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Habitat suitability and environmental niche comparison of cold-water coral species along the Brazilian continental margin

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1           **Habitat suitability and environmental niche comparison**  
2           **of cold-water coral species along the Brazilian continental margin**

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16          KEYWORDS

17          Deep-sea corals, habitat suitability modelling, *Lophelia pertusa*, environmental niche,  
18          Southwestern Atlantic, Octocorallia, Scleractinia.

19

## 20 ABSTRACT

21 In face of increasing anthropogenic disturbance in the deep sea, it is a priority to better  
22 understand the regional distribution of cold-water corals (CWC). These organisms  
23 create some of the most species-rich habitats in the deep sea and, for this reason, they  
24 must be properly protected and managed. In this study, we aimed to identify suitable  
25 habitat for multiple CWC taxa off the Brazilian continental margin and compare their  
26 environmental niches. Habitat suitability models were developed using the Maxent  
27 approach, which allowed for the prediction of species distribution and for the  
28 identification of potential 'hot spot' areas that may be important for biodiversity  
29 conservation. Ecological niches were determined by a PCA-env approach, and niche  
30 similarity and equivalence were evaluated based on niche overlap using the Schoener's  
31  $D$  metric. Potentially suitable habitat for Octocorallia covered a broad latitudinal range  
32 encompassing nearly the entire Brazilian continental margin, whereas Scleractinia had  
33 greater potentially suitable habitat in the Central and Southern areas. Scleractinian  
34 species were observed to slightly differ in their environmental niche, with non-reef-  
35 forming species being more tolerant to a wider range of environmental conditions in  
36 comparison with reef-forming species, inhabiting a wider area of the South American  
37 continental margin. Due to the high potential suitability for several CWC species, the  
38 Central and Southern parts of the Brazilian continental margin should be considered as  
39 potential areas high CWC diversity. Considering the current state of the art and strategic  
40 assessment tools, these areas are important targets for conservation, management, and  
41 environmental impact assessment. Most reef-forming species had similar but not  
42 directly equivalent ecological niches, indicating that mapping efforts and management  
43 planning should consider CWCs at the species level.

44

45

## 46 INTRODUCTION

47 The deep sea (>200 m depth), the largest biome on Earth that covers 65% of the  
48 surface, has been recognized to be environmentally and biologically diverse, providing  
49 several important ecosystem services for humans (Thurber et al., 2014). Cold-water  
50 corals (CWC) create highly heterogeneous deep-sea habitats that can be used by other  
51 organisms as feeding grounds, refuge and/or substrate (Henry et al., 2009; Buhl-  
52 Mortensen et al., 2010). In the case of some reef-forming stony coral species (Order  
53 Scleractinia) these habitats can be many kilometers long and hundreds of meters high  
54 (Roberts et al., 2006). Non reef-forming scleractinian species and the soft corals from  
55 the subclass Octocorallia also provide habitat due to their occurrence within dense and  
56 often diverse aggregations known as coral gardens (Roberts et al., 2009) in both hard  
57 and soft bottoms. CWC are azooxanthellate corals and present a wide bathymetric  
58 distribution generally extending deeper than 50 m water depth (Cairns, 2007).  
59 Ecosystems formed by CWC generally have a high biodiversity of associated fauna and  
60 are considered some of the most species-rich habitats in the deep sea (Freiwald et al.,  
61 2004). However, CWC have a slow growth rate, high fragility (Hall-Spencer et al.,  
62 2002) and low recovery potential (Reed et al., 2007; Huvenne et al., 2016),  
63 consequently, they are considered to form vulnerable marine ecosystems (VME).

64 There are six main reef-forming Scleractinian cold-water coral species: *Lophelia*  
65 *pertusa* (= *Desmophyllum pertusum*, Linnaeus, 1758); *Madrepora oculata* Linnaeus,  
66 1758; *Solenosmilia variabilis* Duncan, 1873; *Enallopsammia profunda* Pourtales, 1868;  
67 *Goniocorella dumosa* Alcock, 1902; and *Oculina varicosa* Le Sueur 1820 (Freiwald et  
68 al., 2004). Their importance, distribution and abundance, varies amongst regions  
69 (Freiwald et al., 2004). *L. pertusa* is considered as the primary reef-forming species in  
70 the deep-sea with an almost world-wide distribution (Davies and Guinotte, 2011). *M.*  
71 *oculata* is widely distributed in the Northeast Atlantic and Mediterranean (Reveillaud et  
72 al., 2008; Orejas et al., 2009; Vertino et al., 2010; Gori et al., 2013), whilst *S. variabilis*  
73 is concentrated within New Zealand waters (Cairns, 1995; Tracey et al., 2011). In the  
74 last decade, habitat suitability models have helped to better understand CWC  
75 distribution at both regional and global scales (e.g. Davies et al., 2008; Tittensor et al.,  
76 2009; Davies and Guinotte, 2011; Howell et al., 2011; Yesson et al., 2012; Vierod et al.,  
77 2014; Georgian et al., 2014; Guinotte and Davies, 2014).

78        The area predicted using habitat suitability models is generally related to the  
79 ecological niche breadth of the species considered (Slatyer et al., 2013). Species that are  
80 geographically widespread normally present broader ecological niches given that they  
81 persist in an area with wider range of environmental conditions, whereas species with  
82 restricted distributions would have a narrower niche breadth (Gaston, 1997). Estimating  
83 the environmental niche of a given species allows for comparison between different  
84 species and may also indicate how sensitive species are to changes in the environment.  
85 Although it is possible to test niche similarity from the outputs of habitat suitability  
86 models, conceptual and statistical challenges exist with this approach (Broennimann et  
87 al., 2012). For example, meaningful niche divergences could be confounded with  
88 geographic distance because the environmental data used in species distribution models  
89 are often spatially correlated (McCormack et al., 2010). To address this, Broennimann  
90 et al. (2012) developed a mathematical approach that can describe species niches in a  
91 Principal Component Analyses delimited by the environmental conditions of the study  
92 area (PCA-env). This promising tool for conservation and management, allows the  
93 evaluation of species niche similarity and serves as a useful complement to habitat  
94 suitability models (e.g. Aguirre-Gutiérrez et al., 2015; Zhu et al., 2016).

95        The exploitation of deep-sea resources is increasing worldwide and there is an  
96 urgent need to have an adequate knowledge of the ecology of CWC to ensure that  
97 appropriate management strategies are applied (e.g. Morato et al., 2006; Davies et al.,  
98 2007). For instance, bottom trawling represents a main threat to CWC (Fosså et al.,  
99 2002; Buhl-Mortensen et al., 2016; Buhl-Mortensen, 2017). Oil and gas offshore  
100 activities could potentially impact CWC (reviewed in Cordes et al., 2016) and,  
101 particularly, the 2010 accidental Deepwater Horizon oil spill in the Gulf of Mexico have  
102 showed negative effects on CWC also at 22 km away from the spill site (Fisher et al.,  
103 2014) and even 7 years after (Girard and Fisher, 2018). Furthermore, deep-sea mining  
104 of massive polymetallic sulfates deposits and cobalt-rich ferromanganese crusts may  
105 potentially negatively affect some CWC communities in the near future (Miller et al.,  
106 2018).

107        Three out of six main scleractinian reef-forming species, i.e. *L. pertusa*, *S. variabilis*, *M. oculata*, together with *E. rostrata*, are known to coexist along the  
108 Brazilian continental slope (Castro et al., 2006; Kitahara, 2007; Pires et al., 2007;  
109 Cavalcanti et al., 2017). With a coastline of 7,491 km, Brazil accounts for a large

proportion of the South American continental margin. This is an extensive area where fisheries, oil and gas exploration are important and ongoing activities. Deep-sea fisheries in the South-eastern Brazilian EEZ (Exclusive Economic Zone) have been estimated to have swept the available area more than once from 2003 to 2011 (Port et al., 2016). In addition, fishing intensity has increased, particularly in the continental slope, from 2000 onwards, due to government policies that stimulated foreign trawlers to occupy deep areas (Perez et al., 2009). Furthermore, the oil and gas production has increased during recent years. Approximately 70% of Brazilian oil production occurs within deep-sea basins (Bernardino and Sumida, 2017). Despite the magnitude and potential environmental impacts, there are few studies analysing the impact of these activities on CWC communities within this region (e.g. Kitahara, 2009; Port et al., 2016).

In this study, we evaluated the habitat suitability distribution and niche of several CWC species along the Brazilian continental margin and slope. We aimed to better understand differences in CWC potential distribution and corresponding environmental niches. We compared the Octocorallia Subclass and Scleractinia Order and then focused on several scleractinian species. Six species of scleractinians were studied in order to compare their niche and potential distributions representing diverse types of CWC VMEs. Four reef-forming species *L. pertusa*, *M. oculata*, *S. variabilis* and *E. rostrata* and two non-reef-forming corals, *Cladocora debilis* Milne Edwards and Haime, 1849 and *Deltocyathus* Milne Edwards & Haime, 1848. The former type of species represents reef presence or possible reef-habitat formations and the latter type represents possible coral fields, being *C. debilis* a colonial species and *Deltocyathus* spp. a solitary cup-coral genus. The results presented here are a fundamental step in better understanding CWC distribution and their possible sensitivity to environmental changes both natural and human-induced within the Brazilian continental margin and slope.

138 METHODS

139 *Study area*

140 The present study focused on the Brazilian continental margin and slope, but  
141 also included international waters to 25° W (Figure 1 a). The Brazilian continental  
142 margin was divided into four areas from north to south based upon their oceanographic  
143 and biological characteristics (after the REVIZEE program - Brazilian project on Living  
144 Resources in the Exclusive Economic Zone, Anon. 2006, [www.mma.gov.br/revizee](http://www.mma.gov.br/revizee)) as  
145 follows: (1) The North Brazil Shelf including the Amazonia, hereafter referred as the  
146 "North Area"; (2) the tropical north-eastern Brazil area, including São Pedro and São  
147 Paulo and Fernando de Noronha archipelagos and Rocas Atoll as the "North-eastern  
148 Area"; (3) the Eastern Brazil and Trindade and Martin Vaz Islands as the "Central Area  
149 "; and (4) the warm temperate South-eastern Brazilian area as the "South Area ",  
150 including the Rio Grande Rise (Figure 1 b).

151

152 *Species data*

153 A database was compiled using all available CWC records in the Brazilian  
154 continental margin from three sources: (1) records in available databases, including the  
155 Ocean Biogeographic Information System (OBIS) and the REVIZEE program; (2)  
156 records from specific literature sources, and (3) field observations using remotely  
157 operated vehicles in Campos Basin (Cavalcanti et al., 2017) (Table 1, Supplemental  
158 material). Octocorallia records were mainly from the North and Central Brazilian areas  
159 and principally from 30 to 150 m depth, i.e. mesophotic habitats. In order to exclude  
160 zooxanthellate corals, we used only records deeper than 50 m (Cairns, 2007). To model  
161 habitat suitability of each taxon, all records were filtered to provide only one record per  
162 analysis cell (ca. 1 km<sup>2</sup>) (Table 1, Figure 1 b). We selected mostly published species  
163 records to ensure a good taxonomic classification at species level. Furthermore, records  
164 from other sources were used at taxonomic level higher than genera to avoid possible  
165 identification errors.

166

167 *Environmental data*

168 A total of 34 environmental variables were used to model species habitat  
169 suitability (after Davies and Guinotte, 2011). They were classified in seven broad  
170 categories (after Yesson et al., 2012): carbonate variables (CARB), bathymetric  
171 variables (BATH), hydrodynamic variables (HYDRO), productivity variables (PROD),  
172 oxygen variables (OXY), chemical variables (CHEM), and temperature variable  
173 (TEMP) (Table 2). These categories were selected based on biological knowledge or  
174 single-factor analysis (Yesson et al., 2012). After subset the variables into top-level  
175 categories, only a single variable per category was selected by creating species  
176 distribution models for each variable on its own, calculating the validation area under  
177 the curve (AUC , see below) and retaining the most important variable per category for  
178 the final analysis (Phillips et al., 2009).

179

180 *Maxent model predictions*

181 Maxent version 3.3.3k (Phillips et al., 2006) was used to model habitat  
182 suitability. Presence records were randomly divided in two subsets, one with 70% of  
183 records to train the model and one with the remaining 30% to testing the models.  
184 Models were run with the default parameters of Maxent i.e., convergence threshold of  
185  $10^{-5}$ , a maximum of 500 iterations, and a regularization multiplier of 1. The importance  
186 of each variable on each final model was assessed using a Jackknifing procedure  
187 (Phillips et al., 2009). This procedure compares the contribution of each variable  
188 between two models, one without the variable and a second including it, thereby  
189 determining how much new information the variable contributes to a model and how  
190 much is lost when that variable is omitted. Final model predictions were presented as  
191 maps showing a predicted continuous habitat suitability value. In order to contrast  
192 predictions from different taxonomic groups, these outputs were converted into binary  
193 values (0 = unsuitable, 1 = suitable) based on the maximum sum of sensitivity plus  
194 specificity test threshold (Jiménez-Valverde and Lobo, 2007; Liu et al., 2013). This  
195 representation allowed to identify potentially suitable areas for multiple taxon as  
196 potential areas of hotspot of cold-water coral diversity.

197

198 *Species niche comparisons*

199 In order to describe and compare the environmental niches, we have represented  
200 the species niche in a multivariate space, measured the niche overlap and tested their  
201 similarity and equivalence. The spatial niche occupied by each species was represented  
202 by an environmental principal component analysis (PCA-env) approach (after  
203 Broennimann et al., 2012) using the seven most important environmental variables for  
204 each taxon (see environmental data session for the variables selection). Despite  
205 differences between Octocorallia and Scleractinia carbonate structures (calcite vs  
206 aragonite, respectively), a unique environmental space is needed to compare their  
207 species niche. Then, whilst not biologically relevant for Octocorallia, aragonite  
208 saturation state (AST), which was highly correlated with the Calcite saturation state  
209 (CST) ( $r > 0.9$ ), was used to construct the PCA-env.

210 Species occurrences were disaggregated with a minimum distance equal to the  
211 grid resolution (ca. 1 km) to reduce sampling bias. The environmental space, delimited  
212 by the axes, was set to  $100 \times 100$  cells. These cells were used to generate a ‘smoothed’  
213 Kernel density of the filtered occurrences, as well as of the available environmental  
214 conditions (in the focal areas, Figure 1). The occupancy of the environment by the entity  
215 was calculated in each cell (Broennimann et al., 2012). Niche overlap was estimated  
216 using Schoener’s  $D$  metric, which ranges from 0 (no overlap) to 1 (complete overlap)  
217 (Schoener, 1970). This metric is used to test niche similarity and equivalence,  
218 comparing the observed  $D$  value and the probability distribution of overlap values  
219 resulted from simulated species occurrence distributions (Warren et al., 2008). The  
220 application of a smoother kernel to standardize species densities allowed moving from  
221 the geographical space to the multivariate environmental space, making the analysis  
222 independent of sampling effort and environmental space resolution (Broennimann et al.,  
223 2012).

224 Similarity and equivalence tests are used to evaluate if the environmental niches  
225 of two species are more similar than expected by chance and if both species have the  
226 same use of the niche space, respectively (Warren et al., 2008). The similarity test for  
227 each species pair (a and b) consisted of two reciprocal comparisons. The observed  $D$   
228 value is compared with the probability distribution of overlap values created from  
229 simulations of random points in the background area. Then, the real overlap is  
230 compared with the overlap between randomly distributed species in the area (same n of  
231 species presence points and with “background” being the studied area). Whereas

232 equivalence test consisted in the comparison of the observed  $D$  value and the probability  
233 distribution of overlap values from simulated species distribution randomly created  
234 from the real presence points of both species (Warren et al., 2008). Since the species  
235 have broad regional and global distributions, high dispersal capacity is expected, thus,  
236 the background area represented a variety of ecological space that they could colonize  
237 as suggested by Barve et al. (2011). The tests were based on 100 iterations. All the  
238 analyses were done in R (R Development Core Team, 2010) with the “ecospat” package  
239 (Broennimann et al., 2016).

240 Niche density center and niche breadth were calculated to determine how the  
241 niches differed, considering the two main principal components. The former indicates  
242 the optimal environmental conditions for the species, while the latter described the  
243 capacity of a species to tolerate deviations from the optima. Smaller values indicated  
244 that the species occupies a more restricted or specialized niche, and larger values that  
245 the species has a wider environmental niche. Niche density center was calculated as the  
246 mean of the Kernel's density value calculated from 10000 random points inside of the  
247 environmental niche space of each taxon. Niche breadth was estimated as the proportion  
248 of the available environmental conditions delimited by the axes (100 × 100 cells) that  
249 were estimated as occupied in the PCA-env, i.e., the percentage of available conditions  
250 inhabited by the species (represented as percentage). To better represent niche center  
251 position differences, the change from Scleractinia niche center to the specific species  
252 was represented with an arrow in the representation of its environmental niche plot.

253

254 RESULTS

255 *Occupied environmental conditions*

256 The environmental conditions occupied by Octocorallia and Scleractinia were  
 257 mostly in waters saturated with calcite and aragonite respectively (i.e.,  $\Omega \geq 1$ ), although  
 258 there were some Scleractinia occurrences found in aragonite-depleted waters (Fig 2a).  
 259 Octocorallia and Scleractinia were mainly present in depth shallower than 1250 m (Fig  
 260 2b). Octocorallia occurrences were found across a broad range of current velocities  
 261 from 0 to 0.20 m s<sup>-1</sup>, whereas Scleractinia were found at sites with velocities lower than  
 262 0.1 m s<sup>-1</sup> (Fig 2c). Both, Octocorallia and Scleractinia were found in sites with POC that  
 263 ranged from 0 to 50 gC C<sub>org</sub> m<sup>-2</sup> y<sup>-1</sup> and in a range of dissolved oxygen conditions  
 264 ranging between 4 and 5.5-mL l<sup>-1</sup>, and silicate < 50 μmol l<sup>-1</sup> (Fig 2d, e and f,  
 265 respectively). Octocorallia occupied a wider temperature range (ca. 0-30 °C), while  
 266 Scleractinia occupied waters less than 25 °C (Fig 2g).

267 The individual scleractinian species had slight differences between them: *E. rostrata*,  
*M. oculata*, *L. pertusa* and *S. variabilis* were restricted to current velocities  
 268 lower than 0.5m s<sup>-1</sup> (Fig 2j) and, together with *C. debilis* were limited to sites with POC  
 269 lower than 20 g C<sub>org</sub> m<sup>-2</sup> y<sup>-1</sup> (Fig 2k); *C. debilis* and *Deltocyathus* spp. were found in a  
 270 smaller range of dissolved oxygen conditions, between 4.5- and 5.5-mL l<sup>-1</sup> (Fig 2l), and  
 271 were found in waters with silicate concentrations < 50 μmol l<sup>-1</sup> (Figure 2m and n,  
 272 respectively): *L. pertusa* and *S. variabilis*, that were mainly restricted to < 20 μmol l<sup>-1</sup>  
 273 (Fig 2m): *S. variabilis* had the narrowest temperature range, with most occurrences in a  
 274 maximum of 10 °C (Fig 2n).

276

277 *Variable selection and contribution*

278 Variables with the highest AUC from each category were selected for model  
 279 construction, with the exception of aragonite saturation state (AST), which was selected  
 280 for Scleractinia and each scleractinian species as they have aragonitic skeletons.  
 281 Variables selected for final models of Octocorallia and Scleractinia were the same, with  
 282 the exception of the carbonate variable (Table 3). The variables that most contributed to  
 283 the final model for Octocorallia were calcite saturation state (CST), dissolved oxygen  
 284 and temperature, whereas for Scleractinia were AST, depth and temperature (Table 4).  
 285 Variables selected for specific models of *Deltocyathus* spp., *E. rostrata*, *M. oculata* and

286 *L. pertusa* were AST, depth, current velocity, POC, dissolved oxygen, silicate and  
 287 temperature (Table 3). Whereas for *C. debilis* oxygen utilization was selected instead of  
 288 dissolved oxygen and for *S. variabilis* salinity in place of silicate (Table 3). The final  
 289 models demonstrated differences in the three variables that contributed most. *C. debilis*,  
 290 *Deltocyathus* spp., *E. rostrata*, *L. pertusa* and *M. oculata* all showed that AST, depth  
 291 and temperature were the best contributors for these species, whilst depth, POC and  
 292 salinity were best for *S. variabilis* (Table 4).

293

294 *Model performance and habitat suitable area*

295 Octocorallia and Scleractinia models performed well, with AUC of 0.9681 and  
 296 0.9551 from test data, respectively. The distribution of suitable habitat for Octocorallia  
 297 encompassed along the entire Brazilian continental margin, including the Vitória-  
 298 Trindade seamount chain and Rio Grande Rise (30°S, 35°W) (Fig 3). Whereas the  
 299 habitat suitability distribution of Scleractinia was more restricted to the Central and  
 300 South area of Brazil, between 20°S 37°W and 30°S 50°W, including the Rio Grande  
 301 Rise (Fig 3, ESM Fig 1 and 2, respectively). Both, Scleractinia and Octocorallia  
 302 demonstrated an overlap in suitable habitat within the Central and South region, as well  
 303 as in the Rio Grande Rise (Fig 3).

304 The scleractinian species-level models also exhibited acceptable model  
 305 performance (Test-AUC: *C. debilis*, 0.9857; *Deltocyathus* spp., 0.9412; *E. rostrata*,  
 306 0.997; *L. pertusa*, 0.9902; *M. oculata*, 0.975; *S. variabilis*, 0.9935). Both, *C. debilis* and  
 307 *Deltocyathus* spp., demonstrated suitable habitat around the South and Central areas,  
 308 between 20°S 40°W and 42°S 23°W, covering a greater area of continental slope, in  
 309 terms of bathymetric extent, than reef-forming species (Fig 3, ESM Fig 3 and 4). The  
 310 reef-forming species *L. pertusa* and *M. oculata* were concentrated around the Northeast,  
 311 Central and South area (ESM Fig 5 and 6), whilst *E. rostrata* and *S. variabilis* were  
 312 restricted to the Central and South area, especially the Vitória-Trindade seamount chain  
 313 and Campos and Santos Basins (i.e., between 20°S 40°W and 42°S 23°W) (Fig 3 B and  
 314 ESM Fig 7 and 8). Most scleractinian species overlapped in predicted suitable habitat in  
 315 some regions of the Northeast area (Fig 3 b, i and ii); the Central area (in Vitoria-  
 316 Trindade chain) (Fig 3 b, iii); the South area (Fig 3 b, iv); and the Rio Grande rise (Fig 3  
 317 b, v).

318

319 *Ecological species niche comparison*

320 Environmental niches of Scleractinia and Octocorallia were determined mainly  
321 by temperature, depth, CST, POC and regional flux (water current velocity) on the  
322 principal component 1 (PC1) and by dissolved oxygen and silicate on the second  
323 principal component (PC2). These two components explained ca. 65.5% and 18.5%,  
324 respectively, of the environmental conditions occupied (Fig 4 c). Octocorals had a wider  
325 environmental niche than Scleractinia, mainly along the PC1, covering 30% and 16% of  
326 the environmental conditions of the region, respectively (Fig 4 a and 4 b). The center of  
327 density of niches were highly differentiated between both groups reflecting the low  
328 niche overlap between Octocorallia and Scleractinia ( $D=0.28$ ) (Table 5).

329 The environmental niche of Scleractinia presented two subcenters;  
330 corresponding to reef-forming and non-reef-forming species (Fig 4 b). The non-reef-  
331 forming species, i.e. *C. debilis* and *Deltocyathus* spp., had their density center displaced  
332 to the down-left indicating that their niches were determined by higher temperature,  
333 POC, current velocity, AST and dissolved oxygen, as well as shallower depths and  
334 lower silicate concentration (Fig 4 d and e). Both species had an environmental niche  
335 that covered the 8% of the environmental conditions available in the region. Reef-  
336 forming species had the niche density center displaced to the top-right showing opposite  
337 patterns to non-reef-forming species (Fig 4 f to i). The environmental niche of *E.*  
338 *rostrata*, *L. pertusa*, *M. oculata* and *S. variabilis* covered 4%, 8%, 7% and 5% of the  
339 environmental conditions available in the region, respectively. The similarity niche  
340 hypothesis was accepted for most pairs of scleractinian species in both directions,  
341 except for *E. rostrata* compared to *C. debilis*, *Deltocyathus* spp. to *L. pertusa*, and for  
342 *M. oculata* to *S. variabilis*, in both directions (Table 5). The niche equivalence  
343 hypothesis was rejected for all Scleractinia species.

344

345

346 **DISCUSSION**

347 In this study, we developed habitat suitability distribution models built  
348 specifically for the main CWC taxa found along the Brazilian continental margin. These  
349 results represent significant improvement over previous model predictions for this  
350 region, which were derived from global scale predictions (i.e. Davies et al., 2008; 2011;  
351 Yesson et al., 2012). This improvement is largely determined by the new region-specific  
352 compilation of occurrence records and also the construction of a regional scale model,  
353 which has a higher capability to identify specific niche features as result of the use of a  
354 more focused range of background environmental conditions (Vierod et al., 2014). In  
355 addition, widely distributed species could exhibit regional or local niche differences for  
356 a variety of evolutionary and non-evolutionary reasons (Pianka, 1988; Lesica and  
357 Allendorf, 1995; Leibold et al., 2019) that are not captured in larger scale models.  
358 Representing regional ecological and environmental features allows for a stronger local  
359 predictive power (Osborne and Suarez-Seoane, 2002; Murphy and Lovett-Doust, 2007).  
360 This approach can thus greatly enhance the understanding of CWC habitat suitability  
361 within the Brazilian continental margin and also allowed for an evaluation of the  
362 overlap between the CWCs found within the region.

363 We observed geographical overlap in the predicted suitable habitat for  
364 Octocorallia and Scleractinia, as well as between individual scleractinian species in the  
365 Campos Basin, Santos Basin, Vitória-Trindade chain, Rio Grande rise and Pelotas Basin  
366 (South area). As CWCs constitute high biodiversity habitats in the deep (Henry and  
367 Roberts, 2017), we suggest that these areas may be of special interest, particularly for  
368 biodiversity conservation. This reinforces previous studies that highlight the regional  
369 importance of the Vitória-Trindade chain as a priority area for conservation (Meirelles  
370 et al., 2015; Pinheiro et al., 2015) and addresses the lack of information about the deep-  
371 sea biodiversity in the region. In the Southern area and Rio Grande Rise, however, the  
372 substantial overlap in Octocorallia and Scleractinia habitat suitability needs to be  
373 validated given there are no published presence records of octocorals from the Southern  
374 area, and there are no CWC records from the Rio Grande Rise. This highlights the need  
375 of surveys in these regions, particularly in Rio Grande rise, which could be a site for  
376 future mineral extraction of cobalt crusts, which could impact coral communities and  
377 their associated biodiversity if they are found there.

378 Suitable habitat for Octocorallia covered a broad latitudinal range that  
379 encompassed nearly the entire Brazilian continental margin, with large areas of highly  
380 suitable habitat in the Central, North and Northeast areas. In the North area (Amazon  
381 Basin), there was high predicted suitability for Octocorallia in the mesophotic region,  
382 which agrees with the many occurrence records (approximately 75%) that were between  
383 50-150 m depth. Their distribution around this region has been recently corroborated by  
384 the observation of several important communities (Cordeiro et al., 2015; Moura et al.,  
385 2016). Even though there are no published records of octocorals in the South area and  
386 the Rio Grande Rise, where our models have shown potentially suitable conditions (Fig  
387 2), several unpublished records from these areas validate our results (M.V. Kitahara and  
388 P.Y.G. Sumida pers. obs.). The wide distribution of Octocorallia was related with a  
389 wide environmental niche breadth, which covered 30% of the available environmental  
390 conditions of the Brazilian continental margin, suggesting that they may be more  
391 common than previously thought.

392 In contrast, Scleractinia had a far narrower habitat suitability distribution, mainly  
393 along the Central and South areas of the Brazilian continental margin, and a lower  
394 habitat suitability around the North-east. The deep sea in these three areas is dominated  
395 by the presence of Antarctic Intermediate Water (AIW) (Wilson et al., 2007), which has  
396 been found to be associated with several scleractinian species in this region between  
397 550-1200 m depth (Viana et al., 1998; Sumida et al., 2004; Arantes et al., 2009). The  
398 broader habitat suitability distribution of Octocorallia compared to Scleractinia can be  
399 translated into a potentially higher tolerance to physical-chemical conditions in the  
400 environment by Octocorallia (e.g. mesophotic corals at shallower depths), which  
401 generally allows for a wider geographic distribution (Slatyer et al., 2013).

402 Substrate is a fundamental factor for the settlement of CWC and its availability  
403 strongly control their colonization. Nevertheless, the availability of this information is  
404 generally limited, particularly for big areas as the entire Brazilian continental margin.  
405 Therefore, the realized distribution of corals could be far smaller in area than the  
406 potential one we are presenting here (Guinotte and Davies, 2014; Anderson et al.,  
407 2016). CWC that settle in hard-bottom substrate are likely more restricted than soft-  
408 bottom substrate colonizing species. Then, the larger morphological variety of  
409 octocorals, which can present a peduncle for anchoring in mud and sand (order  
410 Pennatulacea), a basal disk for fixation in hard substrates, or a basal rootlike processes

411 to anchor in sediment substrates (Bayer, 1961), may allow them to inhabit both substrate  
412 types. Contrary to Octocorallia, most scleractinians are restricted to hard-substrate, but  
413 some species, such as the cup coral *Deltocyathus* genus inhabit soft substrates. For  
414 instance, octocorals have been observed colonizing shells and rock fragments due to the  
415 scarcity of common hard substrates in the Amazon Basin (Cordeiro et al., 2015).  
416 Whereas in the southeastern area (in Campos basin), the occurrence of diverse  
417 Octocorallia species indicated the presence of both hard and soft habitats along the  
418 continental slope (Arantes et al., 2009). Arantes et al. (2009) observed co-occurrence of  
419 octocorals of both type of substrates and scleractinians in the middle slope, which  
420 corroborates the observed overlap in their suitable distribution (Fig 3 a-i).

421 CST, depth, and temperature accounted for the highest contributions to corals  
422 suitability predictions and agree with findings from previous studies about CWC  
423 distributions (Davies et al, 2008; Dullo et al., 2008; Tittensor et al., 2009; Davies and  
424 Guinotte, 2011). CST and AST have been found to be strong predictors in many CWC  
425 species distribution models, mainly at global scales (Davies et al., 2008; Tittensor et al.,  
426 2009; Davies and Guinotte, 2011; Yesson et al., 2012) and in some specific regions,  
427 such as the Pacific Ocean (Anderson et al., 2016). POC is the main food source for  
428 many cold-water coral species (Kiriakoulakis et al., 2004; 2007), but in this study it was  
429 an important predictor only for *S. variabilis*. POC concentration was relatively low in  
430 many areas where corals were found, as has been observed in other regions, such as in  
431 the Northwestern Pacific (Guinotte and Davies, 2014). Nevertheless, these low values  
432 observed here could be due to the fact that POC was calculated as an annual mean and  
433 would underrepresent important seasonal pulses. For instance, increases in POC  
434 resulting from down-welling events or water movements due to internal waves are  
435 important for some coral species, such as *L. pertusa* (Davies et al., 2009; Purser et al.,  
436 2010; van Oevelen et al., 2016). Silicate environmental conditions have been indicated  
437 to have a negative relationship with *L. pertusa* global distribution (Davies et al., 2008),  
438 and a strong negative correlation with coral species richness (especially within the  
439 north-east Pacific) (Reyes Bonilla and Cruz Piñón, 2002). Low silicate concentration is  
440 associated with low primary productivity waters (Longhurst and Pauly, 1987). Here,  
441 silicate was an important factor to predict species suitability distribution. Silicate was  
442 related with depth and could be an indicator of productivity along the Brazilian

443 continental margin that particularly differentiated the more productive conditions  
 444 inhabited by Octocorallia compared with Scleractinia.

445 There were clear differences in environmental niche of the scleractinian species  
 446 investigated in this study. Reef-forming species were found in conditions with higher  
 447 silicate and depth but in a lower dissolved oxygen concentration range (a minimum of  
 448 4.5 ml l<sup>-1</sup>), AST, POC, temperature and regional flow conditions compared with non-  
 449 reef-forming species. Non-reef-forming species niches were associated to a larger range  
 450 of silicate conditions, regional flow and POC conditions (Fig. 2 and 4). These results  
 451 suggest that non-reef-forming species are not limited by environmental conditions as the  
 452 studied reef-forming species within the Brazilian continental margin. This is  
 453 corroborated by their wide distribution in the neighbor Colombian Caribbean region  
 454 between 10-153m and 70-520m, respectively (Santodomingo et al., 2013).

455 Based on the niche conservation theory ecological niches are thought to be more  
 456 similar between close-related taxa (reviewed in Wiens and Grahams, 2005). Within both  
 457 groups, reef forming and non-reef-forming species, there were significant niche  
 458 similarities and differences that were not related with their phylogenetic proximity. For  
 459 instance, *E. rostrata* and *M. oculata* are two reef-forming species that present similar  
 460 environmental niches and belong to different clades of Scleractinia, i.e., the “Complex”  
 461 and “Robust” clades, respectively (Stolarski et al., 2011). On the other hand, *E. rostrata*  
 462 and *Deltocyathus* spp., a reef-forming and non-reef-forming species, respectively, are  
 463 from the “Complex” clade but presented a non-similar environmental niche. This  
 464 suggests that the differentiation between reef-forming and non-reef-forming species  
 465 could imply a divergence in the environmental niche, which is likely independent from  
 466 the evolutionary divergence of “Complex” and “Robust” clades. The diversity of niche  
 467 relationships observed between the studied scleractinian species, with no pattern related  
 468 with evolutionary relationships, reflects the complex and poorly understood evolution of  
 469 Scleractinia.

470 *L. pertusa*, *M. oculata* and *S. variabilis* and *E. rostrata* are widely considered the  
 471 main reef-forming species in the central and south Brazilian areas (Kitahara et al., 2009,  
 472 Cavalcanti et al., 2017). In this study, we observed that *E. rostrata* had a predicted  
 473 distribution that overlapped with *M. oculata* and *S. variabilis* in the South and Central  
 474 area of Brazil, with all having significantly similar niche. This corroborates their role of  
 475 reef-forming species in Brazilian waters. It is important to highlight that *E. rostrata*, as

476 well as *S. variabilis*, had a restricted environmental niche (due to inhabit a more  
477 restricted range of temperature, depth, POC, AST and regional flux). Thus, *E. rostrata*  
478 and *S. variabilis* niches were quite different to the other species niches, showing a non-  
479 similar niche with *L. pertusa* and *C. debilis*, and with *M. oculata*, respectively. Despite  
480 their restricted niche at regional scale, both species are known to be particularly  
481 abundant in Campos basin (Cavalcanti et al., 2017). *E. rostrata* and *S. variabilis* are  
482 more abundant in the South-west Pacific Ocean, and are infrequently observed in the  
483 North Atlantic (Davies and Guinotte, 2011; Roberts et al., 2006).

484 As discussed for Scleractinia and Octocorallia, substrate habitat type may  
485 determine the real distribution, inside the predicted potential distribution areas of the  
486 scleractinian species. All reef-forming species together with the non-reef-forming *C.*  
487 *debilis* inhabit hard-bottom substrate, whereas *Deltocyathus* spp. inhabit soft-bottom  
488 substrate. For instance, *D. italicus* and *Deltocyathus* sp., solitary species with  
489 unattached bases, were registered in both mid and lower slope in Campos basin  
490 (Arantes et al., 2009). These cup corals can also create large dense fields, as observed in  
491 La Foneca canyon by *Desmophyllum dianthus* (Ayma et al., 2019; Lastras et al., 2019),  
492 providing hard substrata and increasing local biodiversity. This indicates that diverse  
493 kind of VME are likely distributed along the Brazilian continental margin. Particularly  
494 in the central and south areas, were a high number of species share habitat suitability  
495 (Fig 2 b - ii and iv).

496 Species niche properties as niche breadth are indicators of species sensitivity  
497 (Kotiaho et al., 2005; Thuiller et al., 2005) and generally, species with a restricted or  
498 smaller niche, have been shown to be more sensitive to the loss of habitat caused by  
499 disturbances such as those produced by climate change (e.g., fish: Munday, 2004; birds:  
500 Seaone and Carrascal, 2008). Given that *E. rostrata* and *S. variabilis* had smaller niches  
501 than other species in this study, they may be the most sensitive species to variations in  
502 environmental conditions. Conversely, those species with a wider environmental niche,  
503 such as *C. debilis*, *Deltocyathus* spp., *L. pertusa* and *M. oculata* may be less sensitive to  
504 environmental changes. Despite this assumption, some species could be overly  
505 susceptible to changes in one particular environmental factor. For instance, *C. debilis* is  
506 likely to be more sensitive to changes in the dissolved oxygen and silicate concentration  
507 than to other factors studied (Fig 4d). Specific biological traits, such as acclimatization  
508 or adaptive capacity will also influence the species response to environmental changes.

509 For example, *L. pertusa* has a higher acclimatization capacity to lower temperature than  
510 *M. oculata* (Naumann et al., 2014). However, *M. oculata* fossils indicate a wider  
511 tolerance to changes in environmental conditions than *L. pertusa* in the Gulf of Cádiz  
512 (Wienberg et al., 2009). Specific experimental research of organisms inhabiting  
513 different regions are fundamental to understanding their ecological niche, physiology  
514 and additional sources of uncertainty that might influence their survival under future  
515 environmental disturbances.

516

#### 517 *Approach limitations*

518 Whilst habitat suitability modeling has been widely used to determine the potential distribution of deep-sea species (e.g., Guinotte et al., 2010; Davies and  
519 Guinotte, 2011; Tracey et al., 2011; Yesson et al., 2012), there are still limitations that  
520 should be considered during the modeling approach (Vierod et al., 2014, Anderson et  
521 al., 2016). For example, a regularly spaced sampling regime that covers the entirety of  
522 the environmental conditions observed in the region of interest is important (Hirzel and  
523 Guisan, 2002). Independent species presence and/or absence data is also an important  
524 aid for model validation (Anderson et al., 2016). However, deep-sea surveys with this  
525 characteristic are extremely limited due to high cost and significant logistical  
526 restrictions such as access to both ship-time and high-quality sampling equipment.  
527 These limitations lead to a disproportionate effect on sampling quality in some regions,  
528 particularly in areas such as the South Atlantic Ocean, where many countries have  
529 restricted access to ocean-going research vessels. In this study, the focus on the  
530 collection of new region-specific occurrences that were not present within international  
531 datasets led to substantial improvements in the quality and utility of predictions in this  
532 region. Nevertheless, future surveys must be carried out in order to validate the present  
533 predictions, principally in the North and Northeast areas for scleractinian and in the  
534 South area to octocorals.

536 It is essential to note that this study only presents suitable areas, which are statistically likely to contain species presences based upon the environmental data used  
537 in the models. There will be other variables or factors that were not included in the  
538 analysis which could influence these predictions, such as substrate availability and type.  
539 Hard substrate presence is highly variable over small spatial scales and is a strong

541 constraining variable that limits the distribution of many coral species (Davies and  
542 Guinotte, 2011; Tracey et al., 2011; Guinotte and Davies, 2014; Mackay et al., 2014).  
543 For example, suitable predicted areas for reef-forming species in the flat tops of some  
544 seamounts in the South Pacific, were dominated by sand, an unsuitable substrate for  
545 most stony coral species settlement (Anderson et al., 2016). Furthermore, the SRTM30  
546 bathymetry data have shown to overestimate suitable area for some deep-sea corals  
547 (Marshall, 2011; Ross et al., 2015), particularly in regions where local bathymetric data  
548 does not exist (Anderson et al., 2016). Better local surveys and the collection of high-  
549 resolution bathymetric data will improve bathymetric representation. This may provide  
550 a representation of sea-bed physiographical features of importance for the presence of  
551 corals and provide the potential for the elucidation of substrate type, which will  
552 substantially improve regional and local habitat suitability models (e.g., Howell et al.,  
553 2011; Rengstorf et al., 2013; 2014; García-Alegre et al., 2014; Georgian et al., 2014).

554

### 555 *Conclusions*

556 The information presented in this study represents the first regional scale habitat  
557 suitability modelling effort for CWCs along the Brazilian margin. This study represents  
558 a fundamental step in better understanding the distribution of Brazilian CWCs and  
559 provides essential information to guide future surveys and conservation plans in the  
560 region. For instance, future surveys must be oriented to describe the presence of both,  
561 octocorals and scleractinians corals, to validate the predictions, mainly where suitability  
562 is observed with no presence records. Based upon the areas of predicted suitable  
563 habitats for CWC, we highlight the importance of management plans that combine the  
564 oil and gas exploration areas with conservation and mitigation of potential impacts to  
565 these communities in Campos Basin, Santos Basin, Vitoria-Trindade chain, Rio Grande  
566 rise and Pelotas Basin (South area). Particularly, the Rio Grande Rise area must be  
567 characterized in terms of biodiversity composition, since it contains cobalt crusts and a  
568 possible future extraction of minerals could impact coral communities that may be  
569 currently unknown. The broader habitat suitability distribution of Octocorallia  
570 compared to Scleractinia is related to a broader environmental niche breadth, likely due  
571 to the variety of physiological adaptations of this group. Non-reef-forming scleractinian  
572 species were less restricted by environmental conditions, when compared to reef-  
573 forming species, allowing them to potentially inhabit a broader area of the Brazilian

574 continental margin. Most reef-forming species presented similar but not equivalent  
575 ecological niche, indicating that management planning, conservation efforts and cruise  
576 planning should consider the species individual environmental requirements to be more  
577 efficient. For instance, priority consideration may need to be given to *S. variabilis* and  
578 *E. rostrata* since they had smaller niche breadth and may be more sensitive to changes  
579 in the environment.

580

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## 909 FIGURES AND TABLES

910 **Figure 1.** (a) Overview of the study area localization. (b) The Brazilian continental  
 911 margin with the CWC presence points of Octocorallia and Scleractinia (light blue and  
 912 light grey, respectively), in the focal areas used in the present study. The boundaries of  
 913 the Brazilian EEZ along the Brazilian coast are represented by the grey line.

914 **Figure 2.** Kernel density curves of the environmental conditions occupied by corals  
 915 from the Brazilian continental margin. Octocorallia (dotted line) and Scleractinia  
 916 (continuous line) are shown to the left of the figure, and *Cladocora debilis* (black dotted  
 917 line), *Deltocyathus* spp. (yellow dotted line), *Enallopsammia rostrata* (red line),  
 918 *Lophelia pertusa* (dark green line), *Madrepora oculata* (grey line), and *Solenosmilia*  
 919 *variabilis* (blue line), to the right. Carbonate condition represent aragonite saturation  
 920 state ( $\Omega$ ) for Scleractinia and scleractinian species, and calcite saturation state for  
 921 Octocorallia.

922

923 **Figure 3.** Potential distribution areas and the overlap between the different taxa. A)  
 924 Octocorallia (light blue) and Scleractinia group (blue) with their overlapped area  
 925 (marine blue). Main overlapping areas: Central area, Rio Grande rise, South area; B)  
 926 Scleractinian species (*Cladocora debilis*, *Deltocyathus* spp., *Enallopsammia rostrata*,  
 927 *Lophelia pertusa*, *Madrepora oculata* and *Solenosmilia variabilis*) overlap, showed as  
 928 the number of species potentially distributed in the same area, along the Brazilian  
 929 continental margin. Areas with higher number of species potentially distributed there:  
 930 north of the Northeast score in front of the Rio Grande do Norte state, ii) east slope of  
 931 the Northeast area in front of Bahia state, Central area, including the margins of  
 932 submersed islands of the Vitoria-Trindade chain, South area, from Cape of São Tomé to  
 933 30° S in Rio Grande do Sul state, and Rio Grande rise, in Southwestern Atlantic  
 934 International waters. Potential distribution areas are represented with the maximum  
 935 sensitivity plus specificity test threshold.

936

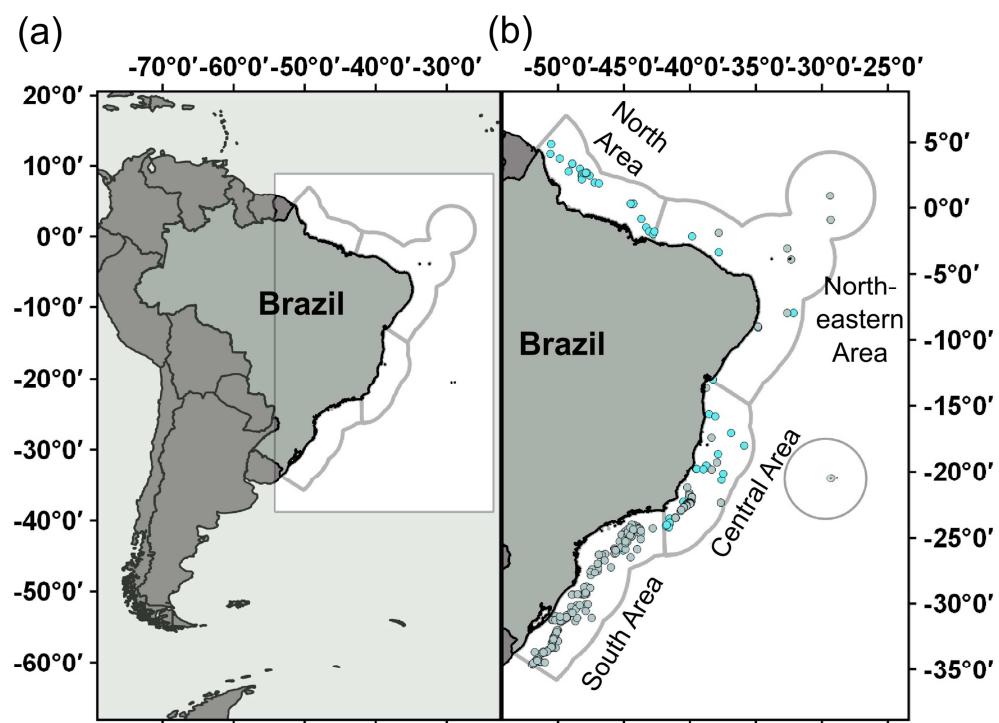
937 **Figure 4.** Ecological niche of the cold-water coral species studied in the environmental  
 938 space produced by the principal component analysis method and the variables  
 939 contribution for loading their two principal components (PC) (c). The results represent  
 940 the niche of the species in the two main axes determining different environmental  
 941 condition. The grey to black shading represents the grid cell Kernel density of the

942 species occurrences, black being the highest density. Dashed lines represent the 50% of  
943 the available environmental conditions in the Brazilian continental margin, and the solid  
944 line represent the 100%. Red arrows connect density center of the species niche to the  
945 density center of Scleractinia and illustrate their differences. In (c), POC in abbreviation  
946 for particulate organic carbon and AST, aragonite saturation state.

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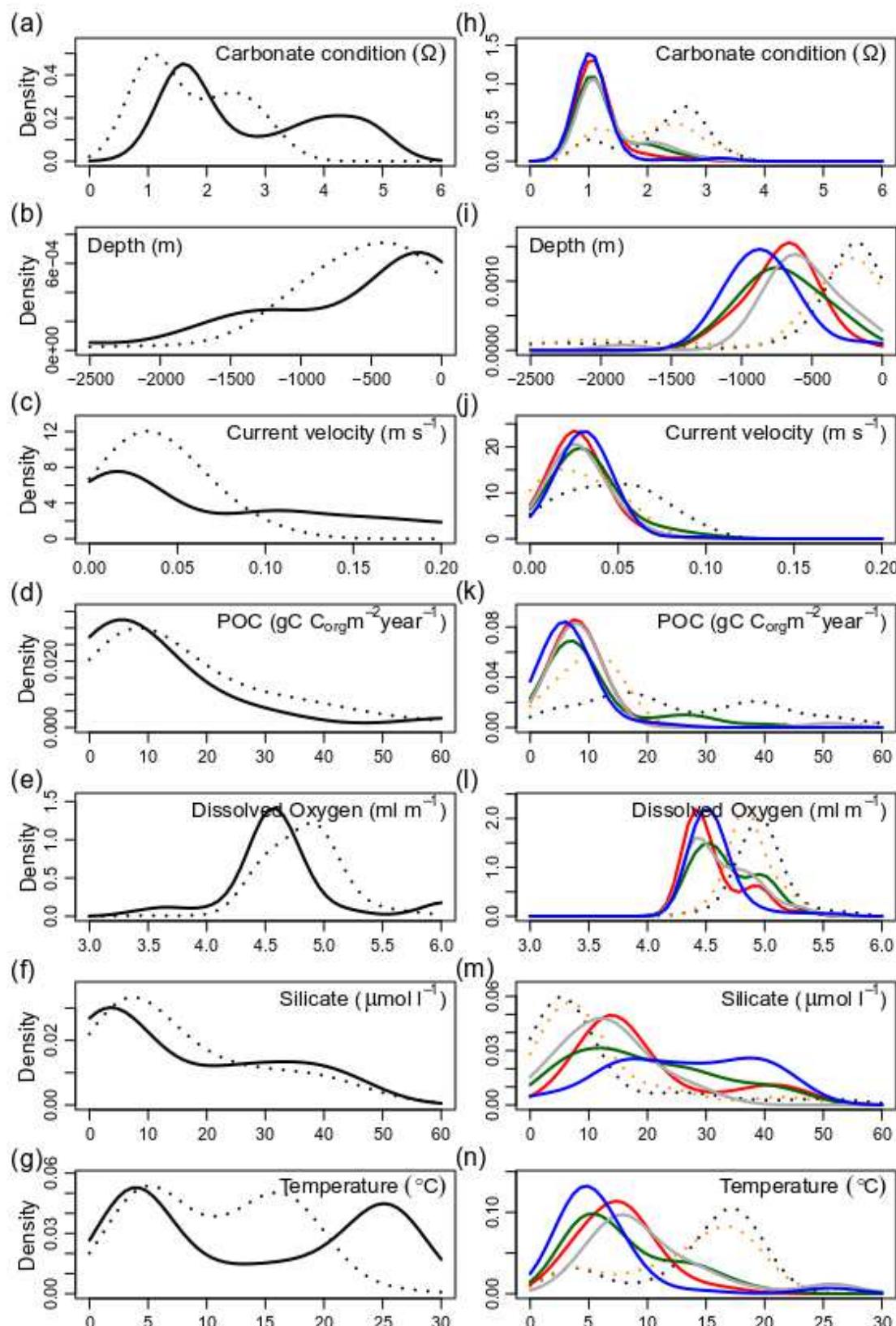
949 Figure 1



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Figure 3

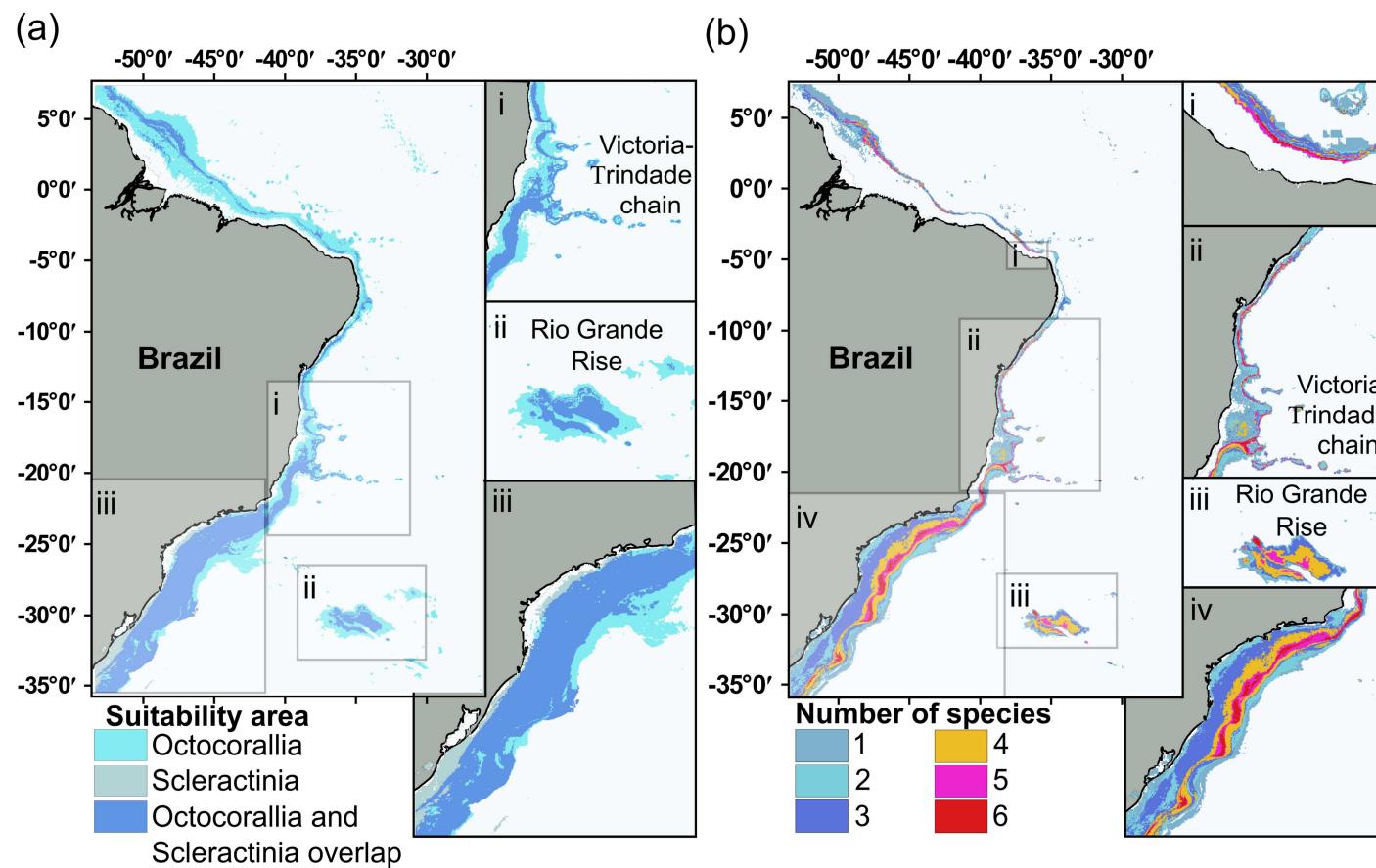
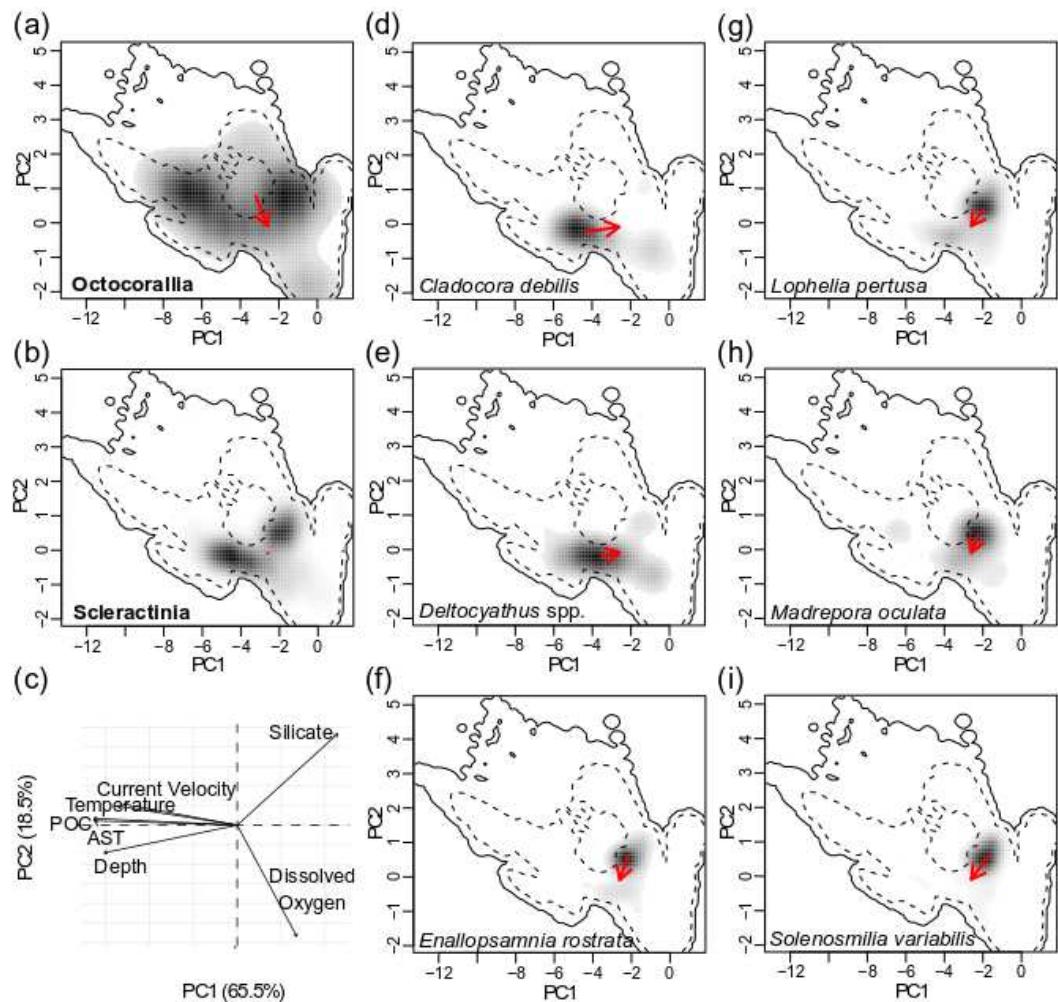


Figure 4



**Table 1.** Number of occurrence records of azooxanthellate corals from the Brazilian continental margin and slope, including historical records from published sources (see references in supplementary Table 1) and new scleractinian records from Cavalcanti et al. (2017), and the filtered total number of records (with one record for analysis cell) that were used to model habitat suitability.

Taxonomic group	Historical records	New records	Total records used in models
<b>Order Scleractinia</b>	396	1147	259
<b>Subclass Octocorallia</b>	151		60
<b>Species</b>			
<i>Cladocora debilis</i>	57		54
<i>Deltocyathus</i> spp.	36		33
<i>Enallopсammia rostrata</i>	8	222	33
<i>Lophelia pertusa</i>	77	342	75
<i>Madrepora oculata</i>	21	97	29
<i>Solenosmilia variabilis</i>	26	486	72

**Table 2.** Environmental variables used to the variables selection divided in seven categories: carbonate variables (CARB), bathymetric variables (BATH), hydrodynamic variables (HYDRO), productivity variables (PROD), oxygen variables (OXY), chemical variables (CHEM), and temperature (TEMP).

	VARIABLE	NAME	REFERENCE	UNIT
<b>CARB</b>	Aragonite saturation state	arag_orr	Orr et al. (2005)	$\Omega_{ARAG}$
	Aragonite saturation state	arag_stein	Steinacher et al. (2009)	$\Omega_{ARAG}$
	Calcite saturation state	cal_orr	Orr et al. (2005)	$\Omega_{CALC}$
	Calcite saturation state	cal_stein	Steinacher et al. (2009)	$\Omega_{CALC}$
<b>BATH</b>	Aspect	aspect	Jenness (2013)	degrees
	Aspect- Eastness	eastness	Wilson et al. (2007)	-
	Aspect- Northness	northeness	Wilson et al. (2007)	-
	Curvature - Plan	plancurve	Jenness (2013)	-
	Curvature - Profile	profilecurve	Jenness (2013)	-
	Curvature - Tangential	tangcurv	Jenness (2013)	-
	Roughness	roughness	Wilson et al. (2007)	-
	Rugosity	rugosity	Jenness (2013)	-
	Slope	slope	Jenness (2013)	degrees
	Bathymetry	srtm30	Becker et al. (2009)	m
	Terrain Ruggedness Index	tpi	Wilson et al. (2007)	-
	Topographic Position Index	tri	Wilson et al. (2007)	-
<b>HYDRO</b>	Current velocity	regfl	Carton et al. (2005)	$m\ s^{-1}$
	Vertical current velocity	verfl	Carton et al. (2005)	$m\ s^{-1}$
<b>PROD</b>	Seasonal variation index	lutzs	Lutzs et al. (2007)	-
	Primary productivity (maximum)	modismax	NASA Ocean Color	$g\ C\ m^{-2}\ y^{-1}$
	Primary productivity (mean)	modismean	NASA Ocean Color	$g\ C\ m^{-2}\ y^{-1}$
	Primary productivity (minimun)	modismin	NASA Ocean Color	$g\ C\ m^{-2}\ y^{-1}$
	Particulate Organic carbon	poc	Lutz et al. (2007)	$g\ C_{org}\ m^{-2}\ y^{-1}$
	Primary Productivity (Vertically generalised productivity model)	vgpmean	Behrenfeld & Falkowski (1997)	$g\ C\ m^{-2}\ y^{-1}$
<b>OXY</b>	Apparent oxygen utilisation	oaxu	Garcia et al. (2006)	$mol\ O_2$
	Percent oxygen saturation	poxs	Garcia et al. (2006)	% $O_2$
	Dissolved oxygen	disso2	Garcia et al. (2006)	$ml\ l^{-1}$
<b>CHEM</b>	Nitrate	nit	Garcia et al. (2006)	$\mu mol\ l^{-1}$
	Phosphate	phos	Garcia et al. (2006)	$\mu mol\ l^{-1}$
	Salinity	sal	Boyer et al. (2005)	PSS
	Silicate	sil	Garcia et al. (2006)	$\mu mol\ l^{-1}$
<b>TEMP</b>	Temperature	temp	Boyer et al. (2005)	°C

**Table 3.** Test AUC values for Maxent model of Octocorallia and Scleractinia taxa and for six scleractinian species in the Brazilian continental margin, based in a single variable. A value close to 0.5 indicates a model no better than a random prediction, values greater than this and closer to 1 indicate models with better predictive power. A value of 1 indicates a theoretically perfect model. Values in bold indicate the main variable of each categorical group and which were selected to run the final models with the exception of arag\_orr which was used to Scleractinia and the scleractinian species due their ecological importance (See section 2.2. Variables selection and contribution). Category and variable name abbreviations are presented in Table 2.

	VARIABLE	SCLERAC TINIA	OCTOCOR ALLIA	C. DEBIL IS	DELTOCYA THUS SPP.	E. ROSTR ATA	L. PERTU SA	M. OCUL ATA	S. VARIAB ILIS
CARB	arag_orr	<b>0.9525</b>	0.9248	<b>0.9671</b>	<b>0.953</b>	<b>0.9612</b>	<b>0.9624</b>	<b>0.9586</b>	<b>0.9604</b>
	arag_stein	0.9562	0.9233	0.9691	0.9234	0.9588	0.9427	0.9757	0.9135
	cal_orr	0.9579	<b>0.9269</b>	0.9663	0.9524	0.9648	0.9634	0.9637	0.9736
	cal_stein	0.9567	0.9206	0.9697	0.9255	0.9642	0.9487	0.9763	0.9256
BATH	srtm30	<b>0.9664</b>	<b>0.9311</b>	<b>0.9737</b>	<b>0.9659</b>	<b>0.9913</b>	<b>0.9877</b>	<b>0.9951</b>	<b>0.9885</b>
	roughness	0.5204	0.5195	0.475	0.6183	0.6258	0.5883	0.5	0.6505
	rugosity	0.5518	0.6296	0.5243	0.6131	0.3548	0.5759	0.3915	0.6288
	slope	0.599	0.7215	0.4622	0.5222	0.7734	0.7702	0.8024	0.756
	TPI	0.7852	0.5012	0.7461	0.782	0.8196	0.7119	0.9248	0.8564
	TRI	0.7088	0.483	0.6351	0.5874	0.7472	0.6516	0.8489	0.7573
	aspect	0.7332	0.4834	0.6824	0.7362	0.7748	0.6292	0.8729	0.744
	eastness	0.4767	0.5079	0.4937	0.5686	0.431	0.6141	0.5	0.6238
	northeness	0.5467	0.6074	0.5552	0.6484	0.4031	0.5142	0.5	0.5696
	plancurve	0.602	0.7327	0.4447	0.5135	0.763	0.7649	0.8147	0.7787
HY	longcurve	0.7057	0.7277	0.4079	0.5455	0.7977	0.7677	0.8069	0.7629
	tangcurve	0.5981	0.7435	0.4055	0.5352	0.7673	0.7676	0.8106	0.7608
	regfl	<b>0.8705</b>	<b>0.9231</b>	<b>0.9187</b>	<b>0.7648</b>	<b>0.9422</b>	<b>0.8762</b>	<b>0.9566</b>	<b>0.8705</b>
	verfl	0.7004	0.6403	0.33	0.2592	0.743	0.2374	0.7354	0.5
PROD	lutzs	0.8487	0.7848	0.947	0.9316	0.9044	0.8349	0.9645	0.7948
	modismax	0.8086	0.8456	0.9491	0.7766	0.9128	0.8689	0.9669	0.8357
	modismean	0.8351	0.8334	0.9498	0.8157	0.9265	0.9004	0.9779	0.8681
	modismin	0.8086	0.8456	0.9491	0.7766	0.9128	0.8689	0.9669	0.8357
	POC	<b>0.9369</b>	<b>0.8621</b>	<b>0.9662</b>	<b>0.9555</b>	<b>0.9878</b>	<b>0.9727</b>	<b>0.9931</b>	<b>0.978</b>
	vgpmean	0.8439	0.809	0.9544	0.8389	0.9449	0.8847	0.9706	0.8819
OXY	aouxu	0.8195	0.8954	<b>0.9126</b>	0.677	0.6107	0.7846	0.6575	0.6625
	disso2	<b>0.8913</b>	<b>0.939</b>	0.8654	<b>0.8969</b>	<b>0.9083</b>	<b>0.9375</b>	<b>0.9671</b>	<b>0.9477</b>
	poxs	0.7796	0.8992	0.894	0.6299	0.5998	0.7486	0.4196	0.7295
	dic_stein	0.8889	0.9214	0.9345	0.7986	0.8179	0.7632	0.9426	0.6993
	nit	0.8281	0.8829	0.8761	0.7474	0.5964	0.8172	0.6385	0.6625

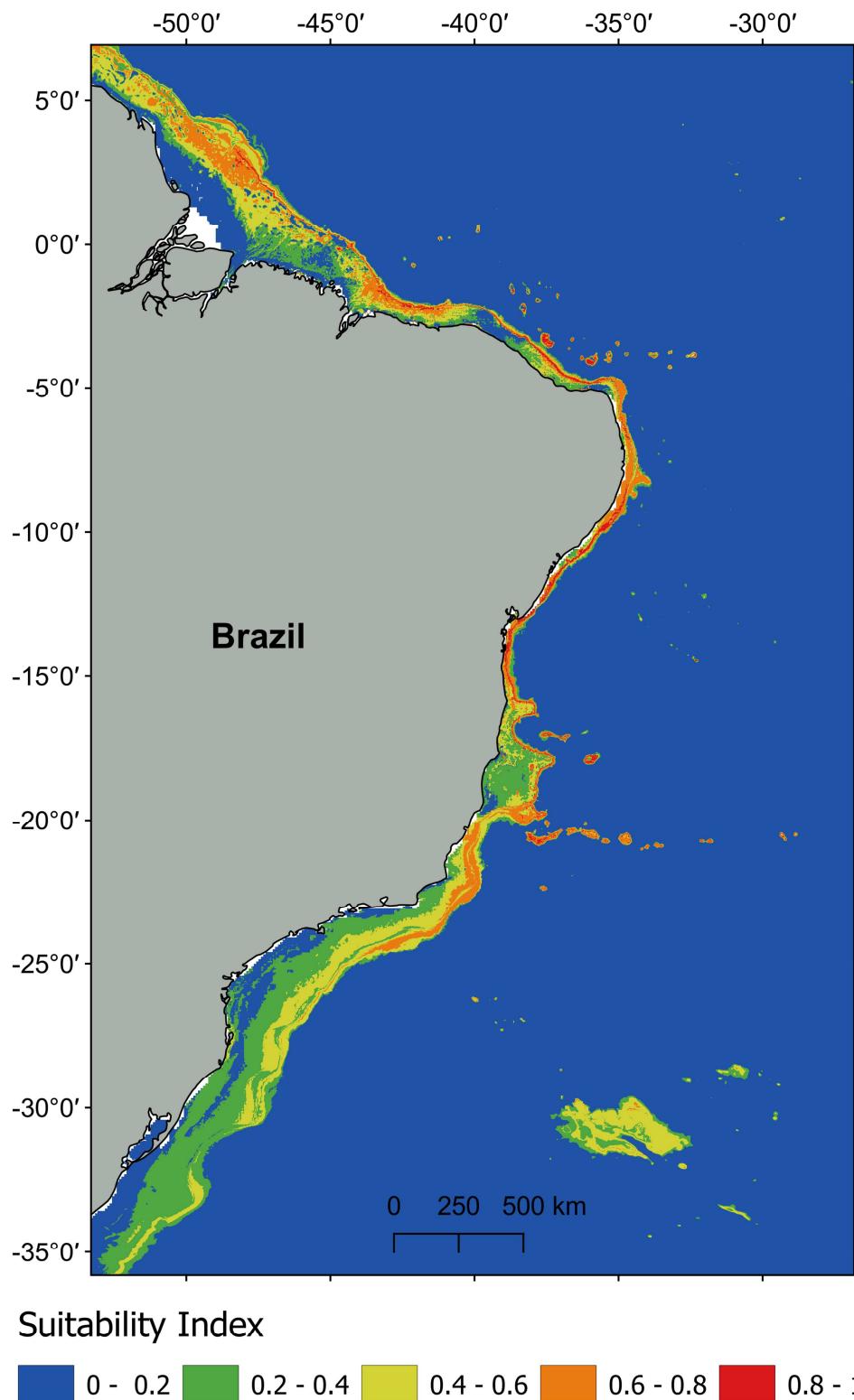
Journal Pre-proof									
CHEM	phos	0.8442	0.9249	0.8669	0.8148	0.6673	0.868	0.6667	0.7377
	sal	0.8962	0.9082	0.8425	0.6082	0.784	0.8779	0.5401	<b>0.9445</b>
	sil	<b>0.9145</b>	<b>0.9273</b>	<b>0.9422</b>	<b>0.8868</b>	<b>0.9312</b>	<b>0.9158</b>	<b>0.9782</b>	0.8753
TEMP	temp	<b>0.9618</b>	<b>0.9309</b>	<b>0.9678</b>	<b>0.953</b>	<b>0.9855</b>	<b>0.9825</b>	<b>0.9951</b>	<b>0.9776</b>

**Table 4.** Test AUC values for Scleractinia, Octocorallia and six different scleractinian species models, based in a single variable model. Values corresponding to the three most significant variables for each taxon are in bold. Variable name abbreviations are presented in Table 2.

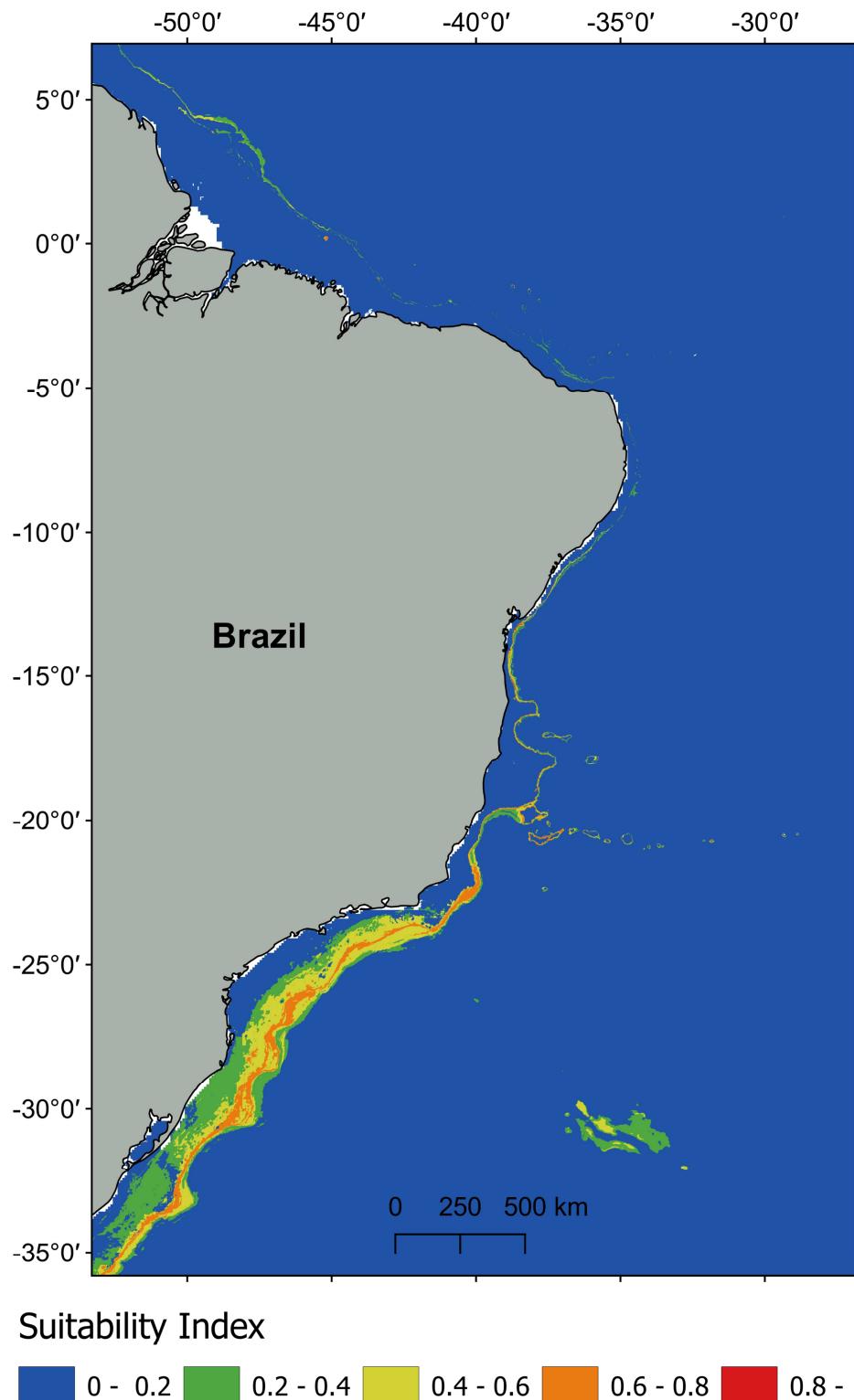
	<i>Scleractinia</i>	<i>Octocorallia</i>	<i>C. debilis</i>	<i>L. pertusa</i>	<i>M. oculata</i>	<i>S. variabilis</i>	<i>E. rostrata</i>	<i>Deltocyathus</i> spp.
AUC								
calc-orr		<b>0.9403</b>						
arag-orr	<b>0.9457</b>		<b>0.9694</b>	<b>0.9565</b>	<b>0.9543</b>	0.9671	<b>0.9403</b>	<b>0.9683</b>
srtm30	<b>0.9518</b>	<b>0.9492</b>	<b>0.9784</b>	<b>0.9882</b>	<b>0.9812</b>	<b>0.9877</b>	<b>0.9493</b>	<b>0.9595</b>
regfl	0.8812	0.8234	0.9223	0.8743	0.916	0.8874	0.8234	0.6203
POC	0.9214	0.8326	0.9685	0.9335	0.8644	<b>0.9748</b>	0.8326	0.9434
diso2	0.8941	0.9206		0.934	0.8869	0.9431	0.9206	0.8913
aouxu			0.8877					
sil	0.8864	0.8639	0.9358	0.9088	0.9527		0.8639	0.9484
sal						<b>0.9905</b>		
temp	<b>0.9424</b>	<b>0.9281</b>	<b>0.9698</b>	<b>0.98</b>	<b>0.9761</b>	0.969	<b>0.9281</b>	<b>0.9635</b>

**Table 5.** Niche comparison for cold water corals in the Brazilian continental margin. Niche overlap values Schoener's  $D$  (Schoener, 1970; Broennimann et al., 2012) and the significance of similarity and equivalence tests are giving for each pair-wise comparison (ns: not significant). The higher overlap value is presented in bold and the lowest in italics.

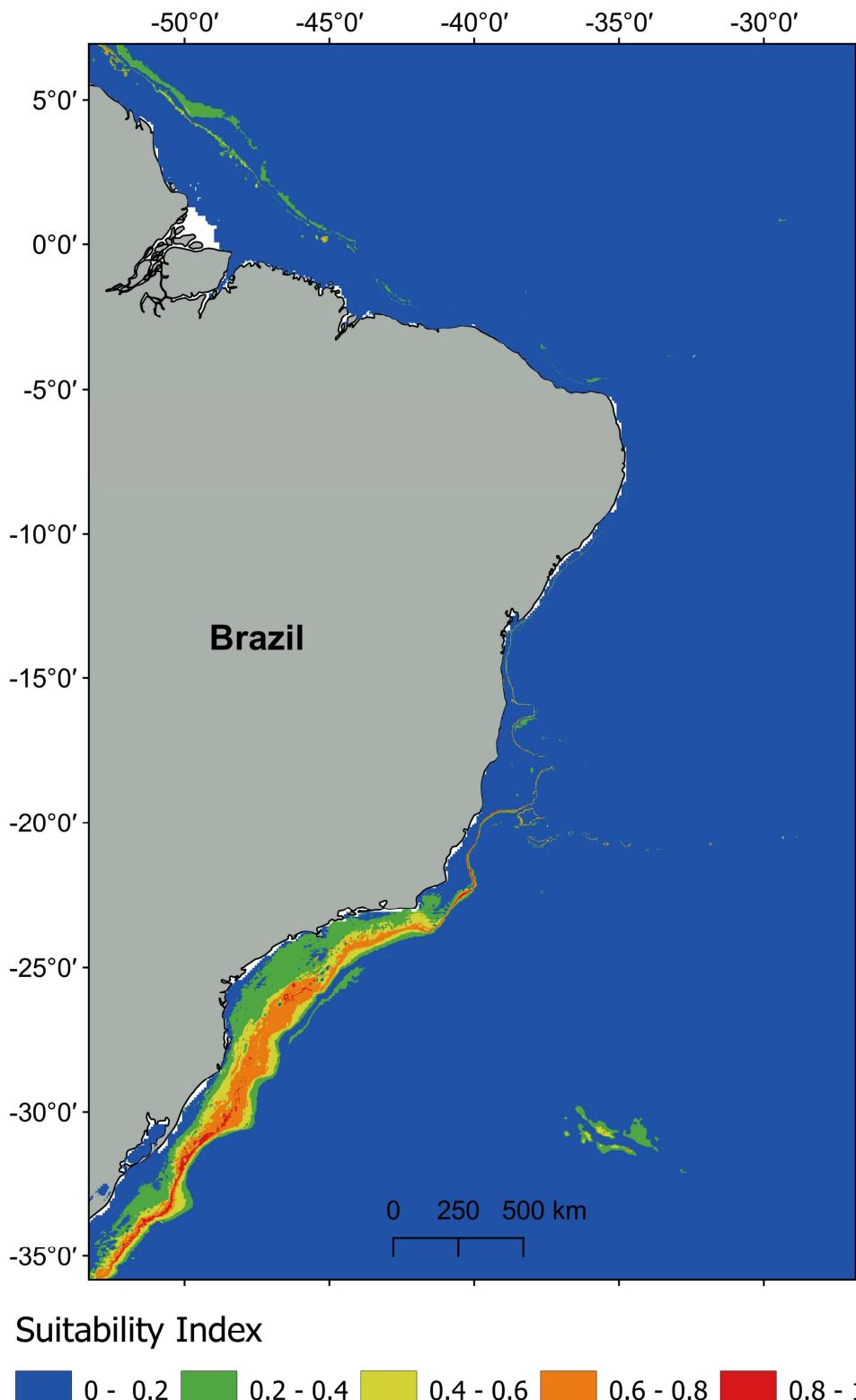
Táxon	<i>a</i>	<i>b</i>	Niche Overlap ( <i>D</i> )	Niche similarit y	Niche equivalence
			<i>a - b and b - a</i>		
<i>C. debilis</i>	<i>Deltocyathus</i> spp.	<b>0.89</b>	Similar	Different	
	<i>E. rostrata</i>	0.01	ns	Different	
	<i>L. pertusa</i>	0.72	Similar	Different	
	<i>M. oculata</i>	0.32	Similar	Different	
	<i>S. variabilis</i>	<i>0.008</i>	Similar	Different	
<i>Deltocyathus</i> spp.	<i>E. rostrata</i>	0.04	ns	Different	
	<i>L. pertusa</i>	0.80	Similar	Different	
	<i>M. oculata</i>	0.40	Similar	Different	
	<i>S. variabilis</i>	0.035	Similar	Different	
<i>E. rostrata</i>	<i>L. pertusa</i>	0.21	ns	Different	
	<i>M. oculata</i>	0.48	Similar	Different	
	<i>S. variabilis</i>	0.77	Similar	Different	
<i>L. pertusa</i>	<i>M. oculata</i>	0.57	Similar	Different	
	<i>S. variabilis</i>	0.20	Similar	Different	
<i>M. oculata</i>	<i>S. variabilis</i>	0.41	ns	Different	
<b>Octocorallia</b>	Scleractinia	0.28	ns	Different	

**Electronic supplementary materials**

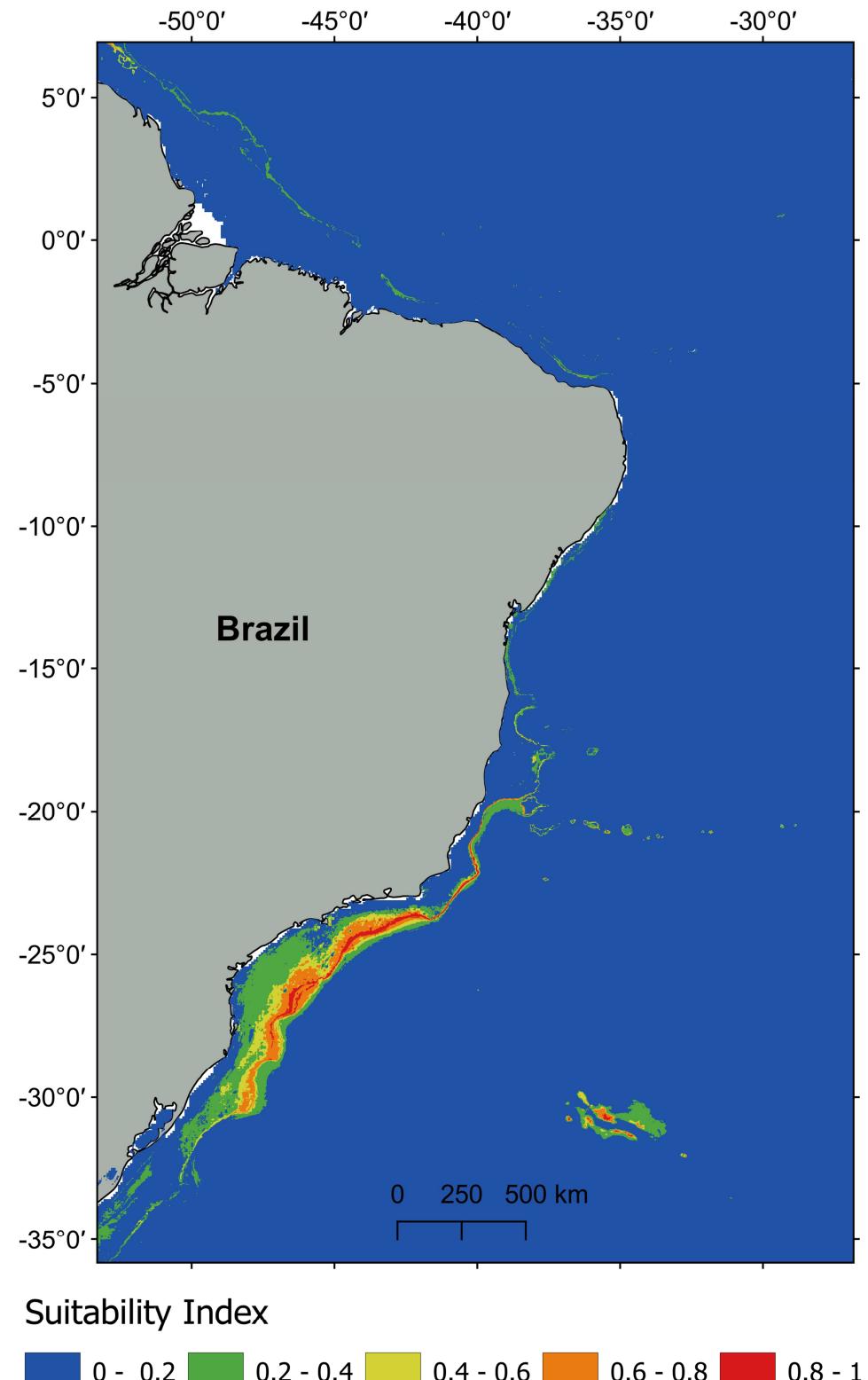
**Figure 1.** Habitat suitability prediction for Octocorallia in the southwest Atlantic Ocean. The legend indicates the habitat suitability index from 0 to 1 as the maximum suitable pixels.



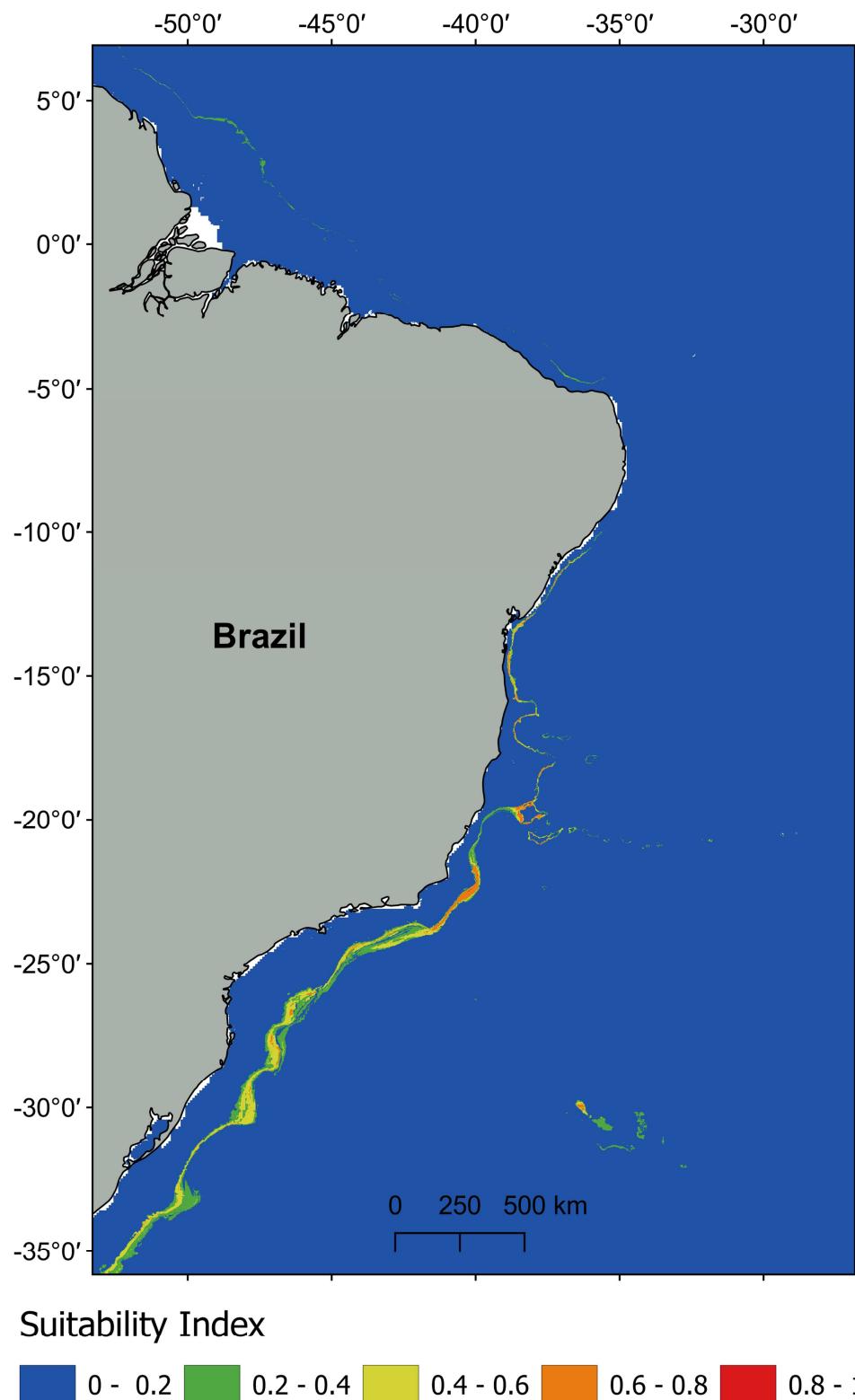
**Figure 2.** Habitat suitability prediction for Scleractinia in the Brazilian continental margin. The legend indicates the habitat suitability index from 0 to 1 as the maximum suitable pixels.



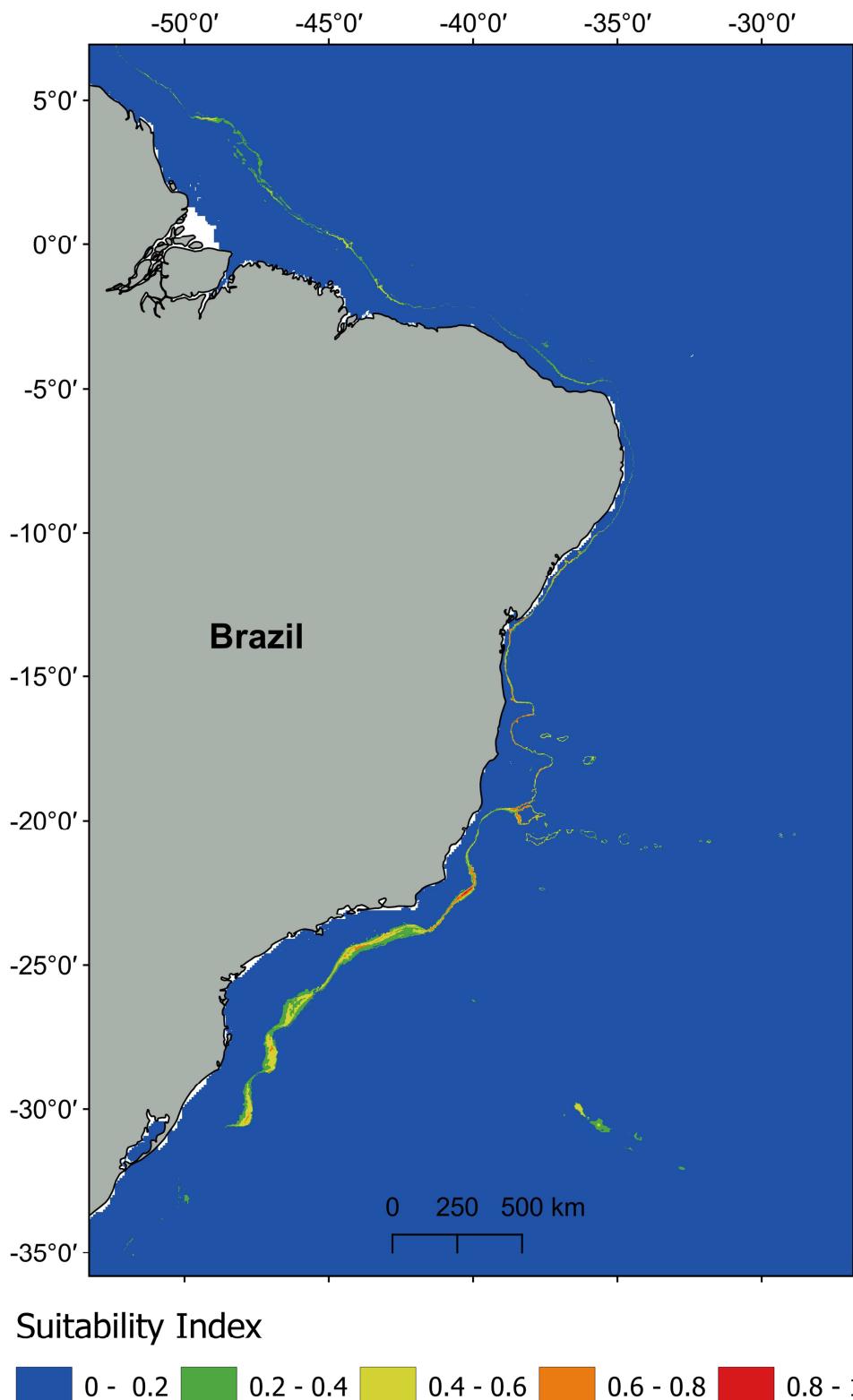
**Figure 3.** Habitat suitability prediction for *Cladocora debilis* in the Brazilian continental margin. The legend indicates the habitat suitability index from 0 to 1 as the maximum suitable pixels.



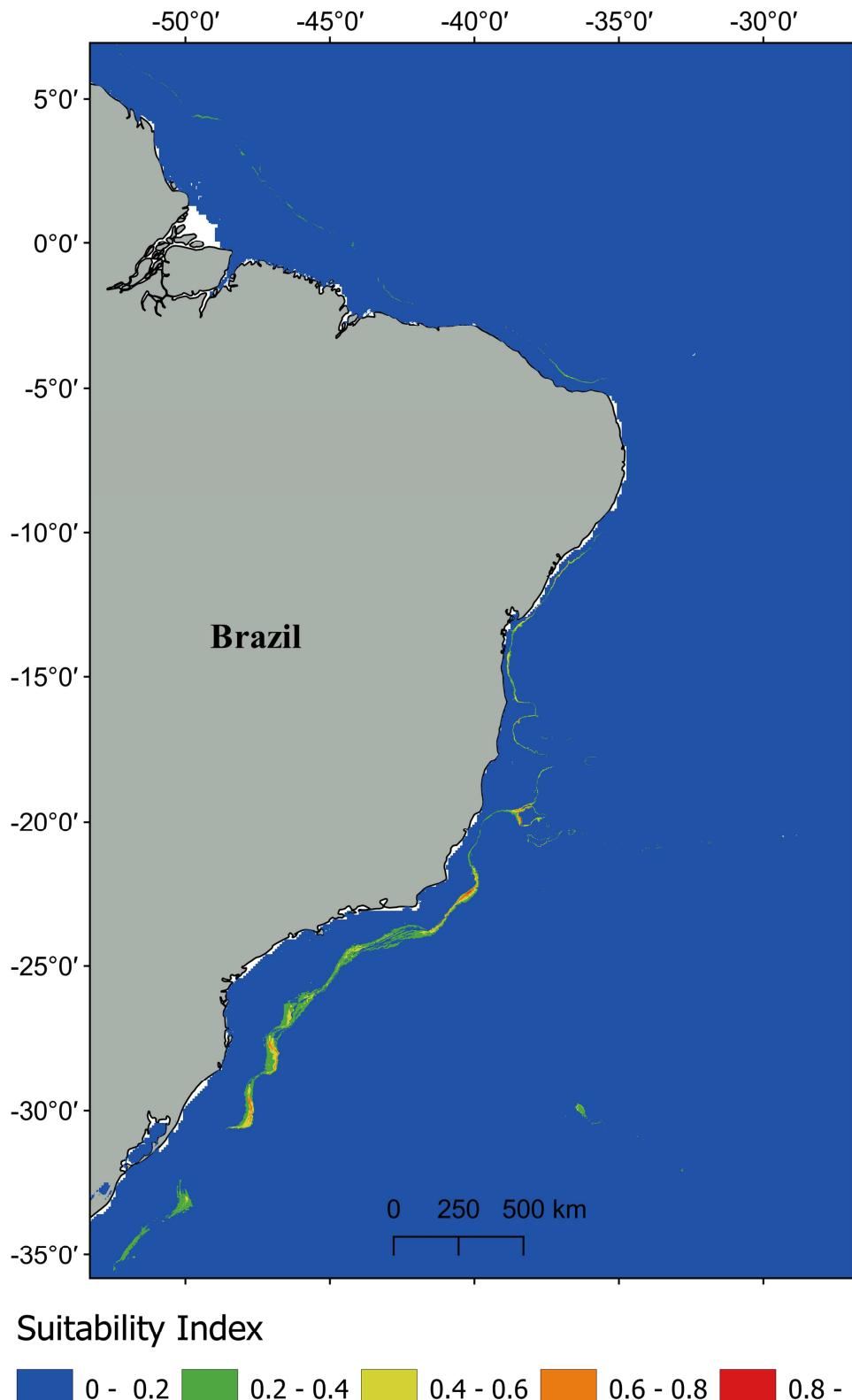
**Figure 4.** Habitat suitability prediction for *Deltocyathus* spp. in the Brazilian continental margin. The legend indicates the habitat suitability index from 0 to 1 as the maximum suitable pixels.



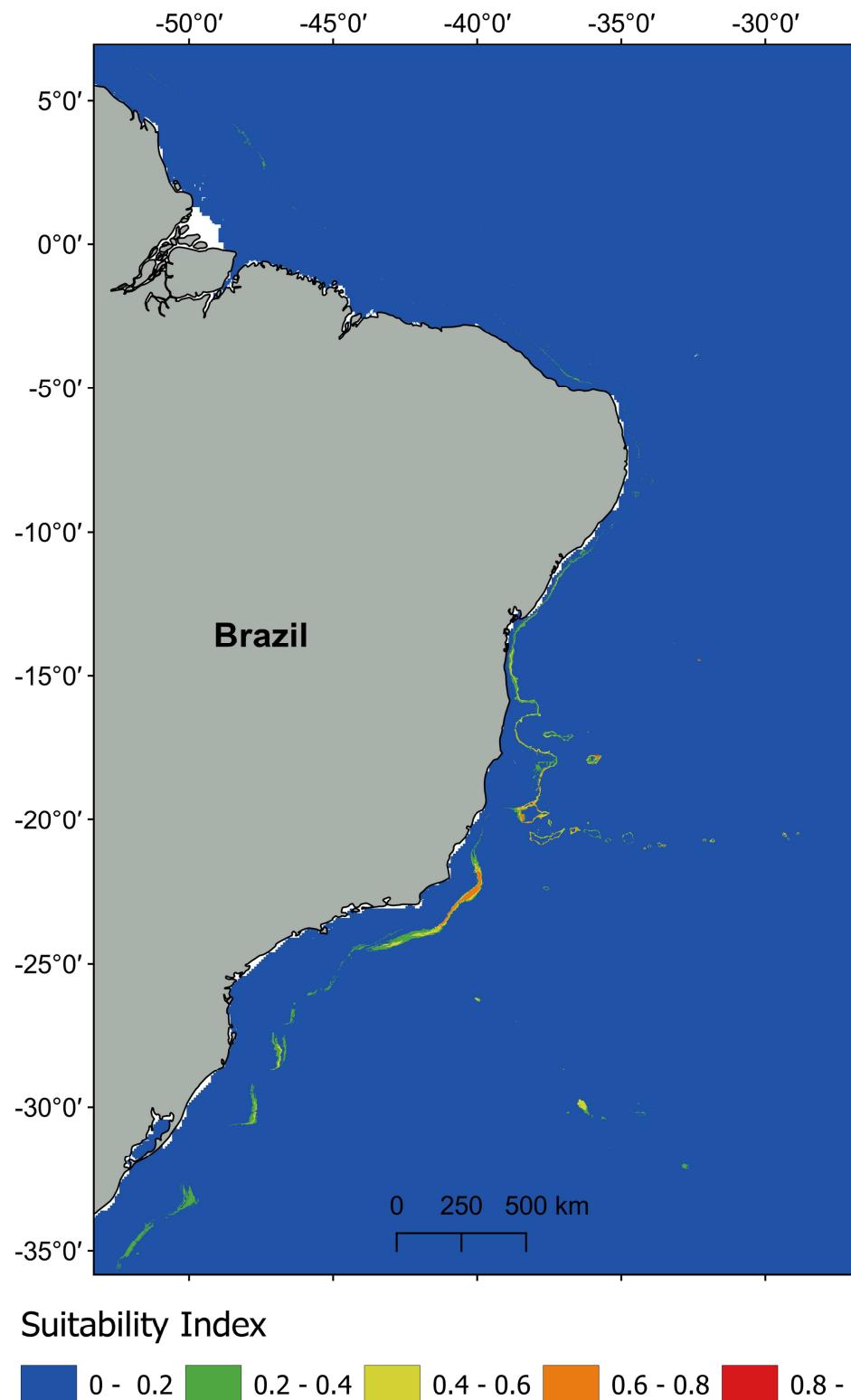
**Figure 5.** Habitat suitability prediction for *Lophelia pertusa* in the Brazilian continental margin. The legend indicates the habitat suitability index from 0 to 1 as the maximum suitable pixels.



**Figure 6.** Habitat suitability prediction for *Madrepora oculata* in the Brazilian continental margin. The legend indicates the habitat suitability index from 0 to 1 as the maximum suitable pixels.



**Figure 7.** Habitat suitability prediction for *Enallopssammia rostrata* in the Brazilian continental margin. The legend indicates the habitat suitability index from 0 to 1 as the maximum suitable pixels.



**Figure 8.** Habitat suitability prediction for *Solenosmilia variabilis* in the Brazilian continental margin. The legend indicates the habitat suitability index from 0 to 1 as the maximum suitable pixels.

**Table 1.** Number of occurrence records of azooxanthellate corals from the Brazilian continental margin and slope, including historical records from published sources (see references in supplementary Table 1) and new scleractinian records from Cavalcanti et al. (2017), and the filtered total number of records (with one record for analysis cell) that were used to model habitat suitability.

Taxonomic group	Historical records	New records	Total records used in models
<b>Order Scleractinia</b>	396	1147	259
<b>Subclass Octocorallia</b>	151		60
<b>Species</b>			
<i>Cladocora debilis</i>	57		54
<i>Deltocyathus</i> spp.	36		33
<i>Enallopсammia rostrata</i>	8	222	33
<i>Lophelia pertusa</i>	77	342	75
<i>Madrepora oculata</i>	21	97	29
<i>Solenosmilia variabilis</i>	26	486	72

**Table 2.** Environmental variables used to the variables selection divided in seven categories: carbonate variables (CARB), bathymetric variables (BATH), hydrodynamic variables (HYDRO), productivity variables (PROD), oxygen variables (OXY), chemical variables (CHEM), and temperature (TEMP).

	VARIABLE	NAME	REFERENCE	UNIT
<b>CARB</b>	Aragonite saturation state	arag_orr	Orr et al. (2005)	$\Omega_{\text{ARAG}}$
	Aragonite saturation state	arag_stein	Steinacher et al. (2009)	$\Omega_{\text{ARAG}}$
	Calcite saturation state	cal_orr	Orr et al. (2005)	$\Omega_{\text{CALC}}$
	Calcite saturation state	cal_stein	Steinacher et al.(2009)	$\Omega_{\text{CALC}}$
<b>BATH</b>	Aspect	aspect	Jenness (2013)	degrees
	Aspect- Eastness	eastness	Wilson et al. (2007)	-
	Aspect- Northness	northeness	Wilson et al. (2007)	-
	Curvature - Plan	plancurve	Jenness (2013)	-
	Curvature - Profile	profilecurve	Jenness (2013)	-
	Curvature - Tangential	tangcurv	Jenness (2013)	-
	Roughness	roughness	Wilson et al. (2007)	-
	Rugosity	rugosity	Jenness (2013)	-
	Slope	slope	Jenness (2013)	degrees
	Bathymetry	srtm30	Becker et al. (2009)	m
	Terrain Ruggedness Index	tpi	Wilson et al. (2007)	-
	Topographic Position Index	tri	Wilson et al. (2007)	-
<b>HYDRO</b>	Current velocity	regfl	Carton et al. (2005)	$\text{m s}^{-1}$
	Vertical current velocity	verfl	Carton et al. (2005)	$\text{m s}^{-1}$
<b>PROD</b>	Seasonal variation index	lutzs	Lutzs et al. (2007)	-
	Primary productivity (maximum)	modismax	NASA Ocean Color	$\text{g C m}^{-2} \text{y}^{-1}$
	Primary productivity (mean)	modismean	NASA Ocean Color	$\text{g C m}^{-2} \text{y}^{-1}$
	Primary productivity (minimun)	modismin	NASA Ocean Color	$\text{g C m}^{-2} \text{y}^{-1}$
	Particulate Organic carbon	poc	Lutz et al. (2007)	$\text{g C}_{\text{org}} \text{m}^{-2} \text{y}^{-1}$
	Primary Productivity (Vertically generalised productivity model)	vgpmean	Behrenfeld & Falkowski (1997)	$\text{g C m}^{-2} \text{y}^{-1}$
	Apparent oxygen utilisation	oaxu	Garcia et al. (2006)	$\text{mol O}_2$
<b>OXY</b>	Percent oxygen saturation	poxs	Garcia et al. (2006)	% $\text{O}_2$
	Dissolved oxygen	disso2	Garcia et al. (2006)	$\text{ml l}^{-1}$
	Nitrate	nit	Garcia et al. (2006)	$\mu\text{mol l}^{-1}$
<b>CHEM</b>	Phosphate	phos	Garcia et al. (2006)	$\mu\text{mol l}^{-1}$
	Salinity	sal	Boyer et al. (2005)	PSS

	Silicate Temperature	sil temp	Garcia et al. (2006) Boyer et al. (2005)	$\mu\text{mol l}^{-1}$ °C
<b>TEMP</b>				

**Table 3.** Test AUC values for Maxent model of Octocorallia and Scleractinia taxa and for six scleractinian species in the Brazilian continental margin, based in a single variable. A value close to 0.5 indicates a model no better than a random prediction, values greater than this and closer to 1 indicate models with better predictive power. A value of 1 indicates a theoretically perfect model. Values in bold indicate the main variable of each categorical group and which were selected to run the final models with the exception of arag\_orr which was used to Scleractinia and the scleractinian species due their ecological importance (See section 2.2. Variables selection and contribution). Category and variable name abbreviations are presented in Table 2.

	VARIABLE	SCLERACTINIA	OCTOCORALLIA	C. DEBILIS	DELTOCYATHUS SPP.	E. ROSTRATA	L. PERTUSA	M. OCULATA	S. VARIABILIS
<b>CARB</b>	arag_orr	<b>0.9525</b>	0.9248	<b>0.9671</b>	<b>0.953</b>	<b>0.9612</b>	<b>0.9624</b>	<b>0.9586</b>	<b>0.9604</b>
	arag_stein	0.9562	0.9233	0.9691	0.9234	0.9588	0.9427	0.9757	0.9135
	cal_orr	0.9579	<b>0.9269</b>	0.9663	0.9524	0.9648	0.9634	0.9637	0.9736
	cal_stein	0.9567	0.9206	0.9697	0.9255	0.9642	0.9487	0.9763	0.9256
<b>BATH</b>	srtm30	<b>0.9664</b>	<b>0.9311</b>	<b>0.9737</b>	<b>0.9659</b>	<b>0.9913</b>	<b>0.9877</b>	<b>0.9951</b>	<b>0.9885</b>
	roughness	0.5204	0.5195	0.475	0.6183	0.6258	0.5883	0.5	0.6505
	rugosity	0.5518	0.6296	0.5243	0.6131	0.3548	0.5759	0.3915	0.6288
	slope	0.599	0.7215	0.4622	0.5222	0.7734	0.7702	0.8024	0.756
	TPI	0.7852	0.5012	0.7461	0.782	0.8196	0.7119	0.9248	0.8564
	TRI	0.7088	0.483	0.6351	0.5874	0.7472	0.6516	0.8489	0.7573
	aspect	0.7332	0.4834	0.6824	0.7362	0.7748	0.6292	0.8729	0.744
	eastness	0.4767	0.5079	0.4937	0.5686	0.431	0.6141	0.5	0.6238
	northeness	0.5467	0.6074	0.5552	0.6484	0.4031	0.5142	0.5	0.5696
	plancurve	0.602	0.7327	0.4447	0.5135	0.763	0.7649	0.8147	0.7787
<b>HY</b>	longcurve	0.7057	0.7277	0.4079	0.5455	0.7977	0.7677	0.8069	0.7629
	tangcurve	0.5981	0.7435	0.4055	0.5352	0.7673	0.7676	0.8106	0.7608
<b>PROD</b>	regfl	<b>0.8705</b>	<b>0.9231</b>	<b>0.9187</b>	<b>0.7648</b>	<b>0.9422</b>	<b>0.8762</b>	<b>0.9566</b>	<b>0.8705</b>
	verfl	0.7004	0.6403	0.33	0.2592	0.743	0.2374	0.7354	0.5
<b>OXY</b>	lutzs	0.8487	0.7848	0.947	0.9316	0.9044	0.8349	0.9645	0.7948
	modismax	0.8086	0.8456	0.9491	0.7766	0.9128	0.8689	0.9669	0.8357
	modismean	0.8351	0.8334	0.9498	0.8157	0.9265	0.9004	0.9779	0.8681
	modismin	0.8086	0.8456	0.9491	0.7766	0.9128	0.8689	0.9669	0.8357
	POC	<b>0.9369</b>	<b>0.8621</b>	<b>0.9662</b>	<b>0.9555</b>	<b>0.9878</b>	<b>0.9727</b>	<b>0.9931</b>	<b>0.978</b>
	vgpmean	0.8439	0.809	0.9544	0.8389	0.9449	0.8847	0.9706	0.8819
	aoux	0.8195	0.8954	<b>0.9126</b>	0.677	0.6107	0.7846	0.6575	0.6625
	disso2	<b>0.8913</b>	<b>0.939</b>	0.8654	<b>0.8969</b>	<b>0.9083</b>	<b>0.9375</b>	<b>0.9671</b>	<b>0.9477</b>
	poxs	0.7796	0.8992	0.894	0.6299	0.5998	0.7486	0.4196	0.7295
	dic_stein	0.8889	0.9214	0.9345	0.7986	0.8179	0.7632	0.9426	0.6993

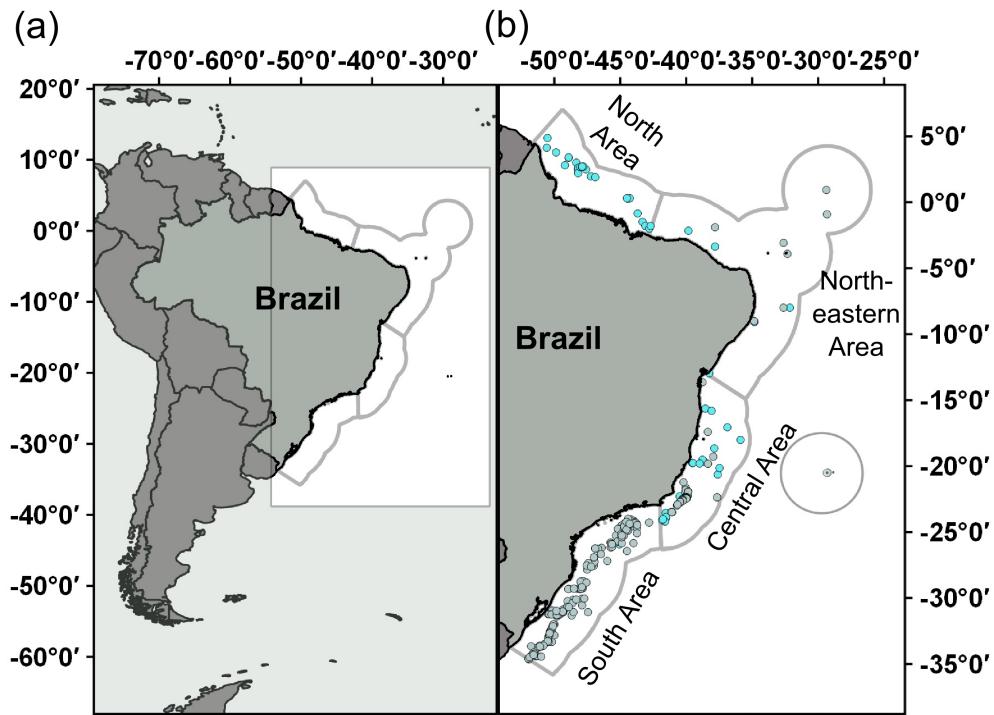
	nit	0.8281	0.8829	0.8761	0.7474	0.5964	0.8172	0.6385	0.6625
CHEM	phos	0.8442	0.9249	0.8669	0.8148	0.6673	0.868	0.6667	0.7377
	sal	0.8962	0.9082	0.8425	0.6082	0.784	0.8779	0.5401	<b>0.9445</b>
	sil	<b>0.9145</b>	<b>0.9273</b>	<b>0.9422</b>	<b>0.8868</b>	<b>0.9312</b>	<b>0.9158</b>	<b>0.9782</b>	0.8753
TEMP	temp	<b>0.9618</b>	<b>0.9309</b>	<b>0.9678</b>	<b>0.953</b>	<b>0.9855</b>	<b>0.9825</b>	<b>0.9951</b>	<b>0.9776</b>

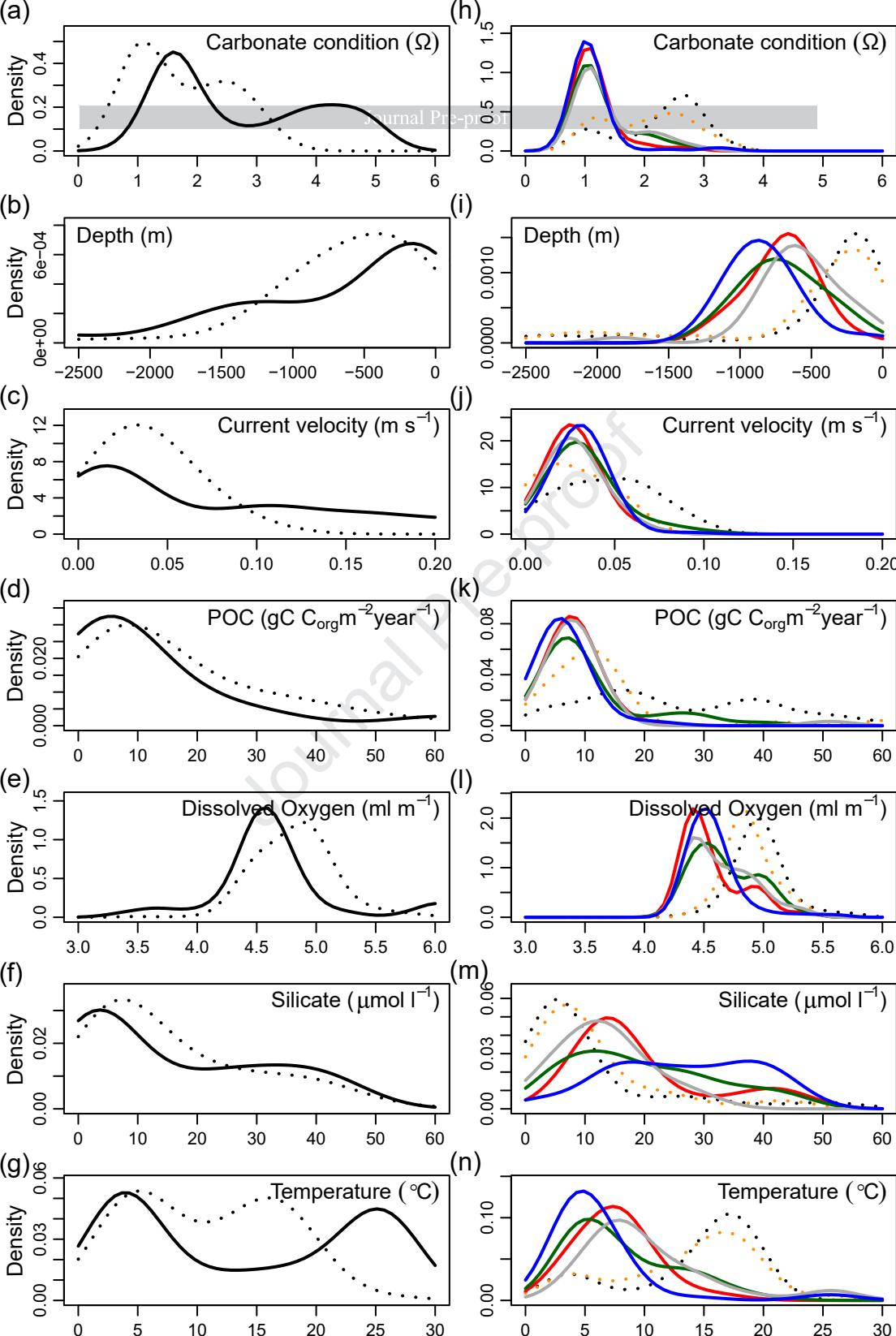
**Table 4.** Test AUC values for Scleractinia, Octocorallia and six different scleractinian species models, based in a single variable model. Values corresponding to the three most significant variables for each taxon are in bold. Variable name abbreviations are presented in Table 2.

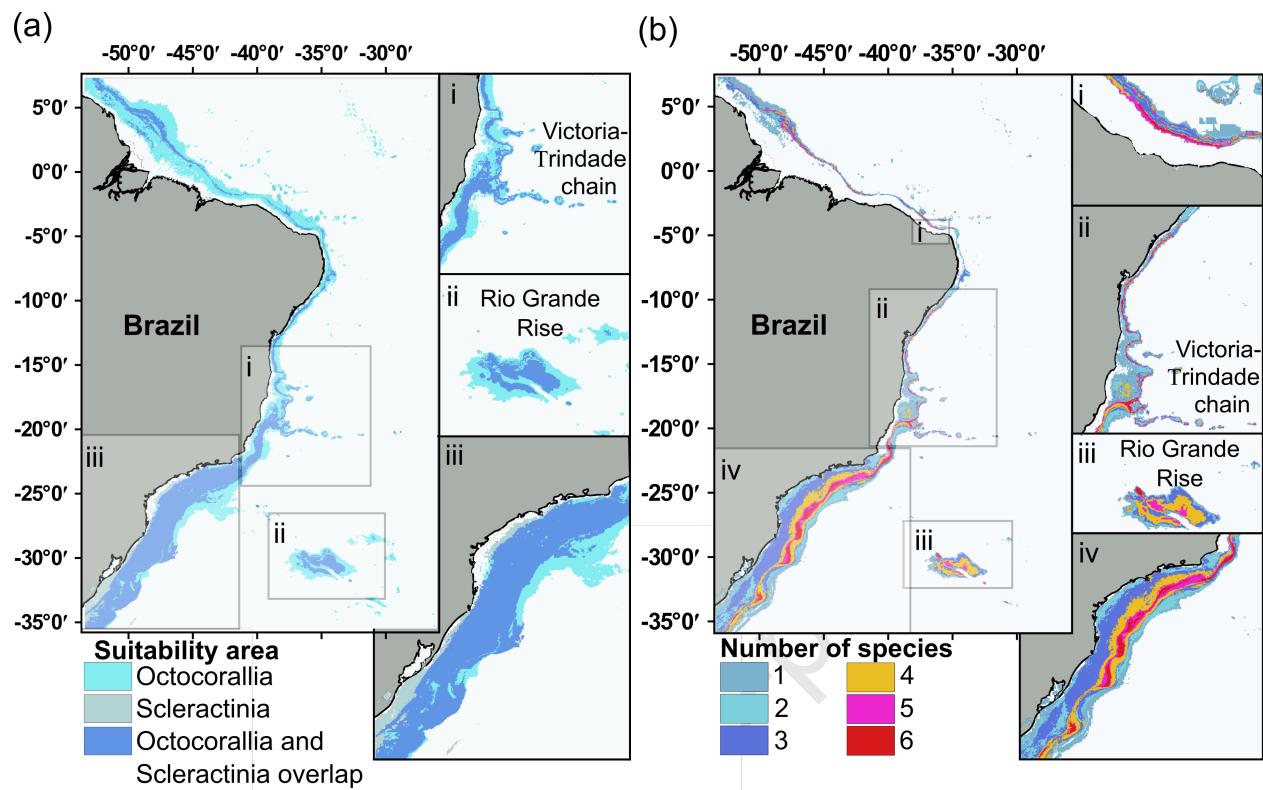
	<i>Scleractinia</i>	<i>Octocorallia</i>	<i>C. debilis</i>	<i>L. pertusa</i>	<i>M. oculata</i>	<i>S. variabilis</i>	<i>E. rostrata</i>	<i>Deltocyathus</i> spp.
AUC								
calc-orr		<b>0.9403</b>						
arag-orr	<b>0.9457</b>		<b>0.9694</b>	<b>0.9565</b>	<b>0.9543</b>	0.9671	<b>0.9403</b>	<b>0.9683</b>
srtm30	<b>0.9518</b>	<b>0.9492</b>	<b>0.9784</b>	<b>0.9882</b>	<b>0.9812</b>	<b>0.9877</b>	<b>0.9493</b>	<b>0.9595</b>
regfl	0.8812	0.8234	0.9223	0.8743	0.916	0.8874	0.8234	0.6203
POC	0.9214	0.8326	0.9685	0.9335	0.8644	<b>0.9748</b>	0.8326	0.9434
diso2	0.8941	0.9206		0.934	0.8869	0.9431	0.9206	0.8913
aouxu			0.8877					
sil	0.8864	0.8639	0.9358	0.9088	0.9527		0.8639	0.9484
sal						<b>0.9905</b>		
temp	<b>0.9424</b>	<b>0.9281</b>	<b>0.9698</b>	<b>0.98</b>	<b>0.9761</b>	0.969	<b>0.9281</b>	<b>0.9635</b>

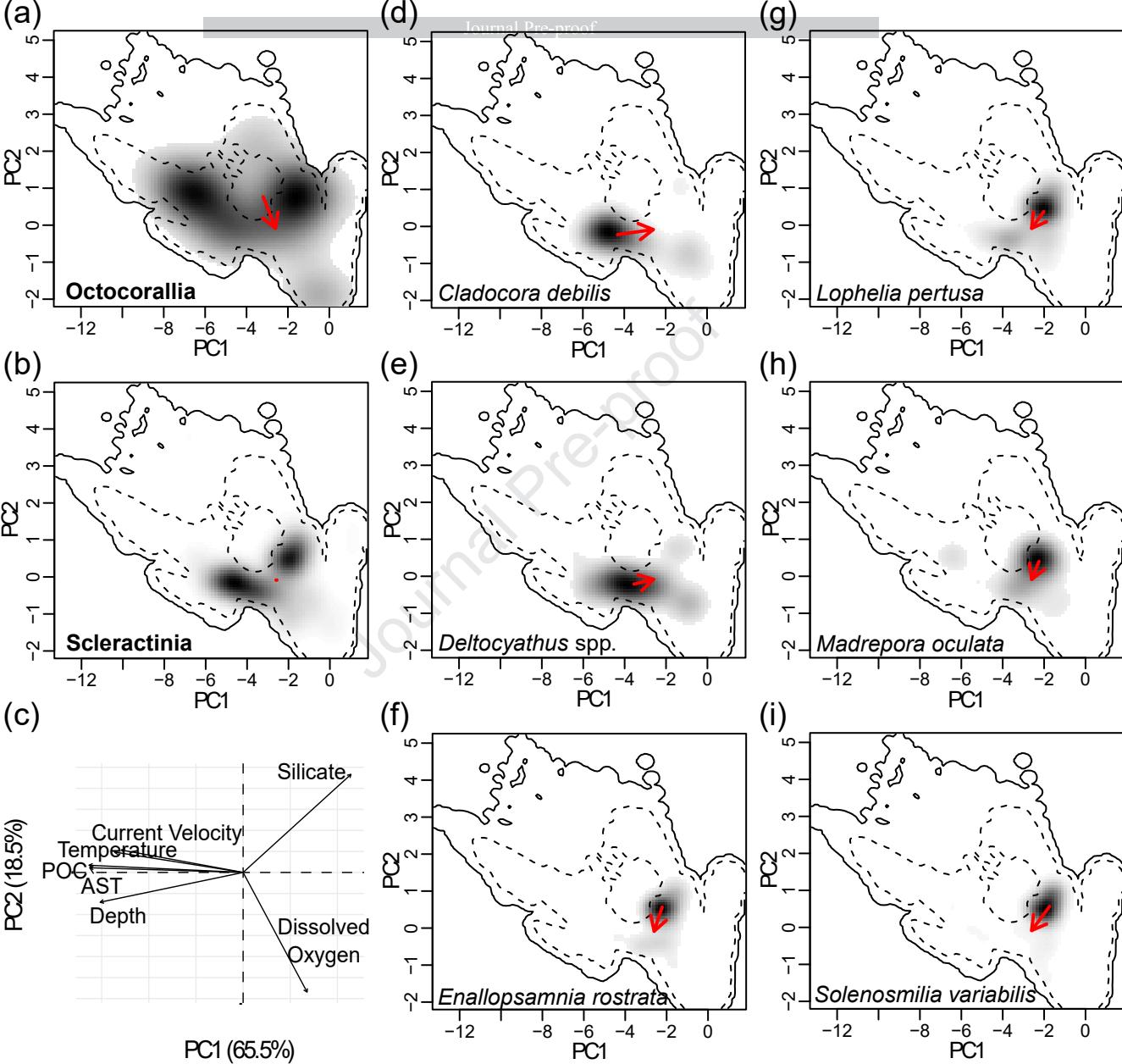
**Table 5.** Niche comparison for cold water corals in the Brazilian continental margin. Niche overlap values Schoener's  $D$  (Schoener, 1970; Broennimann et al., 2012) and the significance of similarity and equivalence tests are giving for each pair-wise comparison (ns: not significant). The higher overlap value is presented in bold and the lowest in italics.

Taxon	<b>Niche Overlap (D)</b>	<b>Niche similarity</b>		<b>Niche equivalence</b>
		<i>a</i>	<i>b</i>	
<i>C. debilis</i>	<i>Deltocyathus</i> spp.	<b>0.89</b>	Similar	Different
	<i>E. rostrata</i>	0.01	ns	Different
	<i>L. pertusa</i>	0.72	Similar	Different
	<i>M. oculata</i>	0.32	Similar	Different
	<i>S. variabilis</i>	<i>0.008</i>	Similar	Different
<i>Deltocyathus</i> spp.	<i>E. rostrata</i>	0.04	ns	Different
	<i>L. pertusa</i>	0.80	Similar	Different
	<i>M. oculata</i>	0.40	Similar	Different
	<i>S. variabilis</i>	0.035	Similar	Different
<i>E. rostrata</i>	<i>L. pertusa</i>	0.21	ns	Different
	<i>M. oculata</i>	0.48	Similar	Different
	<i>S. variabilis</i>	0.77	Similar	Different
<i>L. pertusa</i>	<i>M. oculata</i>	0.57	Similar	Different
	<i>S. variabilis</i>	0.20	Similar	Different
<i>M. oculata</i>	<i>S. variabilis</i>	0.41	ns	Different
<b>Octocorallia</b>	Scleractinia	0.28	ns	Different









## HIGHLIGHTS

- Octocorallia demonstrated potentially suitable habitat that encompassed nearly the entire Brazilian continental margin, covering a wider range than Scleractinia, which covered principally the Central and Southern areas.
- The Central and Southern parts of the Brazilian continental margin should be considered as areas of potentially high cold-water corals diversity.
- Reef-forming cold-water coral species had similar but not equivalent ecological niches.
- The mapping efforts and management planning should consider cold-water coral at the species level.

The authors declare that there is no conflict of interest.