis Santos Sampaio^j, João Lucas Leão Feitosa^{b,k,l}

3. Institutional affiliations

- a - Universidade Federal de Pernambuco - Departamento de Oceanografia, Brazil
Av. da Arquitetura s/n, Recife - PE, 50740-540
- b - Grupo de Ictiologia Marinha Tropical (IMAT) - Brazil
Research group - no postal address
- c - Ramkhamhaeng University, Faculty of Science - Department of Biology, Thailand
Ramkhamhaeng Road, Huamark, Bangkok, 10240
- d - Universidade Federal de Pernambuco - Departamento de Botânica, Brazil
Av. Professor Moraes Rego s/n, Recife - PE, 50670-420
- e - Council of the Haida Nation - Marine Planning Department, Canada
Box 98, Queen Charlotte - BC, V0T 1S0
- f - Universidade Federal do Ceará - Instituto de Ciências do Mar, Brazil
Av. da Abolição, 3207, Fortaleza - CE, 60165-081
- g - Universidade Federal do Sul da Bahia - Centro de Formação em Ciências Ambientais, Brazil
Rodovia Joel Mares, BR 367, Km 10, s/n, Porto Seguro - BA, 458010-000
- h - Universidade Federal do Maranhão - Departamento de Oceanografia e Limnologia, Brazil
Av. dos Portugueses, 1966, São Luís - MA, 65080-805
- i - Universidade Federal da Bahia - Instituto de Geociências, Brazil
R. Barão de Jeremoabo, s/n - Ondina, Salvador - BA, 40170-290
- j - Universidade Federal de Alagoas - Unidade de Ensino Penedo, Brazil
Av. Beira Rio, s/n - Centro, Penedo - AL, 57200-000
- k - Universidade Federal de Pernambuco - Departamento de Zoologia, Brazil
Av. Professor Moraes Rego s/n, Recife - PE, 50670-420

l - Corresponding Author:

feitosajll@gmail.com,

Av. Professor Moraes Rego s/n, Recife - PE, 50670-420,

+5581 21268353

Author's contacts and other resources:

Maria Elisabeth de Araújo

e-mail: betharau08@gmail.com

<https://orcid.org/0000-0001-9747-092X>

Felipe Monteiro Gomes de Mattos

e-mail: felipemgmattos@hotmail.com

<https://orcid.org/0000-0002-9061-9207>

Felipe Pimentel Lopes de Melo

e-mail: fplmelo@gmail.com

<https://orcid.org/0000-0002-1271-3214>

Lais de Carvalho Teixeira Chaves

e-mail: lctchaves@gmail.com
<https://orcid.org/0000-0001-8575-7261>

Caroline Vieira Feitosa
e-mail: carol_feitosa@hotmail.com
<https://orcid.org/0000-0002-6143-0544>

Daniel Lino Lippi
e-mail: daniel_lippi@hotmail.com
<https://orcid.org/0000-0003-0272-9420>

Fabiana César Félix Hackradt
e-mail: fabianacfh@ufsb.edu.br
<https://orcid.org/0000-0001-7119-7128>

Carlos Werner Hackradt
e-mail: carlos.hackradt@csc.ufsb.edu.br
<https://orcid.org/0000-0002-8326-6503>

Jorge Luiz Silva Nunes
e-mail: silvanunes@yahoo.com
<https://orcid.org/0000-0001-6223-1785>

Zelinda Margarida de Andrade Nery Leão
e-mail: zelinda.leao@gmail.com
<https://orcid.org/0000-0001-7016-0139>

Ruy Kenji Papa de Kikuchi
e-mail: ruykenji@gmail.com
<https://orcid.org/0000-0002-6271-7491>

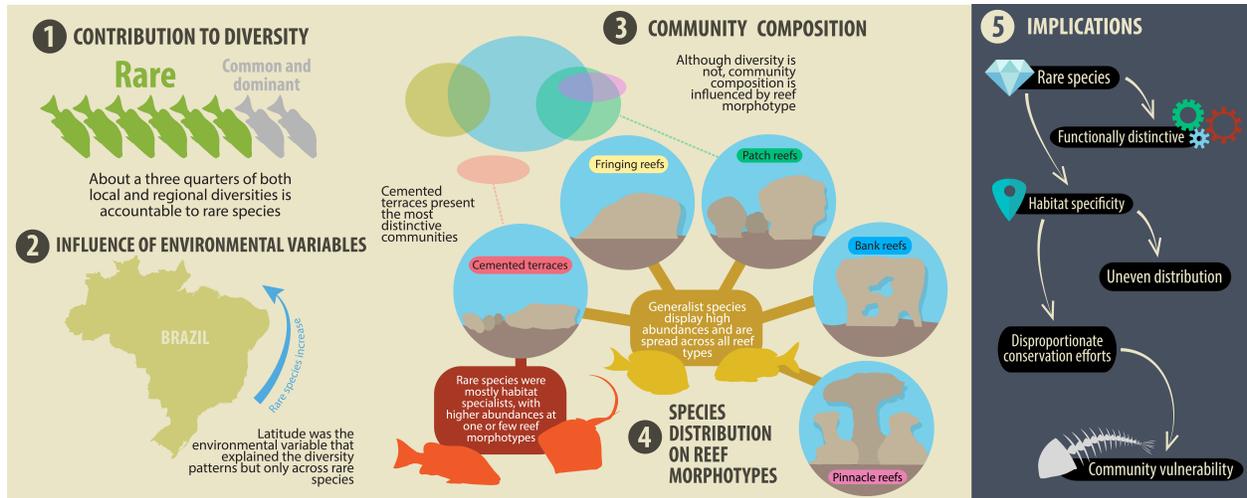
Antonio Vicente Ferreira Junior
e-mail: ferreirajr_av@hotmail.com
<https://orcid.org/0000-0002-6721-4076>

Pedro Henrique Cipresso Pereira
e-mail: pedrohcp2@yahoo.com.br

Cláudio Henrique Rodrigues Macedo
e-mail: claudiohrm@yahoo.com.br

Cláudio Luis Santos Sampaio
e-mail: claudio.sampaio@penedo.ufal.br
<https://orcid.org/0000-0002-0389-2302>

João Lucas Leão Feitosa
e-mail: feitosajll@gmail.com
<https://orcid.org/0000-0003-1257-2340>



Journal Pre-proof

Diversity patterns of reef fish along the Brazilian tropical coast

Abstract

Causal mechanisms for broad-scale reef fish diversity patterns are poorly understood and current knowledge is limited to trends of species richness. This work compared the effects of ecological drivers on components of fish diversity across reefs spanning over 2,000 km of the tropical Brazilian coastline. A quarter of communities' diversity is accountable to common and dominant species, while remaining species are rare. Low-latitude sites were more diverse in rare species. Communities along the coast share common and dominant species, which display high densities across all reefs, but differ in rare species that show abundance peaks in particular reef morphotypes. The disproportionate distribution of rare species reveals a higher vulnerability of these communities to impacts and stochastic density fluctuations. Uneven conservation efforts directed to these morphotypes pose a threat to the maintenance of a paramount component of the reef fish diversity represented by rare species.

Keywords: Brazilian reefs, Conservation, Diversity, Effects-population, Marine ecology, Latitudinal effects, Rare species, Reef fish distribution, Reef morphotype, Species Abundance

1. Introduction

Coral reefs host the most diverse communities of marine fish, yet, identifying the processes underlying reef fish diversity patterns is a challenging task. Fundamentally, widely accepted ecological drivers of diversity patterns in terrestrial communities, such as area effects and isolation, the mid-domain effect, Rapoport's rule, or the intermediate disturbance hypothesis, seem to be inconsistent for reef fish communities across different scales (Rogers, 1993; Rohde, Heap & Heap, 1993; Bellwood & Hughes, 2001; Connolly, Bellwood & Hughes, 2003; Mora & Robertson, 2005; Parravicini et al., 2013; Mora, 2015). Furthermore, there are several limitations to studies attempting to identify causal mechanisms for broad-scale reef fish diversity patterns. Most of current work on this topic is based on the compilation of species checklists gathered from literature (Mora, 2015) and, although of great value, available inventories still present issues, such as misidentifications (which mistakenly extends some species ranges), invalid and outdated species names. Current estimates suggest that only 24% of the world's oceans area hold checklists covering more than 80% of local fish species (Mora, Tittensor & Myers, 2008).

Additionally, multiple methods are applied to assess species' abundances, and to avoid the

36 potential biases (Usseglio, 2015), broad-scale studies are constrained to assumptions based solely on
37 richness patterns (Mora, 2015). The lack of comparable empirical support has then impaired assessing
38 reef diversity while accounting for species abundance over a larger scale, precluding our understanding
39 of the contribution of dominant, common or rare species to major patterns of diversity. In fact, the role
40 of rare species to community functioning has been identified as one of the 20-most fundamental
41 questions in community ecology (Sutherland et al. 2013), a subject yet to be elucidated for the reef fish
42 realm. Conversely, rarity has been often identified as a notorious component of reef fish communities
43 and is a regular topic in numerous reef fish studies (for reviews, refer to Jones, Munday & Caley, 2002,
44 MacNeil & Conolly, 2015 and Mora, 2015), but often overlooked at local studies. Ultimately,
45 abundance is generally applied to categorize species or to find a threshold to narrow community
46 structure patterns, while contribution of rare species to community diversity and functioning is widely
47 ignored.

48 Despite several classification systems in place to discern rare species, ‘rare’ is generally
49 applied to species with low local abundances and/or small geographical ranges (Gaston, 1997).
50 Excluding endemic species from remote islands, rare reef fishes are mostly those with limited local
51 densities, even if their distribution cover quite extensive ranges. For instance, Luiz Jr. et al. (2013)
52 analyzed a database of roughly 600 reef fish species and found that only seven species had geographical
53 ranges of less than 1,000 kilometers, but over 300 species are distributed within a range of more than
54 10,000 kilometers. In fact, reef fish communities widely diverge from the conceptual ecological
55 framework recognized for their terrestrial counterparts. All reef-dependent populations are locally
56 disjunct, thus intrinsically behaving in a metapopulation structure when the patchiness of reef habitat
57 distribution along the coast is considered (Jones, Munday & Caley, 2002). These local subpopulations
58 are interconnected by the great potential of fish larvae to disperse (Mora & Sale, 2002), so a given
59 community is constantly subjected to immigration, even if parental populations are located hundreds of
60 kilometers away. Local subpopulations are often unsaturated and open to immigration from regional
61 pools of species, and therefore, species are able to persist at local low abundances (Jones, Munday &
62 Caley, 2002). In addition, reef fish recruitment to local populations often follows stochastic patterns and
63 resulting communities are highly dependent of post-recruitment processes. Therefore, regional and local
64 habitat characteristics are also expected to play a major role in shaping communities according to
65 habitat preferences of species (Friedlander & Parrish, 1998).

66 Among the main drivers of local diversity patterns - at varied levels of importance and
67 response discrepancies - reef structure, depth, isolation and temperature have been repeatedly
68 emphasized as major influences on richness trends (e.g. Bender et al., 2017; Komyakova, Jones &
69 Munday, 2018; Barneche et al. 2019; Quimbayo et al., 2019). Reef structure, translated as rugosity
70 and/or other proxies for structural complexity, is one of the most consistent drivers of local number of
71 fish species (Gratwicke & Speight, 2005). Increasing depth was once thought to result in reduced fish
72 richness, but ever-growing research conducted at mesophotic reefs have found exactly the opposite (e.g.
73 Pinheiro et al., 2016; Soares, Davis, Paiva & Carneiro, 2016; Lesser, Slattery & Mobley, 2018).
74 Isolation is particularly dependent on species dispersion capabilities and local ocean currents (Mora &
75 Sale, 2002), not consistently affecting local diversity. Likewise, latitude, a common surrogate for the
76 effects of temperature and primary productivity, is found to leverage species abundance, physiological
77 tolerance and rates of speciation at broader scales (e.g. Mittelbach et al., 2007; Stuart-Smith et al.,
78 2013). Nevertheless, latitude has elicited variable responses from the local number of species.
79 Considering the aforementioned hindrances, largely applied to reef fish diversity patterns, most studies
80 approach these factors solely in terms of richness; species abundances at a broader scale, are still
81 understudied.

82 On that note, the present work aims to investigate further some questions that remain poorly
83 understood in relation to diversity patterns of reef fishes: (1) How dominant, common and rare species
84 contribute to regional and local trends of diversity? (2) Do the most accepted drivers of richness - reef
85 structure, depth, isolation and latitude - influence local diversity of fish species? (3) Does composition
86 of reef fish species differ among reefs of distinctive structural formations? We compiled a database of
87 fish communities spanning a hundred reefs within a scale of thousands of kilometers along the Brazilian
88 coast in an attempt to answer those questions.

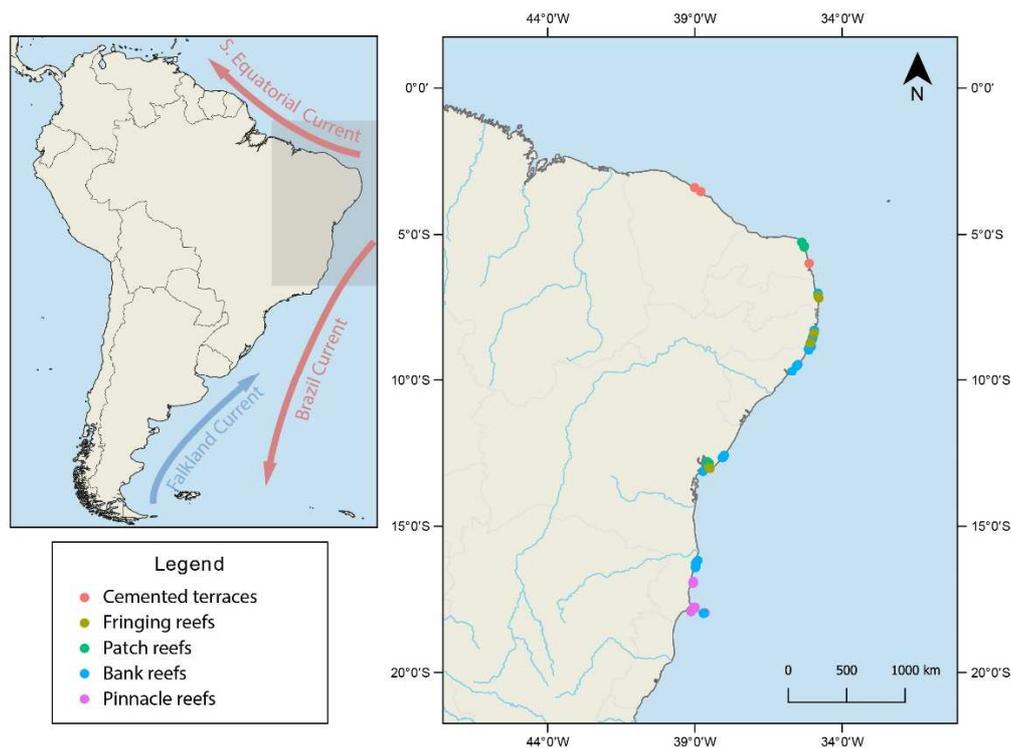
89 2. Methods

90 2.1 - Study area and geomorphology of Brazilian reefs

91 Brazil is the fifth largest country of the world and has a coastline of nearly 8,000 km. Along this
92 extensive coast, several types of reef formations are found, both of biogenic and abiogenic origins.
93 South-Western Atlantic reef fish fauna is limited to the north by the Amazon river plume, to the south
94 by the Malvinas current and to the east by the Mid-Atlantic barrier (Pinheiro et al., 2018). Furthermore,
95 the region differs in species composition between Brazilian and Argentinian provinces, mostly by
96 changes in water temperature, and the influence of a marked coastal upwelling impairing coral growth to
97 the south of Rio de Janeiro, which also presents subtropical to temperate climates. Therefore, the reef
98 formations studied herein were limited to the tropical portion of the Brazilian coast, focusing on the
99 coastal reefs located on the continental shelf, ranging from 3° 23' to 17° 54' S. Those reefs are also
100 subject to a higher stability of climatic conditions, including sea surface temperatures ranging from 20 to
101 27°C and annual average precipitation around 1500 mm (Maida & Ferreira, 1997).

102 Reefs included on this study were categorized based on the morphological complexity of the main
103 reef structures described and characterized by previous authors (see Appendix A in Supporting
104 Information for a detailed description). Brazilian reefs were recognized as (1) Cemented terraces; (2)
105 Fringing reefs; (3) Patch reefs; (4) Bank reefs and (5) Pinnacle reefs. Despite being formed mostly by a
106 distinctive coral fauna with a high degree of endemism to the Brazilian province, most of these types
107 are comparable to reef structures found elsewhere, except for the Pinnacle reefs. These are unique
108 constructions found in Eastern Brazil, formed massively by bryozoans (Bastos et al., 2018) and by a
109 coral species, *Mussismilia braziliensis*, endemic to Bahia and Espírito Santo states (Mazzei et al.,
110 2017).

111 Reef morphotypes are unevenly distributed along the Brazilian coast (Fig. 1). Cemented terraces are
112 the most uncommon morphotype, generally concentrated at lower latitudes (from 3°20'S to 6°13'S).
113 Fringing reefs occur mainly at mid-range latitudes (between 7°06'S and 13°01'). Patch reefs present a
114 disjunct distribution occurring between lower latitudes of 5°15'S and 5°45'S, and again only between
115 12°47'S and 12°50'S. Bank reefs are the most widespread morphotype, occurring at most of the
116 Brazilian coast. Pinnacle reefs are limited to the southernmost boundary of biogenic reef distribution
117 (16°50'S to 17°54'S). Most gaps on reef distribution along the coast are due to freshwater influx from
118 large river basins.



119

120 Figure 1 - Map of the study area, showing sampled reefs along the Brazilian coast and major river
 121 basins. Dot colors indicate reef morphotypes, which are fully described in Appendix A in Supporting
 122 Information.

123

124

2.2 - Fish Communities Database

125

126

127

128

129

130

131

132

133

134

135

136

137

For the purposes of this study, a database composed of both original data and secondary information available on published work was compiled (Table 1). This database included data acquired by three visual census techniques only, belt transects (most of the database), rover-diver censuses (of predetermined reef area) and stationary point counts, all yielding species density information. We followed the procedures in MacNeil et al. (2015) and Cinner et al. (2009), which consider that these census techniques perform equally (Watson & Quinn II, 1997) and assumed no differences on density estimates between methods (Samoilys & Carlos, 2000; Murphy & Jenkins, 2010). Each reef was considered a sample unit for community composition and species density. The latter was standardized by mean density per 100 m². Other criteria used for the standardization of the database, considered the minimum sampled area used per reef (150 m²), as well as a threshold for censuses performed later than year 2000, a maximum depth of 30 m and reefs location restricted to the Brazilian continental shelf. Literature was reviewed extensively and for the communities assessed in previous scientific work, we included only the data were each reef sampled discriminated for local species density and reef mean

138 depth. The resulting database rendered a total of 100 reefs, of which 70 were assessed in the present
 139 study and 30 were compiled from literature information. The bulk of the database (> 75% of samples)
 140 encompasses 1,000 m² of surveyed area per reef and dates from 2010-2016 (~ 70% of samples).

141

Reef morphotype	B	R	S	Number of reefs	Number of censuses	Surveyed area (m ²)	Source
Cemented terraces	X	X		3	142	48,988	Present study, Freitas, Vieira & Araújo (2009)
Fringing reefs		X	X	14	453	27,620	Present study, Ferreira, D'Amico & Reinhardt (2005), Cordeiro (2009), Medeiros (2007)
Patch reefs	X			15	208	23,520	Present study
Bank reefs	X		X	50	1433	71,115	Present study, Grande (2012), Chaves, Nunes, & Sampaio (2010), Querino (2011), Chaves, Pereira & Feitosa (2013)
Pinnacle reefs	X			18	214	21,400	Present study

142

143 Table 1 - Sampling methods, sample size and sources of data for each reef morphotype used to compose
 144 the database of Brazilian reef fish distribution. Letters indicate which visual census technique was
 145 applied: B - Belt transects; R - Rover-diver; S - Stationary point counts.

146

147 2.3 - Data analysis

148 Diversity patterns were investigated using “true diversity” measures (*sensu* Jost, 2006),
 149 considering the effective number of species equal to Hill numbers (^qD) (Hill, 1973). Using this
 150 approach, diversity can be quantified as equally abundant species based on increasing the weight of
 151 abundance by the order of diversity q. When q is 0 (⁰D) species abundances are disregarded, favouring
 152 rare species; ¹D is equivalent to Shannon’s entropy, and can be accounted as the effective number of
 153 common species in a community; at ²D, dominant species are favoured, as disproportionate weight is
 154 given to abundance (Jost, 2007).

155 Diversity was partitioned into overall number of species (γ diversity, $D\gamma$), mean number of
 156 species per reef (α diversity, $D\alpha$) and number of effectively distinct communities (β diversity, $D\beta$),
 157 using the decomposition described in Marcon, Hérault, Baraloto & Lang (2012). Diversities were

158 computed with 'entropart' package (Marcon & Hérault, 2015) in R 3.5.0 (R Core Team, 2018), using
159 sampled area per reef as community weights. Results were plotted as partitioned diversity profiles for
160 Brazilian reefs pooled and local diversities ($D\alpha$ per reef) were used for further analysis.

161 The relationships between local-scale diversity and reef morphotype, depth, isolation and
162 latitude were investigated using Generalized Linear Models (GLMs). $D\alpha$ of orders 0, 1 and 2 were used
163 as gaussian dependent variables to fit models, since they were found to adjust to normal distributions
164 (under Shapiro- Wilk tests). Reef morphotype was treated as a categorical predictor, with five levels
165 corresponding to Brazilian reef morphological structures (cemented terraces, fringing, patch, bank and
166 pinnacle reefs). Depth, as the average depth of the reef in meters, measured *in situ*, and isolation, as the
167 linear distance between the reef to the nearest point in mainland, were accounted as continuous factors.
168 Latitude was also included as a continuous predictor, measured in decimal degrees at the mid-point of
169 the reef extension. GLMs were computed using 'glm' function of the 'stats' package and best fitted
170 models were selected based on the lowest value of AIC (Akaike Information Criterion), using the
171 'dredge' function of 'MuMin' package. Pairwise comparisons between reef morphotypes through
172 Tukey's tests performed with the function 'glht' of the 'multcomp' package in R 3.5.0 (R Core Team,
173 2018).

174 To investigate the distinctiveness among fish communities on different reef morphotypes, we
175 used species composition to perform a non-metric multidimensional scaling (nMDS), followed by a
176 Multi-response Permutation Procedure (MRPP). The choice of use of MRPP followed the rationale that
177 not only a p-value is computed, but also a measure of the distance between pairs of morphotypes is
178 provided, based on the average dissimilarities between groups. This procedure allowed the identification
179 of morphotypes holding more akin fish communities. In both nMDS and MRPP analyses the Jaccard
180 distance was used as a dissimilarity measure, computed as $2B/(1 + B)$, where B is Bray-Curtis
181 dissimilarity. Jaccard distance was preferred instead of Bray-Curtis, once the latter index is semimetric
182 (Oksanen et al. 2010). These analyses were performed at 'vegan' package, using the functions
183 'metaMDS' and 'mrpp'.

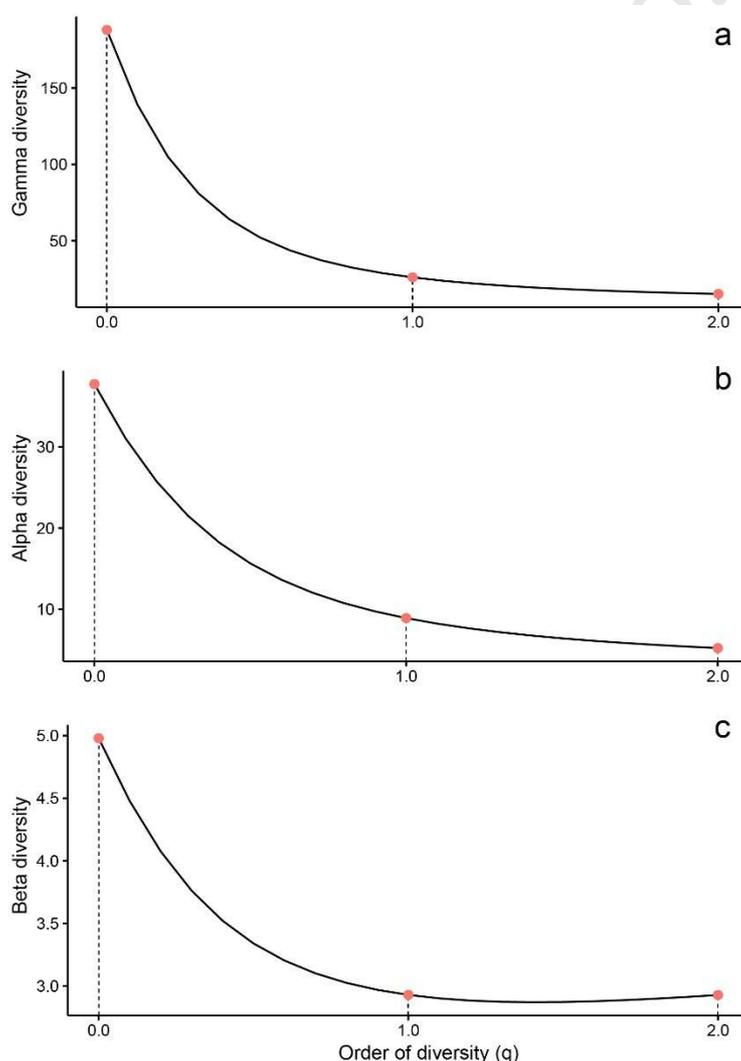
184 Following these analyses, the relationship of species with the morphotypes were calculated
185 based on Indicator Value index (*sensu* Dufrêne & Legendre, 1997), by measuring the association
186 between a species and sites grouped within reef morphotype, following McCune et al. (2002). The values
187 for identifying indicator species are computed based on two conditional components: 'A', or specificity,

188 is the probability of determining reef morphotype given the fact that the species has been found (values
189 close to 1 indicate the species occurs in sites belonging to a particular morphotype only); and 'B', or
190 fidelity, which accounts for the probability of finding the species in sites belonging to a particular
191 morphotype (i.e. values close to 1 show that all sites belonging to a morphotype include the species). As
192 suggested by de Cáceres, Legendre & Moretti (2010), this analysis was improved by considering the
193 association between species and all combinations of reef morphotypes, which also allows for the
194 identification of species that had narrower or broader preferences for particular morphotypes. For the
195 purpose of making comparisons on habitat preferences of species, those chosen as representative of
196 several or all morphotypes were considered as 'habitat generalists', whereas the opposite, species
197 characteristic of few or one morphotype only were treated as 'habitat specialists'. Finally, these
198 relationships were tested for statistical significance using a permutation test (with 999 permutations).
199 Indicator species analyses were performed using 'multipatt' function of R package 'indicspecies' (de
200 Cáceres & Jansen, 2016).

201

202 **3. Results**

203 Considering all reefs pooled, we found very steep diversity profiles for reef fish communities,
 204 suggesting a greater importance of rare species (${}^0D\gamma$) over common (${}^1D\gamma$) and dominant ones (${}^2D\gamma$) (Fig.
 205 2a). From the total of 189 species recorded, about a quarter of the gamma diversity (41 species) can be
 206 considered common or dominant, whereas the remaining are rare. At local scale (each reef), the pattern
 207 was very similar and indicated that rare species (${}^0D\alpha$) account for most of the diversity at local
 208 communities (Fig. 2b). The beta-diversity profile revealed that there must be five effective communities
 209 when considering rare species (${}^0D\beta = 4.98$), and around three when considering common and dominant
 210 species (${}^1D\beta$ and ${}^2D\beta$ both equaling 2.93, Fig. 2c).



211

212 Figure 2 - Diversity profiles by order of diversity (q) of Brazilian reef fish communities. Red points
 213 indicate values of diversity of orders 0, 1 and 2. (a) Gamma diversity profile. (b) Alpha diversity
 214 profile. (c) Beta diversity profile.

215

216

Neither depth nor isolation (i.e. distance to coastline) influenced local reef fish diversity

217 (Appendix B in Supporting Information - Tables B.1-3). Local rare species diversity (${}^0D\alpha$) was the only
 218 measure explained by latitude, and rare fish were more numerous at lower latitudes (regression
 219 coefficient = -0.98, $p = 0.01$) (Fig.3a). Pairwise comparisons of alpha diversities showed no differences
 220 among reef morphotypes, however, slightly higher numbers of both common (${}^1D\alpha$) and dominant (${}^2D\alpha$)
 221 species are found within patch, bank and pinnacle reefs (Fig. 3a-c). The only difference found in
 222 pairwise tests was between bank and fringing reefs, solely for dominant (${}^2D\alpha$) species (Tables S2.3).

223

224

225

226

227

228

229

230

231

232

233

234

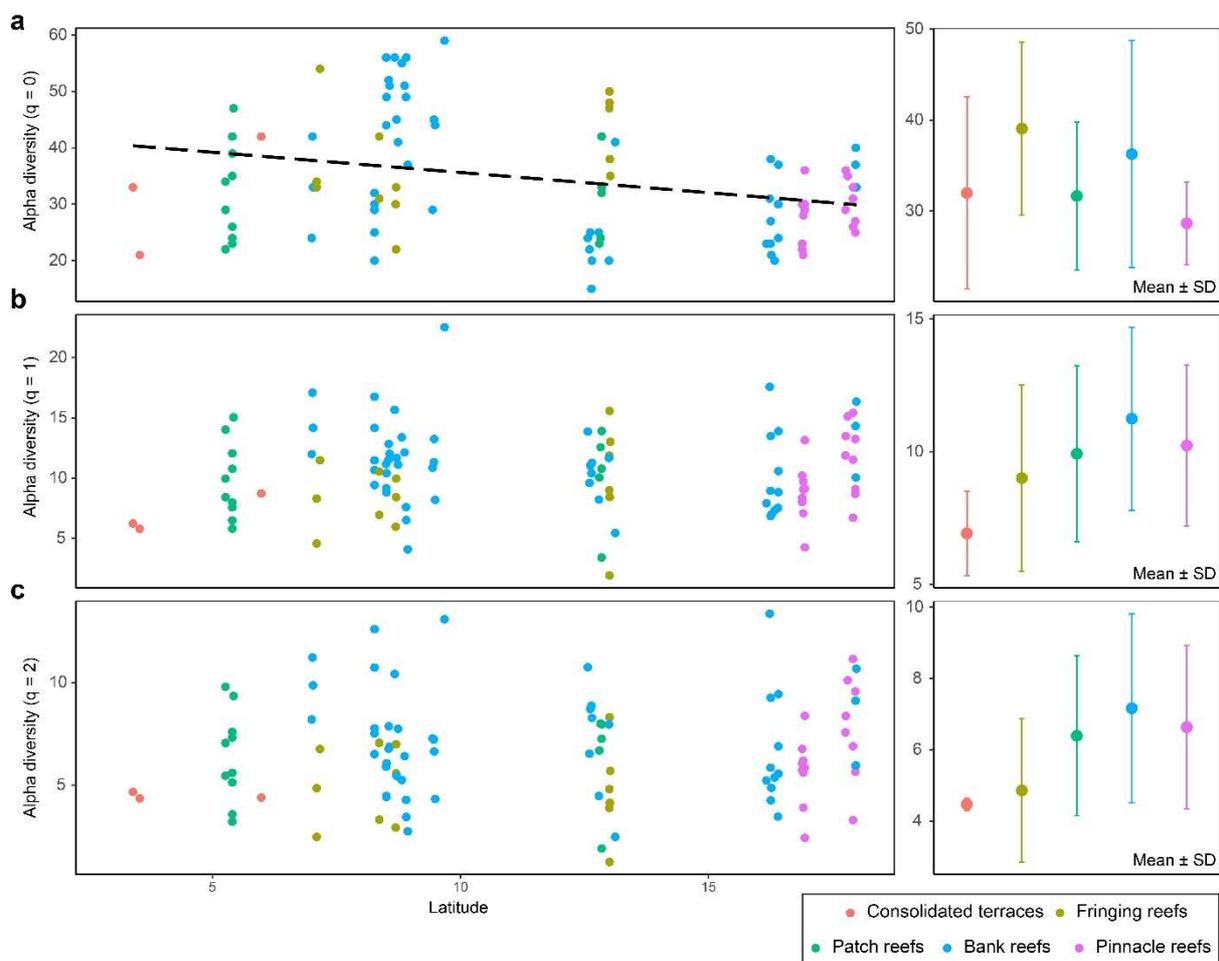
235

236

237

238

239



240 Figure 3 - Latitudinal distribution of reef's alpha diversities along Brazilian coast. Dot colors indicate reef
 241 morphotypes. (a) Rare species (${}^0D\alpha$). (b) Common species (${}^1D\alpha$). (c) Dominant species (${}^2D\alpha$). Panels on the
 242 right indicate mean alpha diversity by reef morphotype (error bars are \pm standard deviation). Dashed line in
 243 (a) shows adjusted alpha diversity relationship with latitude.

244

245

246

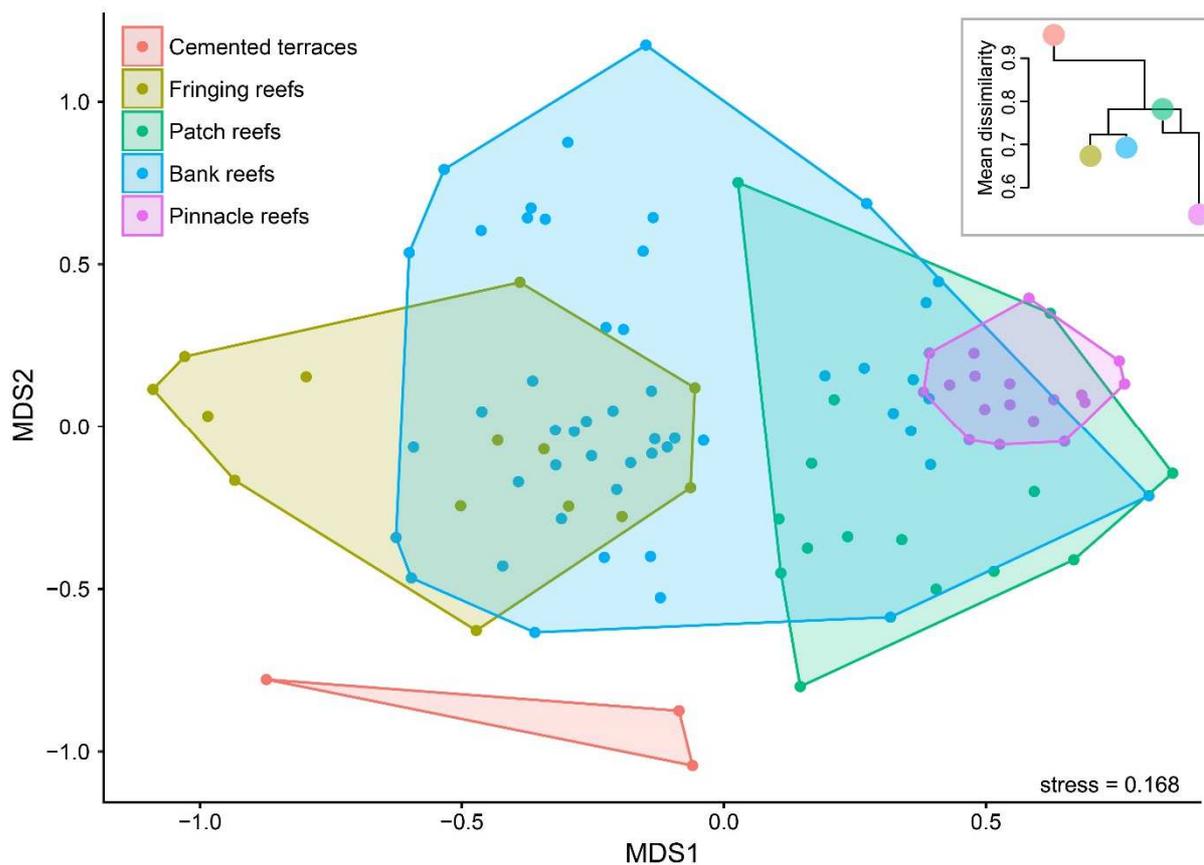
247

248

249

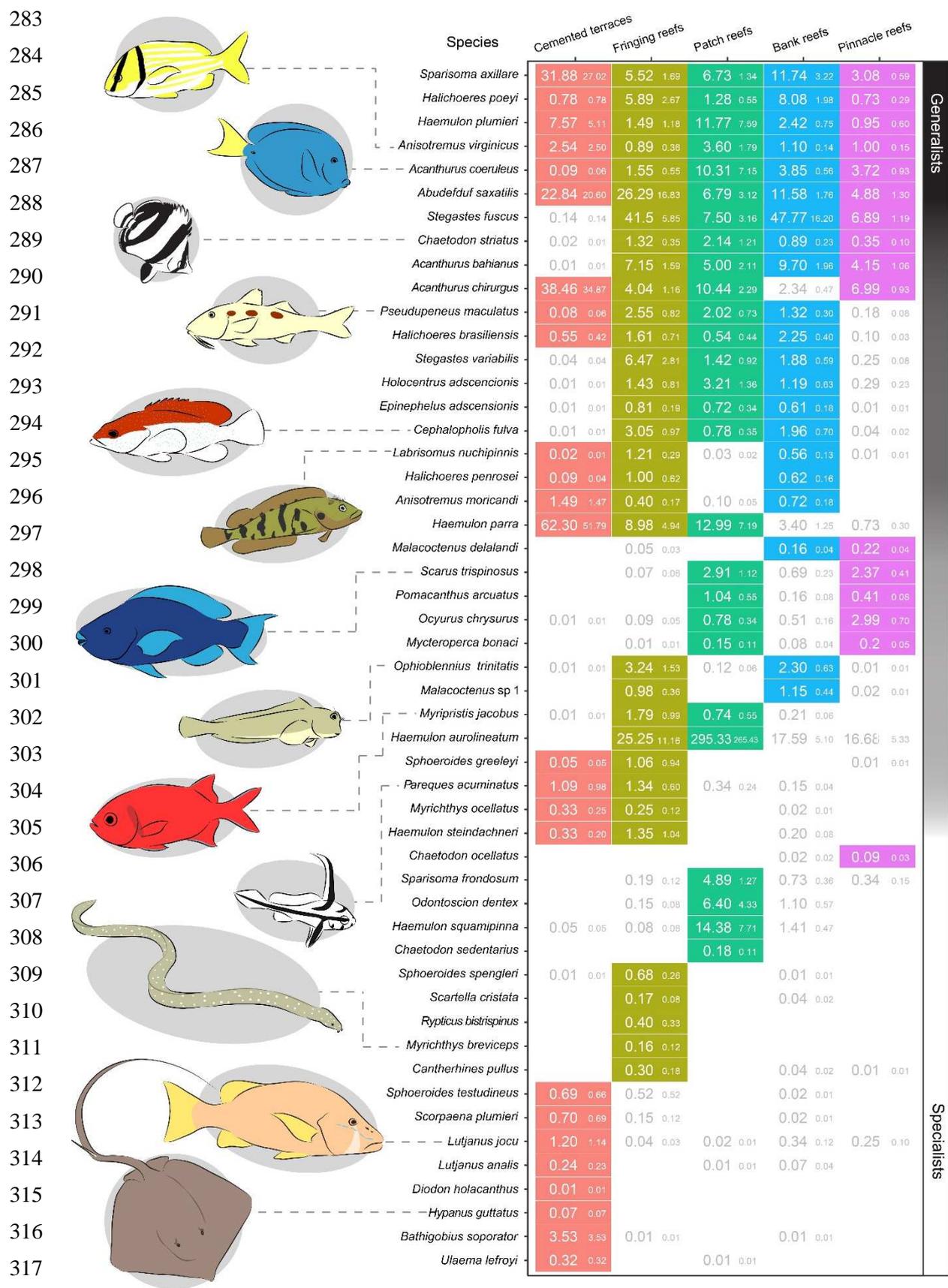
Despite presenting relatively similar numbers of species, reef morphotypes differ in species composition. Reef fish fauna appears to be organized as nested communities, where all but cemented terraces share part of their species (Fig. 4). Specifically, bank reefs seemed to be the most heterogeneous reef morphotype, displaying similarities on fish communities with fringing, patch, and

250 pinnacle reefs. Fringing and patch reefs maintain clearly distinct fish communities relative to one
 251 another, whereas pinnacle reefs sustain mostly a subsample of the species composition found within
 252 patch reefs. The MRPP analysis showed that fish communities were significantly dissimilar between
 253 morphotypes ($\delta = 0.81$, $p = 0.001$), identifying cemented terraces as having the most dissimilar
 254 composition of species, while both fringing and bank reefs, as well as patch and pinnacle reefs present
 255 more similar communities (Fig. 4).



271 Figure 4 - nMDS of reef fish communities for Brazilian coast. Dots represent each reef sampled and
 272 colors identify reef morphotype. The dendrogram represents the output of MRPP analysis, indicating
 273 mean dissimilarities of fish communities between morphotypes. Terminal end of leaves expresses mean
 274 within-group dissimilarity.

275
 276 From a total of 189 species found in this study, 51 were assigned as good indicators of reef
 277 morphotype (detailed statistics are presented in Fig. B.1, in Appendix B). Species selected as indicators
 278 of a single morphotype or two hold lower local densities (generally of less than 1 individual per 100m²)
 279 than the ones emerging as indicators of three or more morphotypes (Fig. 5). This corroborates that
 280 common and dominant coral reef fishes are abundant across the coast, inhabiting several morphotypes,
 281 whereas the distinctiveness observed among morphotypes is due to the turnover of rarer species, which
 282 are particularly more abundant at these sites.



318 Figure 5 - Fish species selected as indicators of Brazilian reef morphotypes. Larger numbers are species
 319 densities (mean individuals per 100 m²) and smaller numbers denote standard deviation. Colored
 320 backgrounds indicate species selected as typical of this morphotype after analyses of indicator species.
 321 Fish drawings are examples of species selected in the analysis.

322 **4. Discussion**

323 **4.1 - General patterns**

324 Communities of coral reef fishes across the Brazilian coast share, both locally and regionally,
325 the common and dominant species, but differ in rare species. These communities can be grouped by the
326 type of reef they inhabit. Bank reefs seemed to be the most heterogeneous reef morphotype, displaying
327 similarities on fish communities with fringing, patch, and pinnacle reefs. Only roughly a quarter of both
328 local and regional richness accounts for pooled common and dominant species, while the remaining
329 species are rare. Latitude was the only environmental variable that affected fish communities in terms of
330 diversity but only across rare species. Finally, habitat generalist species are spread across all reef types
331 while specialist ones are those that responded most for changes in beta diversity. Our study suggests
332 that there is a strong relationship between species abundance and occupancy among coral reef fish
333 communities.

334 In most communities, few species are common and dominant. Their abundances are high,
335 compared to a much greater proportion of species represented by few individuals, a consistent pattern
336 observed across several taxa and ecosystems. Rarity is often associated to species' traits, such as those
337 influencing population dynamics and replenishment (e.g. slow growth rates, long generation times and
338 low reproductive outputs) or the ones that relate to species' requirements (such as complex social
339 structures, large home ranges, large body sizes/ higher trophic levels or high ecological specialization)
340 (Flather & Sieg, 2007). Few reef fish species have "slow" population dynamics, as species generally
341 adopt fast growth/reproduction and high fecundity strategies, thus for most reef fish species, low
342 abundances must be due to relatively narrow habitat requirements. One of our findings that support this
343 view is that reef morphotype was found to be a critical driver of abundance for nearly a third of the
344 species in our study. The most common and dominant species are found to thrive in most or all
345 morphotypes, whereas rare species were consistently associated with higher local abundances at one or
346 two morphotypes only (Figure 5). In fact, local ecosystem characteristics, competition and species
347 specificity interact for determining local abundances (Flather & Sieg, 2007; Andrades, Reis-Filho,
348 Macieira, Giarrizzo & Joyeux, 2018): if suitable habitats are more available, we may find higher
349 abundances of these habitat specialist fish and this may be one of the main factors assigning reef fish
350 into distinctive communities across these morphotypes.

351 In general, rare species tend to occupy more specific niches than common ones, and by the

352 combination of different biological traits, the number of unique functional entities is higher among rare
353 species (Violle et al., 2017). A negative correlation has already been observed between commonness
354 and functional distinctiveness in reef fishes (Mouillot et al., 2013). The loss of such rare species might
355 encompass a greater reduction of functional diversity and environmental effects than randomized
356 extinctions (Bracken & Low, 2012; Leitão et al., 2016; Säterberg, Jonsson, Yearsley, Berg & Ebenman,
357 2019), which could also be translated into lower functional redundancy (Teichert et al., 2017). These
358 results are especially worrisome to Brazilian's reefs, which harbour fewer species in comparison to
359 other reef systems, such as the Great Barrier Reef and the Caribbean Province. The Brazilian province
360 is also recognized as a hotspot of functional rarity for coral reef fishes, since even a comparatively
361 poorer fish fauna still allows these communities to share most of the key ecosystem functions with the
362 Indo-Pacific region, that is, a higher functional distinctiveness between species but also higher
363 vulnerability (Mouillot et al., 2014; Grenié et al., 2018). Due to the important contribution of rare fishes
364 to diversity patterns of Brazilian coral reefs, as pinpointed by our study, we suggest further evaluation
365 to the risk of losing the functional roles associated with rare species.

366 Although little can be inferred, the number of locally common and dominant species changed
367 among morphotypes, and marginally increased with structural habitat heterogeneity. This driver has
368 been proven quite difficult to evaluate within the marine realm (Bergman et al., 2000; Wilson, Graham
369 & Polunin, 2007). The proposed scale, where Brazilian reefs were categorized of into five morphotypes,
370 did not allowed us to fully assess the contribution of minor changes in reef structural complexity and,
371 consequently, its influence on local patterns of diversity at a finer-scale. Nevertheless, we believe that
372 this driver can still leverage the diversity of common and dominant fish species by means of increased
373 resource availability. Homogenous reefs typically support lower fish abundance, fewer species, and
374 increased evenness in comparison to complex reefs (Lewis, 1997; Syms & Jones, 2000; Messmer et al.,
375 2011; Komyakova, Jones & Munday, 2018). Similarly, it has been found that habitat structure mediates
376 species-specific habitat preferences (Syms & Jones, 2000; Godbold, Bulling & Solan, 2011). Also,
377 evidence suggests that specialist taxa are most likely selected in homogenous environments, where
378 increased competition acts narrowing niche breath (Kassen, 2002; Büchi & Vuilleimier, 2014).
379 Therefore, habitat homogeneity may also be the reason behind the greater number of rare species at
380 cemented terraces and fringing reefs. If this is proven true, the difference in the number of dominant
381 species between bank and fringing reefs could be a result of higher habitat heterogeneity of bank reefs.

382 Yet, a new set of evidence is needed to comprehensively address these patterns.

383 Specialist species are generally confined to a small part of the ecological space where they can
384 outcompete generalists, which are less adapted to these specific habitats (Lennon, Beale, Reid, Kent &
385 Pakeman, 2011; Boulangeat, Lavergne, Es, Garraud & Thuiller, 2012). Additionally, models indicate
386 that specialists experience greater shifts and achieve higher fitness when in proper habitats, while
387 generalists show a constant, low variation in fitness across several habitats (Clavel, Julliard & Devictor,
388 2011; Kassen, 2002). So, the practical consequence of such scenario is that these habitat-specialized
389 species experience higher abundance declines than generalists over local environmental disturbances,
390 resulting on a higher rate of specialist species loss at a global scale (McKinney, 1997; Jablonski, 2004;
391 Wilson et al., 2008; Clavel, Julliard & Devictor, 2011; Harnik, Simpson & Payne, 2012). Furthermore,
392 extinction risk is enhanced when species with narrow niche breaths also occur in low abundances
393 (Harnik, Simpson & Payne, 2012) as observed for several species in this study, leading to a higher
394 vulnerability for the communities they are part of.

395 Tropical communities are classically believed to have more specialized species than their
396 temperate counterparts (Klopfer & MacArthur, 1961; Brown, 2014). However, this trend seems to vary
397 across taxa and latitudinal ranges (Hubbell, 2001; Mouillot et al., 2013) and is yet to achieve a
398 definitive explanation (Willig, Kaufman & Stevens, 2003; Pennell, 2019). Although current evidence
399 suggests faster speciation rates at higher temperatures (Brown, 2014; Worm & Titteson, 2018, Barneche
400 et al 2019), there is also indication of the contrary (Mora & Robertson, 2005; Schluter, 2016; Rabosky
401 et al., 2018). Regardless of this controversy, common and rare species tend to respond similarly to
402 major environmental gradients, while rare species abundances have a tendency to be driven by other
403 local factors (Siqueira et al., 2011; Lennon, Beale, Reid, Kent & Pakeman, 2011). Given the available
404 evidence, we find that the observed patterns in Brazilian reefs - where rare species were the only found
405 to respond to latitude - are not linked to temperature but to other aspects associated with latitude.

406 The accumulation of species in lower latitudes have been previously found to be a result of
407 regional differences in the distribution and spatial connectivity among reefs (Floeter, Ferreira,
408 Dominici-Arosemena & Zalmon, 2004; Mora & Robertson, 2005, Parravicini et al., 2013, Barneche et
409 al., 2019). As described in our study, the longest continuum of reef environments along the Brazilian
410 tropical coast can be found at lower latitudes (between 5 and 10°S). This stretch of coastline is also
411 where four different reef morphotypes are found. We believe that the proximity among these reefs

412 supports higher species interchange across a range of morphotypes, whereas the southernmost reefs
413 become gradually remote, with concurrent reduction in morphotype diversity (Figure 1 and 3).
414 Furthermore, ocean circulation patterns may enhance the accumulation and/or retention of rare species
415 at lower latitudes, due to the influence of the South-Equatorial Current (Floeter et al., 2001). This
416 current reaches this latitude range then breaks into two branches before running southwards as the
417 Brazilian Current. The importance of these currents to larval dispersion and adult fish movement is key
418 to further elucidate the patterns of distribution of reef fishes in Brazilian waters, and once addressed,
419 will allow properly managed resources by creating a series of well-designed and highly connected
420 Marine Protected Areas.

421 Other explanations for latitudinal trends lie on species distribution ranges. Southwestern Atlantic reef
422 fishes present about 24% of endemism (Pinheiro et al., 2018), and half of these endemics are limited to
423 Brazilian coastal waters; but endemism was not related to rarity. Distributions of coastal endemics in Brazil
424 extend far beyond our studied area (Floeter et al 2003, Pinheiro et al, 2018), and several of these were
425 identified as dominant species along all Brazilian tropical coast (e.g. *Stegastes fuscus* and *Sparisoma*
426 *axillare*, Figure 5). Endemism is generally related to greater extinction risks (Işık, 2011). In the case of
427 Brazilian coastal reef fishes, endemism is not directly translated to limited distribution ranges, small local
428 populations and/or narrow habitat requirements. In fact, the discrepancy between local richness and
429 endemism was previously identified by Hughes et al. (2002), which acknowledged that increased richness
430 is associated to the accumulation of species with wide distribution ranges more often than the number of
431 endemics present.

432

433 **4.2 - Implications for conservation**

434 We still fail in properly identifying critical populations to prioritize in our conservation efforts,
435 thus ensuring the least extinction risk for species (Harrison, 1991, 1994; Watson et al., 2011). Rare
436 species, in particular, do not receive the attention needed, since their low abundance and/or cryptic
437 habits make them a difficult subject to study. With the exception of rare fishes targeted for aquarium
438 trade, most of them are not economically valuable given their small local populations. Even though they
439 can still be indirectly and directly affected by human activities. The disproportionate distribution of rare
440 species, as found in this study, reveals a higher vulnerability of these communities to impacts and
441 stochastic density fluctuations, and based on previous studies, their removal can lead to greater than

442 expected ecosystem losses (Bracken & Low, 2012; Mouillot et al., 2013; Leitão et al., 2016; Violle et
443 al., 2017; Säterberg, Jonsson, Yearsley, Berg & Ebenman, 2019). According to our results, several rare
444 species attain higher abundances at determined reef morphotypes, which can be defensibly considered
445 hotspots for these species in the Brazilian coast.

446 The mechanisms that regulate reef fish populations in the Brazilian province, however, are still
447 understudied (Endo, Gherardi, Pezzi & Lima, 2018). It is difficult to identify at this point whether the
448 reef morphotypes studied serve as source or sink for populations of these species (Bay, Caley &
449 Crozier, 2008; Gagiotti, 2017), however, small reefs had been previously identified as source
450 populations for some fish species, and their conjoint larval supply can sometimes surpass those of larger
451 habitats, contributing up to 90% of to metapopulation total biomass (Watson et al., 2011). Considering that
452 immigration is essential to maintain genetic diversity and populations resilience (Shulman, 1998;
453 Planes, 2002; Mora, Metzger, Rollo & Myers, 2007), maintaining connectivity between these local
454 populations is of major importance for the resilience of reef communities in the Brazilian coast,
455 Regardless of their contribution to species metapopulations, it is important to consider these
456 concentrations of rare species as critical genetic pools that should be a priority for conservation and
457 MPA design.

458 Marine protection policies in Brazilian waters are still far behind international commitments.
459 The Conservation efforts directed at reefs are those aimed at protecting species at immediate extinction
460 risk, at best. For instance, the Black grouper *Mycteroperca bonaci*, the Dog and Mutton snappers
461 *Lutjanus jocu* and *L. analis* and the Greenback parrotfish *Scarus trispinosus* are heavily targeted by
462 fisheries and show significant abundance at few reef morphotypes (Figure 5). However, past record
463 shows a widespread distribution of these species along the Brazilian coast, as well as higher overall
464 abundances. These species were historically extirpated from other morphotypes due to uncontrolled
465 fishing, and consequent population declines are the main threats posed (Ferreira et al., 2012; 2018). In
466 fact, *S. trispinosus* is endemic to our study area and is the most threatened parrotfish species in the
467 world (Ferreira et al., 2012). Yet, initiatives to protected these species are few and far between, not to
468 mention challenges in compliance and enforcement.

469 Moreover, from the one hundred reefs studied, 74 maintain some level of protection, but only
470 six are within no-take MPAs, and the five reef morphotypes herein described are not equally represented
471 within these MPAs. While all the surveyed pinnacles and patch reefs are located inside MPAs, only a

472 third of the bank and fringing reefs are protected and only one of the cemented terraces studied is inside
473 a no-take area. The latter MPA is still non-compliant to current no-take regulations, partially allowing
474 artisanal fishing (Soares, Lopez, Muto & Giannini, 2011). Of special concern, are fringing reefs and
475 cemented terraces in Brazil where at least 20 species showed significant densities. These morphotypes
476 are not as common and widespread as others and might be under higher pressure. Some of those are of
477 easy access and located in degraded areas. For instance, Paracuru reefs (one of the cemented terraces
478 assessed) are located in an area targeted for oil exploration (Matthews-Cascon & Lotufo, 2006). All
479 these are symptoms of ill policies to conserve reef systems in Brazil and we suggest MPA design to be
480 reassessed in the light of the disproportionate rare species distribution.

481 We still fail to properly manage the Brazilian reef fauna. The findings of our study are a good
482 starting point to direct future conservation measures in Brazil, but we still have a long journey ahead to
483 to protect a hidden portion of the Brazilian diversity represented by rare reef fish species.

484 5. Acknowledgements

485

486 We would like to thank all researchers and students involved in the collection and compilation of data used in
487 this manuscript, in special, past and current members of the IMAT research group. The National Council for
488 Scientific and Technological Development (CNPq) and The Rufford Foundation (TRF) are acknowledged for
489 partially funding fieldwork (TRF, Grant Number: 14865-1; CNPq, Grant Numbers: 558286/2009-7,
490 478136/2013-7 and 465634/2014-1). M.E.A., F.P.L.M., R.K.P.K., Z.M.A.N.L. are CNPq research fellows.

491

492 Competing Interest Statement

493 The authors have no competing interests to declare

494 **References**

- 495 Andrades, R., Reis-Filho, J. A., Macieira, R. M., Giarrizzo, T., & Joyeux, J. C. (2018). Endemic fish species
496 structuring oceanic intertidal reef assemblages. *Scientific Reports*, 8, 1–9.
497 <https://doi.org/10.1038/s41598-018-29088-0>
- 498 Barneche, D. R., Rezende, E. L., Parravicini, V., Maire, E., Edgar, G. J., Stuart-Smith, R. D., Arias-González,
499 J. E., Ferreira, C. E. L., Friedlander, A. M., Green, A. L., Luiz, O. J., Rodríguez-Zaragoza, F. A.,
500 Vigliola, L., Kulbicki, M., & Floeter, S. R. (2019). Body size, reef area and temperature predict global
501 reef-fish species richness across spatial scales. *Global Ecology and Biogeography*, 28(3), 315–327.
502 <https://doi.org/10.1111/geb.12851>
- 503 Bastos, A. C., Moura, R. L., Moraes, F. C., Vieira, L. S., Braga, J. C., Ramalho, L. V., ... & Webster, J. M.
504 (2018). Bryozoans are major modern builders of South Atlantic oddly shaped reefs. *Scientific reports*,
505 8, 9638.
- 506 Bay, L. K., Caley, J. M., & Crozier, R. H. (2008). Meta-population structure in a coral reef fish demonstrated by
507 genetic data on patterns of migration, extinction and re-colonisation. *BMC Evolutionary Biology*, 8:
508 248. <https://doi.org/10.1186/1471-2148-8-248>
- 509 Bellwood, D. R., & Hughes, T. P. (2001). Regional-Scale Assembly Rules and Biodiversity of Coral Reefs.
510 *Science*, 292(5521), 1532–1535. <https://doi.org/10.1126/science.1058635>
- 511 Bender, M. G., Leprieur, F., Mouillot, D., Kulbicki, M., Parravicini, V., Pie, M. R., ... Floeter, S. R. (2017).
512 Isolation drives taxonomic and functional nestedness in tropical reef fish faunas. *Ecography*, 40, 425–
513 435. <https://doi.org/10.1111/ecog.02293>
- 514 Bergman, K. C., Öhman, M. C., & Svensson, S. (2000). Influence of habitat structure on *Pomacentrus sulfureus*,
515 a Western Indian Ocean reef fish. *Environmental Biology of Fishes*, 59, 243–252.
516 <https://doi.org/10.1023/A:1007610023865>
- 517 Boulangeat, I., Lavergne, S., Es, J. V., Garraud, L., & Thuiller, W. (2012). Niche breadth, rarity and ecological
518 characteristics within a regional flora spanning large environmental gradients. *Journal of*
519 *Biogeography*, 39, 204–214. <https://doi.org/10.1111/j.1365-2699.2011.02581.x>
- 520 Bracken, M. E. S., & Low, N. H. N. (2012). Realistic losses of rare species disproportionately impact higher
521 trophic levels: Loss of rare ‘cornerstone’ species. *Ecology Letters*, 15, 461–467.
522 <https://doi.org/10.1111/j.1461-0248.2012.01758.x>

- 523 Brown, J. H. (2014). Why are there so many species in the tropics? *Journal of Biogeography*, 41, 8–22.
524 <https://doi.org/10.1111/jbi.12228>
- 525 Büchi, L., & Vuilleumier, S. (2014). Coexistence of specialist and generalist species is shaped by dispersal and
526 environmental factors. *The American Naturalist*, 183(5), 612–624. <https://doi.org/10.1086/675756>
- 527 Chaves, L. C. T., Nunes, J. de A. C. C., & Sampaio, C. L. S. (2010). Shallow reef fish communities of South
528 Bahia coast, Brazil. *Brazilian Journal of Oceanography*, 58(SPE4), 33–46.
529 <https://doi.org/10.1590/S1679-87592010000800006>
- 530 Chaves, L. T. C., Pereira, P. H. C., & Feitosa, J. L. L. (2013). Coral reef fish association with macroalgal beds
531 on a tropical reef system in North-eastern Brazil. *Marine and Freshwater Research*, 64, 1101–1111.
532 <https://doi.org/10.1071/MF13054>
- 533 Clavel, J., Julliard, R., & Devictor, V. (2011). Worldwide decline of specialist species: toward a global
534 functional homogenization? *Frontiers in Ecology and the Environment*, 9, 222–228.
535 <https://doi.org/10.1890/080216>
- 536 Connolly, S. R., Bellwood, D. R., & Hughes, T. P. (2003). Indo-pacific biodiversity of coral reefs: Deviations
537 from a mid-domain model. *Ecology*, 84, 2178–2190. <https://doi.org/10.1890/02-0254>
- 538 Cordeiro, C. A. M. M. (2009). Estrutura da comunidade de peixes recifais do litoral sul da Paraíba. (Master
539 Thesis). Retrieved from Universidade Federal da Paraíba.
- 540 de Cáceres, M. D., Legendre, P., & Moretti, M. (2010). Improving indicator species analysis by combining
541 groups of sites. *Oikos*, 119, 1674–1684. <https://doi.org/10.1111/j.1600-0706.2010.18334.x>
- 542 de Cáceres, M. D., Jansen, F. (2016). Package ‘indicspecies’ for R: relationship between species and groups of
543 sites. *Cran*, p. 1–31,
- 544 Dufrêne, M., & Legendre, P. (1997). Species assemblages and indicator species: The need for a flexible
545 asymmetrical approach. *Ecological Monographs*, 67, 345–366. [https://doi.org/10.1890/0012-9615\(1997\)067\[0345:SAIST\]2.0.CO;2](https://doi.org/10.1890/0012-9615(1997)067[0345:SAIST]2.0.CO;2)
- 547 Endo, C. A. K., Gherardi, D. F. M., Pezzi, L. P., & Lima, L. N. (2019). Low connectivity compromises the
548 conservation of reef fishes by marine protected areas in the tropical South Atlantic. *Scientific Reports*,
549 9, 1–11. <https://doi.org/10.1038/s41598-019-45042-0>
- 550 Ferreira, B. P., D’Amico, T. M., & Reinhardt, M. H. (2005). Peixes ornamentais marinhos dos recifes de
551 Tamandaré (PE): Padrões de distribuição, conservação e educação ambiental. *Boletim Técnico*
552 Científico CEPENE, 13, 9-23.

- 553 Ferreira, B. P., Floeter, S., Rocha, L.A., Ferreira, C.E., Francini-Filho, R., Moura, R., ...Feitosa, C. 2012. *Scarus*
554 *trispinosus*. The IUCN Red List of Threatened Species 2012: e.T190748A17786694.
555 <http://dx.doi.org/10.2305/IUCN.UK.2012.RLTS.T190748A17786694.en>
- 556 Ferreira, B. P., Bertoncini, A. A., Pollard, D. A., Erisman, B., Sosa-Cordero, E., Rocha, ...Brule, T. 2018.
557 *Mycteroperca bonaci*. The IUCN Red List of Threatened Species 2018: e.T132724A46916253.
558 <http://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T132724A46916253.en>
- 559 Flather, C. H., & Sieg, C. H. (2007). Species rarity: Definition, causes, and classification. In Raphael, M. G. &
560 Molina, R. (Eds.), *Conservation of rare of little-known species* (pp. 40–66). Washington, D. C.: Island
561 Press.
- 562 Floeter, Sergio R., Guimarães, R. Z. P., Rocha, L. A., Ferreira, C. E. L., Rangel, C. A., & Gasparini, J. L.
563 (2001). Geographic variation in reef-fish assemblages along the Brazilian coast. *Global Ecology and*
564 *Biogeography*, 10(4), 423–431. <https://doi.org/10.1046/j.1466-822X.2001.00245.x>
- 565 Floeter, S., Gasparini, J. L., Rocha, L. A., Ferreira, C. E. L., Rangel, C. A., & Feitosa, B. M. (2003). Brazilian
566 reef fish fauna: checklist and remarks. Brazilian Reef Fish Project.
567 https://www.academia.edu/4807992/Brazilian_reef_fish_fauna_checklist
- 568 Floeter, S. R., Ferreira, C. E. L., Dominici-Arosemena, A., & Zalmon, I. R. (2004). Latitudinal gradients in
569 Atlantic reef fish communities: trophic structure and spatial use patterns: *Journal of Fish Biology*,
570 64(6), 1680–1699. <https://doi.org/10.1111/j.0022-1112.2004.00428.x>
- 571 Floeter, S. R., Behrens, M. D., Ferreira, C. E. L., Paddock, M. J., & Horn, M. H. (2005). Geographical gradients
572 of marine herbivorous fishes: patterns and processes. *Marine Biology*, 147, 1435–1447.
- 573 Freitas, M. C., Vieira, R. H. S. dos F., & Araújo, M. E. (2009). Impact of the construction of the harbor at
574 Pecém (Ceará, Brazil) upon reef fish communities in tide pools. *Brazilian Archives of Biology and*
575 *Technology*, 52, 187–195. <https://doi.org/10.1590/S1516-89132009000100024>
- 576 Friedlander, A. M., & Parrish, J. D. (1998). Habitat characteristics affecting fish assemblages on a Hawaiian
577 coral reef. *Journal of Experimental Marine Biology and Ecology*, 224, 1-30.
578 [https://doi.org/10.1016/S0022-0981\(97\)00164-0](https://doi.org/10.1016/S0022-0981(97)00164-0)
- 579 Gaggiotti, O. E. (2017). Metapopulations of marine species with larval dispersal: A counterpoint to Ilkka's
580 Glanville fritillary metapopulations. *Annales Zoologici Fennici*, 54(1–4), 97–112.
581 <https://doi.org/10.5735/086.054.0110>

- 582 Gaston, K. J. (1997). What is rarity? In W. E. Kunin & K. J. Gaston (Eds.), *The Biology of rarity: Causes and*
583 *consequences of rare-common differences* (pp. 30–47). Dordrecht. Springer Netherlands
584 https://doi.org/10.1007/978-94-011-5874-9_3
- 585 Godbold, J. A., Bulling, M. T., & Solan, M. (2011). Habitat structure mediates biodiversity effects on ecosystem
586 properties. *Proceedings. Biological Sciences*, 278, 2510–2518. <https://doi.org/10.1098/rspb.2010.2414>
- 587 Grande, H. (2012). A influência de variáveis ambientais na distribuição espacial e local em comunidade de
588 peixes de recifes costeiros do Nordeste do Brasil. (Master thesis). Retrieved from Universidade Federal
589 de Alagoas.
- 590 Gratwicke, B., & Speight, M. R. (2005). The relationship between fish species richness, abundance and habitat
591 complexity in a range of shallow tropical marine habitats. *Journal of Fish Biology*, 66, 650–667.
592 <https://doi.org/10.1111/j.0022-1112.2005.00629.x>
- 593 Grenié, M., Mouillot, D., Villéger, S., Denelle, P., Tucker, C. M., Munoz, F., & Violle, C. (2018). Functional
594 rarity of coral reef fishes at the global scale: Hotspots and challenges for conservation. *Biological*
595 *Conservation*, 226, 288–299. <https://doi.org/10.1016/j.biocon.2018.08.011>
- 596 Harnik, P. G., Simpson, C., & Payne, J. L. (2012). Long-term differences in extinction risk among the seven
597 forms of rarity. *Proceedings of the Royal Society B: Biological Sciences*, 279(1749), 4969–4976.
598 <https://doi.org/10.1098/rspb.2012.1902>
- 599 Harrison, S. (1991). Local extinction in a metapopulation context: an empirical evaluation. *Biological Journal of*
600 *the Linnean Society*, 42(1–2), 73–88. <https://doi.org/10.1111/j.1095-8312.1991.tb00552.x>
- 601 Harrison, S. (1994). Metapopulations and conservation. In P. J. Edwards, R. M. May & N. R. Webb (Eds.),
602 *Large-scale ecology and conservation biology* (pp. 111–128), Oxford. Blackwell.
- 603 Hill, M. O. (1973). Diversity and Evenness: A Unifying Notation and Its Consequences. *Ecology*, 54, 427–432.
604 <https://doi.org/10.2307/1934352>
- 605 Hubbell, S. P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography* (MPB-32). Princeton:
606 Princeton University Press. Retrieved from <http://www.jstor.org/stable/j.ctt7rj8w>
- 607 Hughes, T. P., Bellwood, D. R., & Connolly, S. R. (2002). Biodiversity hotspots, centres of endemism, and the
608 conservation of coral reefs: Biodiversity of coral reefs. *Ecology Letters*, 5(6), 775–784.
609 <https://doi.org/10.1046/j.1461-0248.2002.00383.x>
- 610 Işık, K. (2011). Rare and endemic species: why are they prone to extinction?. *Turk J Bot*, 35, 411–417
611 [doi:10.3906/bot-1012-90](https://doi.org/10.3906/bot-1012-90)

- 612 Jablonski, D. (2004). Extinction: past and present. *Nature*, 427, p.589. <https://doi.org/10.1038/427589a>
- 613 Jones, G. P., Munday, P. L., & Caley, M. J. (2002). Rarity in Coral Reef Fish Communities. In P. Sale (Ed.)
614 *Coral Reef Fishes Dynamics and Diversity in a Complex Ecosystem* (pp. 81–101), London, UK.
615 Academic Press. <https://doi.org/10.1016/B978-012615185-5/50006-2>
- 616 Jost, L. (2006). Entropy and diversity. *Oikos*, 113, 363–375. <https://doi.org/10.1111/j.2006.0030-1299.14714.x>
- 617 Jost, L. (2007). Partitioning diversity into independent alpha and beta components. *Ecology*, 88, 2427–2439.
618 <https://doi.org/10.1890/06-1736.1>
- 619 Kassen, R. (2002). The experimental evolution of specialists, generalists, and the maintenance of diversity:
620 Experimental evolution in variable environments. *Journal of Evolutionary Biology*, 15, 173–190.
621 <https://doi.org/10.1046/j.1420-9101.2002.00377.x>
- 622 Klopfer, P. H., & MacArthur, R. H. (1961). On the Causes of Tropical Species Diversity: Niche Overlap. *The*
623 *American Naturalist*, 95, 223–226. <https://www.jstor.org/stable/2458932>
- 624 Komyakova, V., Jones, G. P., & Munday, P. L. (2018). Strong effects of coral species on the diversity and
625 structure of reef fish communities: A multi-scale analysis. *PLOS ONE*, 13, e0202206.
- 626 Leitão, R. P., Zuanon, J., Villéger, S., Williams, S. E., Baraloto, C., Fortunel, C., ... Mouillot, D. (2016). Rare
627 species contribute disproportionately to the functional structure of species assemblages. *Proceedings of*
628 *the Royal Society B: Biological Sciences*, 283: 20160084. <https://doi.org/10.1098/rspb.2016.0084>
- 629 Lennon, J. J., Beale, C. M., Reid, C. L., Kent, M., & Pakeman, R. J. (2011). Are richness patterns of common
630 and rare species equally well explained by environmental variables? *Ecography*, 34, 529–539.
631 <https://doi.org/10.1111/j.1600-0587.2010.06669.x>
- 632 Lesser, M. P., Slattery, M., & Mobley, C. D. (2018). Biodiversity and functional ecology of mesophotic coral
633 reefs. *Annual Review of Ecology, Evolution, and Systematics*, 49, 49–71.
634 <https://doi.org/10.1146/annurev-ecolsys-110617-062423>
- 635 Lewis, A. (1997). Effects of experimental coral disturbance on the structure of fish communities on large patch
636 reefs. *Marine Ecology Progress Series*, 161, 37–50. <https://doi.org/10.3354/meps161037>
- 637 Longo, G. O., Hay, M. E., Ferreira, C. E. L., & Floeter, S. R. (2019). Trophic interactions across 61 degrees of
638 latitude in the Western Atlantic. *Global Ecology and Biogeography*, 28, 107–117.
639 <https://doi.org/10.1111/geb.12806>

- 640 Luiz, O. J., Allen, A. P., Robertson, D. R., Floeter, S. R., Kulbicki, M., Vigliola, L., ... Madin, J. S. (2013).
641 Adult and larval traits as determinants of geographic range size among tropical reef fishes. *Proceedings*
642 of the National Academy of Sciences, 110, 16498–16502. <https://doi.org/10.1073/pnas.1304074110>
- 643 MacNeil, M. A., & Connolly, S. R. (2015). Multi-scale patterns and processes in reef fish abundance. In C.
644 Mora (Ed.) *Ecology of Fishes on Coral Reefs* (pp. 116–124). Cambridge. Cambridge University Press.
645 <https://doi.org/10.1017/CBO9781316105412.014>
- 646 Maida, M., & Ferreira, B. P. (1997). Coral reefs of Brazil: Overview and field guide. *Proc. 8th Int Coral Reef*
647 *Sym*, 1, 263–274.
- 648 Marcon, E., & Hérault, B. (2015). Entropart: An R package to measure and partition diversity. *Journal of*
649 *Statistical Software*, 67, 1–26. <https://doi.org/10.18637/jss.v067.i08>
- 650 Marcon, E., Hérault, B., Baraloto, C., & Lang, G. (2012). The decomposition of Shannon's entropy and a
651 confidence interval for beta diversity. *Oikos*, 121, 516–522. <https://doi.org/10.1111/j.1600->
652 [0706.2011.19267.x](https://doi.org/10.1111/j.1600-0706.2011.19267.x)
- 653 Matthews-Cascon, H., & Lotufo, T. (2006). Biota marinha da costa oeste do estado do Ceará. (No. 24; pp. 248).
654 Brasília: Ministério do Meio Ambiente.
- 655 Mazzei, E. F., Bertoncini, A. A., Pinheiro, H. T., Machado, L. F., Vilar, C. C., Guabiroba, H. C., ... Joyeux, J.-
656 C. (2017). Newly discovered reefs in the southern Abrolhos Bank, Brazil: Anthropogenic impacts and
657 urgent conservation needs. *Marine Pollution Bulletin*, 114, 123–133.
658 <https://doi.org/10.1016/j.marpolbul.2016.08.059>
- 659 McKinney, M. L. (1997). How do rare species avoid extinction? A paleontological view. In W. E. Kunin & K. J.
660 Gaston (Eds.), *The Biology of Rarity: Causes and consequences of rare—common differences* (pp.
661 110–129). Springer Netherlands. https://doi.org/10.1007/978-94-011-5874-9_7
- 662 Medeiros, P. R., Gempel, R. G., Souza, A. T., Ilarri, M. I., & Sampaio, C. L. S. (2007). Effects of recreational
663 activities on the fish assemblage structure in a northeastern Brazilian reef. 2, 288-300.
- 664 Messmer, V., Jones, G. P., Munday, P. L., Holbrook, S. J., Schmitt, R. J., & Brooks, A. J. (2011). Habitat
665 biodiversity as a determinant of fish community structure on coral reefs. *Ecology*, 92, 2285–2298.
666 <https://doi.org/10.1890/11-0037.1>
- 667 Mittelbach, G. G., Schemske, D. W., Cornell, H. V., Allen, A. P., Brown, J. M., Bush, M. B., ... Turelli, M.
668 (2007). Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography.
669 *Ecology Letters*, 10, 315–331. <https://doi.org/10.1111/j.1461-0248.2007.01020.x>

- 670 Mora, C. (2015). Large-scale patterns and processes in reef fish richness. In C. Mora (Ed.), *Ecology of Fishes on*
671 *Coral Reefs* (pp. 88–96). Cambridge: Cambridge University Press.
672 <https://doi.org/10.1017/CBO9781316105412.011>
- 673 Mora, C., & Robertson, D. R. (2005). Causes of latitudinal gradients in species richness: A test with fishes of
674 the tropical eastern Pacific. *Ecology*, 86, 1771–1782. <https://doi.org/10.1890/04-0883>
- 675 Mora, C., & Sale, P. F. (2002). Are populations of coral reef fish open or closed? *Trends in Ecology &*
676 *Evolution*, 17, 422–428. [https://doi.org/10.1016/S0169-5347\(02\)02584-3](https://doi.org/10.1016/S0169-5347(02)02584-3)
- 677 Mora, C., Metzger, R., Rollo, A., & Myers, R. A. (2007). Experimental simulations about the effects of
678 overexploitation and habitat fragmentation on populations facing environmental warming. *Proceedings*
679 *of the Royal Society B: Biological Sciences*, 274(1613), 1023–1028.
680 <https://doi.org/10.1098/rspb.2006.0338>
- 681 Mora, C., Tittensor, D. P., & Myers, R. A. (2008). The completeness of taxonomic inventories for describing the
682 global diversity and distribution of marine fishes. *Proceedings of the Royal Society B: Biological*
683 *Sciences*, 275, 149–155. <https://doi.org/10.1098/rspb.2007.1315>
- 684 Mouillot, D., Bellwood, D. R., Baraloto, C., Chave, J., Galzin, R., Harmelin-Vivien, M., ... Thuiller, W. (2013).
685 Rare species support vulnerable functions in high-diversity ecosystems. *PLoS Biology*, 11, e1001569.
686 <https://doi.org/10.1371/journal.pbio.1001569>
- 687 Mouillot, D., Vileger, S., Parravicini, V., Kulbicki, M., Arias-Gonzalez, J. E., Bender, M., ... Bellwood, D. R.
688 (2014). Functional over-redundancy and high functional vulnerability in global fish faunas on tropical
689 reefs. *Proceedings of the National Academy of Sciences*, 111, 13757–13762.
690 <https://doi.org/10.1073/pnas.1317625111>
- 691 Nakamura, Y., Feary, D. A., Kanda, M., & Yamaoka, K. (2013). Tropical fishes dominate temperate reef fish
692 communities within western Japan. *PloS One*, 8, e81107. <https://doi.org/10.1371/journal.pone.0081107>
- 693 Parravicini, V., Kulbicki, M., Bellwood, D. R., Friedlander, A. M., Arias-Gonzalez, J. E., Chabanet, P., ...
694 Mouillot, D. (2013). Global patterns and predictors of tropical reef fish species richness. *Ecography*,
695 36, 1254–1262. <https://doi.org/10.1111/j.1600-0587.2013.00291.x>
- 696 Pennell, M. W. (2019). What explains latitudinal diversity gradients? *Trends in ecology & evolution*, 34, 390-
697 392. <https://doi.org/10.1016/j.tree.2019.02.011>

- 698 Pinheiro, H. T., Goodbody-Gringley, G., Jessup, M. E., Shepherd, B., Chequer, A. D., & Rocha, L. A. (2016).
699 Upper and lower mesophotic coral reef fish communities evaluated by underwater visual censuses in
700 two Caribbean locations. *Coral Reefs*, 35, 139–151. <https://doi.org/10.1007/s00338-015-1381-0>
- 701 Pinheiro, H. T., Rocha, L. A., Macieira, R. M., Carvalho-Filho, A., Anderson, A. B., Bender, M. G., ... Floeter,
702 S. R. (2018). South-western Atlantic reef fishes: Zoogeographical patterns and ecological drivers reveal
703 a secondary biodiversity centre in the Atlantic Ocean. *Diversity and Distributions*, 24, 951–965.
704 <https://doi.org/10.1111/ddi.12729>
- 705 Planes, S. (2002). Biogeography and larval dispersal inferred from population genetic analysis. In P. F. Sale
706 (Ed.), *Coral Reef Fishes* (pp. 201–220). Cambridge: Cambridge University Press.
707 <https://doi.org/10.1016/B978-012615185-5/50012-8>
- 708 Querino, L. A. C. (2011). Composição e estrutura da comunidade de peixes recifais do parque estadual marinho
709 areia vermelha, Cabedelo, PB. (Master thesis). Retrieved from Universidade Federal da Paraíba
710 <https://repositorio.ufpb.br/jspui/handle/tede/4131>
- 711 Quimbayo, J. P., Dias, M. S., Kulbicki, M., Mendes, T. C., Lamb, R. W., Johnson, A. F., ... Floeter, S. R.
712 (2019). Determinants of reef fish assemblages in tropical Oceanic islands. *Ecography*, 42, 77–87.
713 <https://doi.org/10.1111/ecog.03506>
- 714 R Core Team (2018) R: A Language and Environment for Statistical Computing. R Foundation for Statistical
715 Computing, Vienna. <https://www.R-project.org>
- 716 Rabosky, D. L., Chang, J., Title, P. O., Cowman, P. F., Sallan, L., Friedman, M., ... Alfaro, M. E. (2018). An
717 inverse latitudinal gradient in speciation rate for marine fishes. *Nature*, 559, 392–395.
718 <https://doi.org/10.1038/s41586-018-0273-1>
- 719 Rogers, C. S. (1993). Hurricanes and coral reefs: The intermediate disturbance hypothesis revisited. *Coral*
720 *Reefs*, 12(3–4), 127–137. <https://doi.org/10.1007/BF00334471>
- 721 Rohde, K., Heap, M., & Heap, D. (1993). Rapoport's rule does not apply to marine teleosts and cannot explain
722 latitudinal gradients in species richness. *The American Naturalist*, 142, 1–16.
- 723 Säterberg, T., Jonsson, T., Yearsley, J., Berg, S., & Ebenman, B. (2019). A potential role for rare species in
724 ecosystem dynamics. *Scientific Reports*, 9, 11107. <https://doi.org/10.1038/s41598-019-47541-6>
- 725 Schluter, D. (2016). Speciation, ecological opportunity, and latitude. *The American Naturalist*, 187, 1–18.
726 <https://doi.org/10.1086/684193>

- 727 Shulman, M. J. (1998). What can population genetics tell us about dispersal and biogeographic history of coral-
728 reef fishes? *Austral Ecology*, 23, 216–225. <https://doi.org/10.1111/j.1442-9993.1998.tb00723.x>
- 729 Siqueira, T., Bini, L. M., Roque, F. O., Marques-Couceiro, S. R., Trivinho-Strixino, S., & Cottenie, K. (2012).
730 Common and rare species respond to similar niche processes in macroinvertebrate metacommunities.
731 *Ecography*, 35, 183–192. <https://doi.org/10.1111/j.1600-0587.2011.06875.x>
- 732 Soares, L. S. H., Lopez, J. P., Muto, E. Y., & Giannini, R. (2011). Capture fishery in northern Todos os Santos
733 Bay, tropical southwestern Atlantic, Brazil. *Brazilian Journal of Oceanography*, 59(1), 61–74.
734 <https://doi.org/10.1590/S1679-87592011000100005>
- 735 Soares, M. O., Davis, M., Paiva, C. C., Carneiro, P. B. M. (2016). Mesophotic ecosystems: coral and fish
736 assemblage in a tropical marginal reef (northeastern Brazil). *Marine biodiversity*, 48, 1631-1636.
- 737 Stuart-Smith, R. D., Bates, A. E., Lefcheck, J. S., Duffy, J. E., Baker, S. C., Thomson, R. J., ... Edgar, G. J.
738 (2013). Integrating abundance and functional traits reveals new global hotspots of fish diversity.
739 *Nature*, 501, 539–542. <https://doi.org/10.1038/nature12529>
- 740 Sutherland, W. J., Freckleton, R. P., Godfray, H. C. J., Beissinger, S. R., Benton, T., Cameron, D. D., ...
741 Wiegand, T. (2013). Identification of 100 fundamental ecological questions. *Journal of Ecology*, 101,
742 58–67. <https://doi.org/10.1111/1365-2745.12025>
- 743 Symes, C., & Jones, G. P. (2000). Disturbance, habitat structure, and the dynamics of a coral-reef fish
744 community. *Ecology*, 81, 2714–2729. <https://doi.org/10.2307/177336>
- 745 Teichert, N., Lepage, M., Sagouis, A., Borja, A., Chust, G., Ferreira, M. T., ... Argillier, C. (2017). Functional
746 redundancy and sensitivity of fish assemblages in European rivers, lakes and estuarine ecosystems.
747 *Scientific Reports*, 7, 1–11. <https://doi.org/10.1038/s41598-017-17975-x>
- 748 Usseglio, P. (2015). Quantifying reef fishes: bias in observational approaches. In C. Mora (Ed.), *Ecology of*
749 *Fishes on Coral Reefs* (pp. 270–273). Cambridge: Cambridge University Press.
750 <https://doi.org/10.1017/CBO9781316105412.035>
- 751 Vergés, A., Doropoulos, C., Malcolm, H. A., Skye, M., Garcia-Pizá, M., Marzinelli, E. M., ... & Bozec, Y. M.
752 (2016). Long-term empirical evidence of ocean warming leading to tropicalization of fish communities,
753 increased herbivory, and loss of kelp. *Proceedings of the National Academy of Sciences*, 113, 13791-
754 13796. <https://doi.org/10.1073/pnas.1610725113>

- 755 Violle, C., Thuiller, W., Mouquet, N., Munoz, F., Kraft, N. J. B., Cadotte, M. W., ... Mouillot, D. (2017).
756 Functional rarity: The ecology of outliers. *Trends in Ecology & Evolution*, 32, 356–367.
757 <https://doi.org/10.1016/j.tree.2017.02.002>
- 758 Watson, J. R., Siegel, D. A., Kendall, B. E., Mitarai, S., Rassweiler, A., & Gaines, S. D. (2011). Identifying
759 critical regions in small-world marine metapopulations. *Proceedings of the National Academy of*
760 *Sciences*, 108, E907–E913. <https://doi.org/10.1073/pnas.1111461108>
- 761 Willig, M. R., Kaufman, D. M., & Stevens, R. D. (2003). Latitudinal gradients of biodiversity: pattern, process,
762 scale, and synthesis. *Annual Review of Ecology, Evolution, and Systematics*, 34, 273–309.
763 <https://doi.org/10.1146/annurev.ecolsys.34.012103.144032>
- 764 Wilson, S. K., Graham, N. A. J., & Polunin, N. V. C. (2007). Appraisal of visual assessments of habitat
765 complexity and benthic composition on coral reefs. *Marine Biology*, 151, 1069–1076.
766 <https://doi.org/10.1007/s00227-006-0538-3>
- 767 Wilson, S. K., Burgess, S. C., Cheal, A. J., Emslie, M., Fisher, R., Miller, I., ... Sweatman, H. P. A. (2008).
768 Habitat utilization by coral reef fish: Implications for specialists vs. generalists in a changing
769 environment. *Journal of Animal Ecology*, 77, 220–228. [https://doi.org/10.1111/j.1365-](https://doi.org/10.1111/j.1365-2656.2007.01341.x)
770 [2656.2007.01341.x](https://doi.org/10.1111/j.1365-2656.2007.01341.x)
- 771 Worm, B., & Tittensor, D. P. (2018). *A theory of global biodiversity (MPB-60)*. Princeton, Oxford: Princeton
772 University Press. <http://www.jstor.org/stable/j.ctt1zkjz6q>

Diversity patterns of reef fish along the Brazilian tropical coast - Araújo et al.

Highlights

1. Communities across the coast share dominant species but differ in rare species
2. Rare species make up three quarters of both local and regional diversities
3. Latitude explained the diversity patterns of rare species only
4. Reef structure influences species, affecting rare species occupancy
5. Uneven distribution of rare species reveals a higher community vulnerability

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Journal Pre-proof