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

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KEYWORDS

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

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ABSTRACT

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

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INTRODUCTION

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

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

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

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

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 Brazilian continental slope (Castro et al., 2006; Kitahara, 2007; Pires et al., 2007; Cavalcanti et al., 2017). With a coastline of 7,491 km, Brazil accounts for a large

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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.

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METHODS

Study area

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

Species data

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

Environmental data

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

Maxent model predictions

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

Species niche comparisons

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

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

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

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

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

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RESULTS

Occupied environmental conditions

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

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

Variable selection and contribution

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

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

Model performance and habitat suitable area

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

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

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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.

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DISCUSSION

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

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

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

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

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

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411 to anchor in sediment substrates (Bayer, 1961), may allow then 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

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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^{-1}), 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 Grahan, 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

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

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

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

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

Approach limitations

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

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 in the models. There will be other variables or factors that were not included in the analysis which could influence these predictions, such as substrate availability and type. Hard substrate presence is highly variable over small spatial scales and is a strong

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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 were 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 conservations 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 then to potentially inhabit a broader area of the Brazilian

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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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FIGURES AND TABLES

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

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

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

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

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

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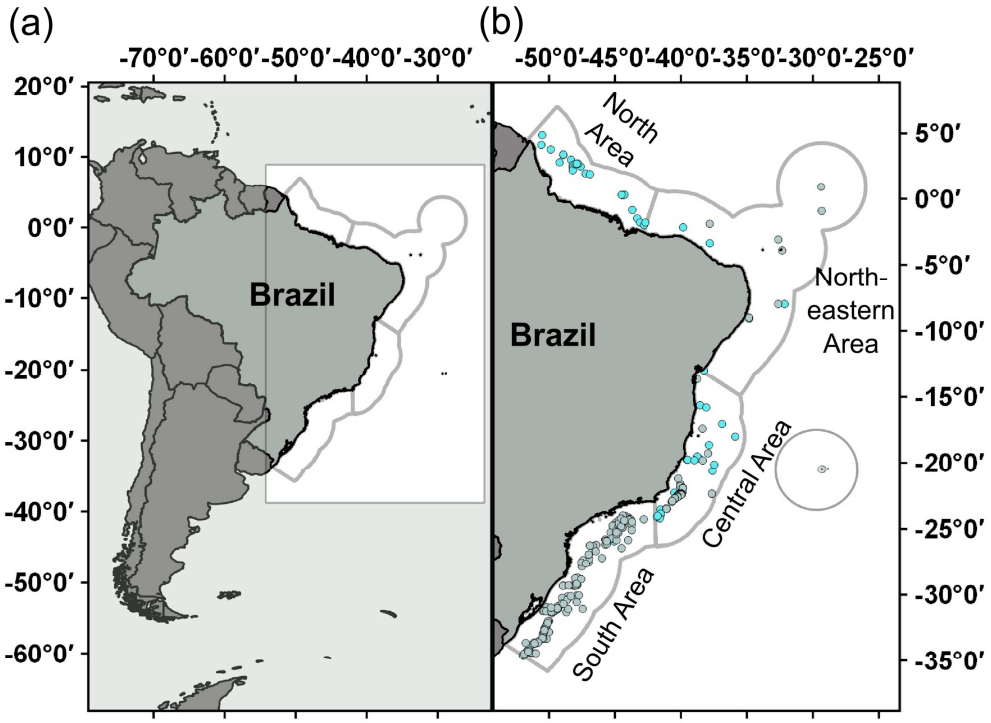
949 Figure 1



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951 Figure 2

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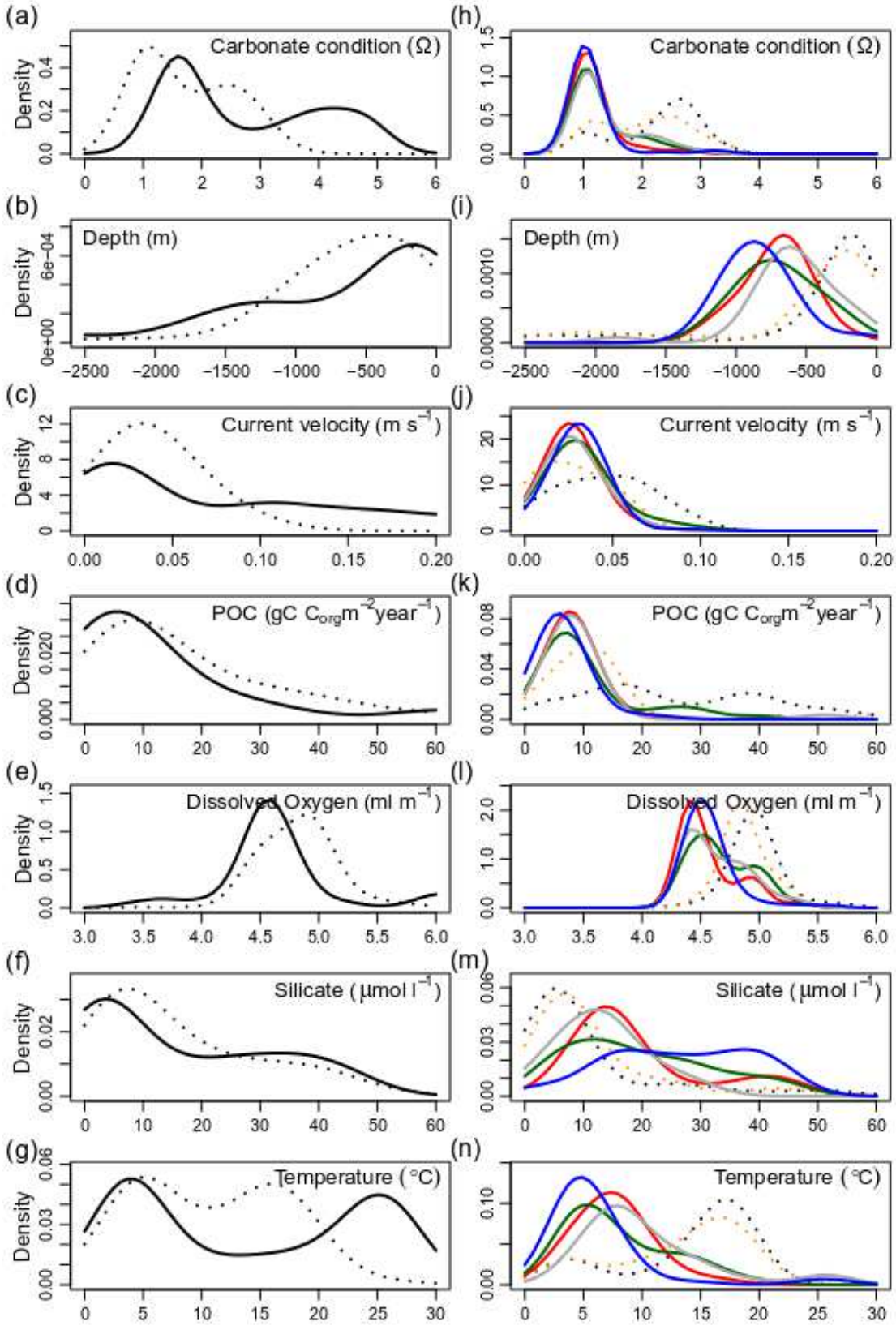

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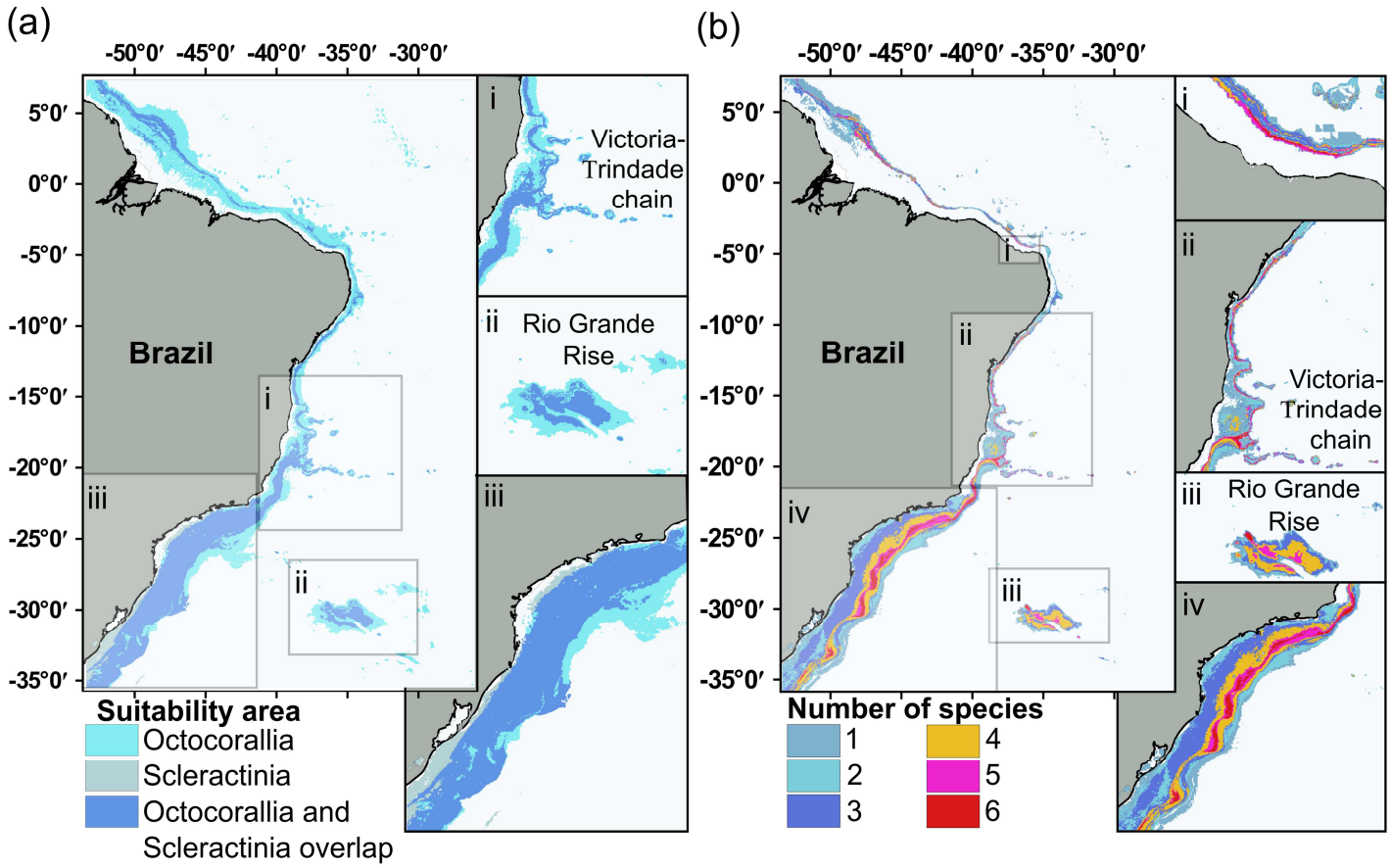
Figure 3


(a)
(b)
-50°0′ -45°0′ -40°0′ -35°0′ -30°0′
5°0′
0°0′
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-10°0′
-15°0′
-20°0′
-25°0′
-30°0′
-35°0′
Brazil
i
ii
iii
iv
Victoria-Trindade chain
Rio Grande Rise
Suitability area
Octocorallia
Scleractinia
Octocorallia and Scleractinia overlap
Number of species
1
2
3
4
5
6

Figure 4

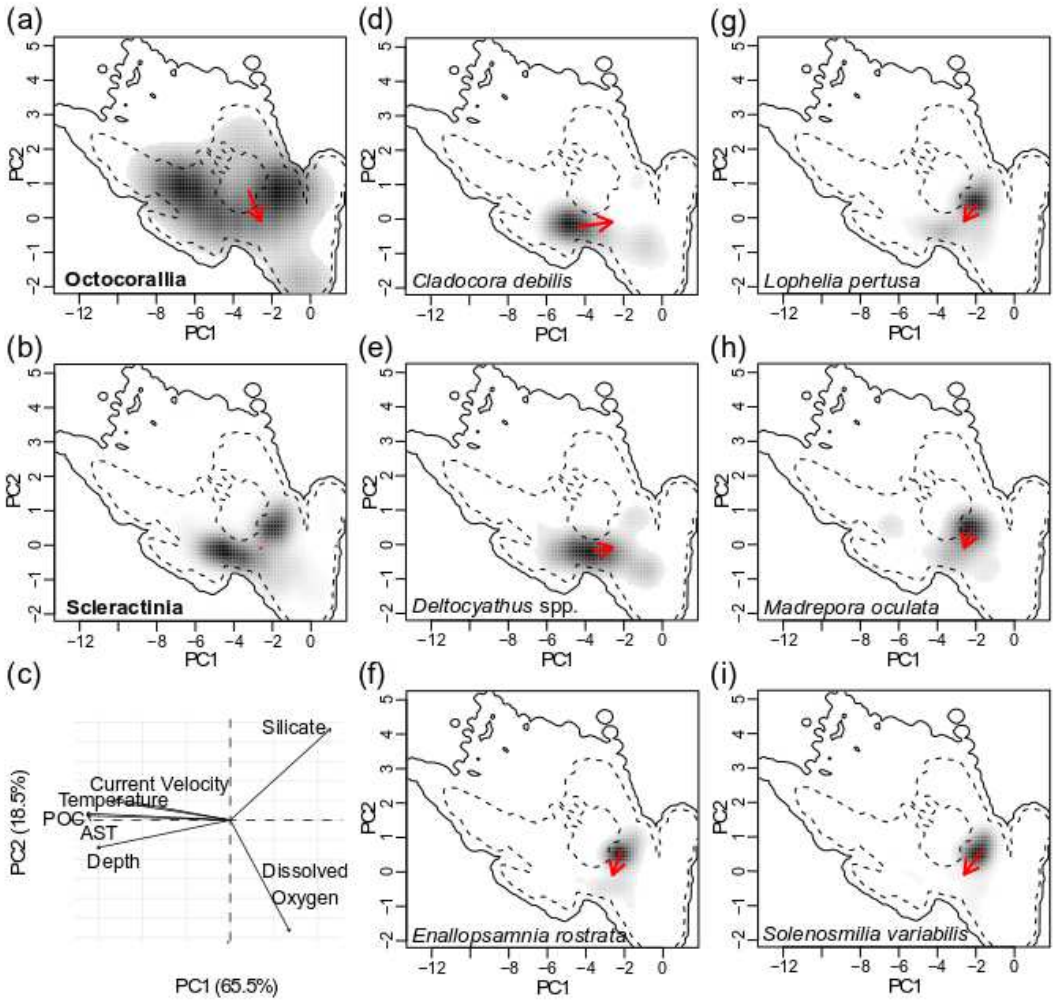
(a)
Octocorallia
(b)
Scleractinia
(c)
Silicate
Current Velocity
Temperature
POC
AST
Depth
Dissolved Oxygen
PC2 (18.5%)
PC1 (65.5%)
(d)
Cladocora debilis
(e)
Deltocyathus spp.
(f)
Enallopsamnia rostrata
(g)
Lophelia pertusa
(h)
Madrepora oculata
(i)
Solenosmilia variabilis
PC1
PC2

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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
Order Scleractinia	396	1147	259
Subclass Octocorallia	151		60
Species			
Cladocora debilis	57		54
***Deltocyathus* spp.**	36		33
Enallopsammia rostrata	8	222	33
Lophelia pertusa	77	342	75
Madrepora oculata	21	97	29
Solenosmilia variabilis	26	486	72

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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
CARB	Aragonite saturation state	arag_orr	Orr et al. (2005)	Ω_{ARAG}
	Aragonite saturation state	arag_stein	Steinacher et al. (2009)	Ω_{ARAG}
	Calcite saturation state	cal_orr	Orr et al. (2005)	Ω_{CALC}
	Calcite saturation state	cal_stein	Steinacher et al.(2009)	Ω_{CALC}
BATH	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)	-
HYDRO	Current velocity	regfl	Carton et al. (2005)	$m\ s^{-1}$
	Vertical current velocity	verfl	Carton et al. (2005)	$m\ s^{-1}$
PROD	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)	$g\ C\ m^{-2}\ y^{-1}$
OXY	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)	$ml\ l^{-1}$
CHEM	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)	$\mu mol\ l^{-1}$
TEMP	Temperature	temp	Boyer et al. (2005)	ºC

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*
CARB	arag_orr	**0.9525**	0.9248	**0.9671**	**0.953**	**0.9612**	**0.9624**	**0.9586**	**0.9604**
	arag_stein	0.9562	0.9233	0.9691	0.9234	0.9588	0.9427	0.9757	0.9135
	cal_orr	0.9579	**0.9269**	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	**0.9664**	**0.9311**	**0.9737**	**0.9659**	**0.9913**	**0.9877**	**0.9951**	**0.9885**
	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
	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
HY	regfl	**0.8705**	**0.9231**	**0.9187**	**0.7648**	**0.9422**	**0.8762**	**0.9566**	**0.8705**
	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	**0.9369**	**0.8621**	**0.9662**	**0.9555**	**0.9878**	**0.9727**	**0.9931**	**0.978**
	vgpmean	0.8439	0.809	0.9544	0.8389	0.9449	0.8847	0.9706	0.8819
OXY	aoxu	0.8195	0.8954	**0.9126**	0.677	0.6107	0.7846	0.6575	0.6625
	disso2	**0.8913**	**0.939**	0.8654	**0.8969**	**0.9083**	**0.9375**	**0.9671**	**0.9477**
	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

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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	**0.9445**
	sil	**0.9145**	**0.9273**	**0.9422**	**0.8868**	**0.9312**	**0.9158**	**0.9782**	0.8753
TEMP	temp	**0.9618**	**0.9309**	**0.9678**	**0.953**	**0.9855**	**0.9825**	**0.9951**	**0.9776**

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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.

	Scleractinia	*Octocorallia*	*C. debilis*	*L. pertusa*	*M. oculata*	*S. variabilis*	*E. rostrata*	*Deltocyathus* spp.
AUC								
calc-orr		**0.9403**						
arag-orr	**0.9457**		**0.9694**	**0.9565**	**0.9543**	0.9671	**0.9403**	**0.9683**
srtm30	**0.9518**	**0.9492**	**0.9784**	**0.9882**	**0.9812**	**0.9877**	**0.9493**	**0.9595**
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	**0.9748**	0.8326	0.9434
diso2	0.8941	0.9206		0.934	0.8869	0.9431	0.9206	0.8913
aoxu			0.8877					
sil	0.8864	0.8639	0.9358	0.9088	0.9527		0.8639	0.9484
sal						**0.9905**		
temp	**0.9424**	**0.9281**	**0.9698**	**0.98**	**0.9761**	0.969	**0.9281**	**0.9635**

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

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Electronic supplementary materials

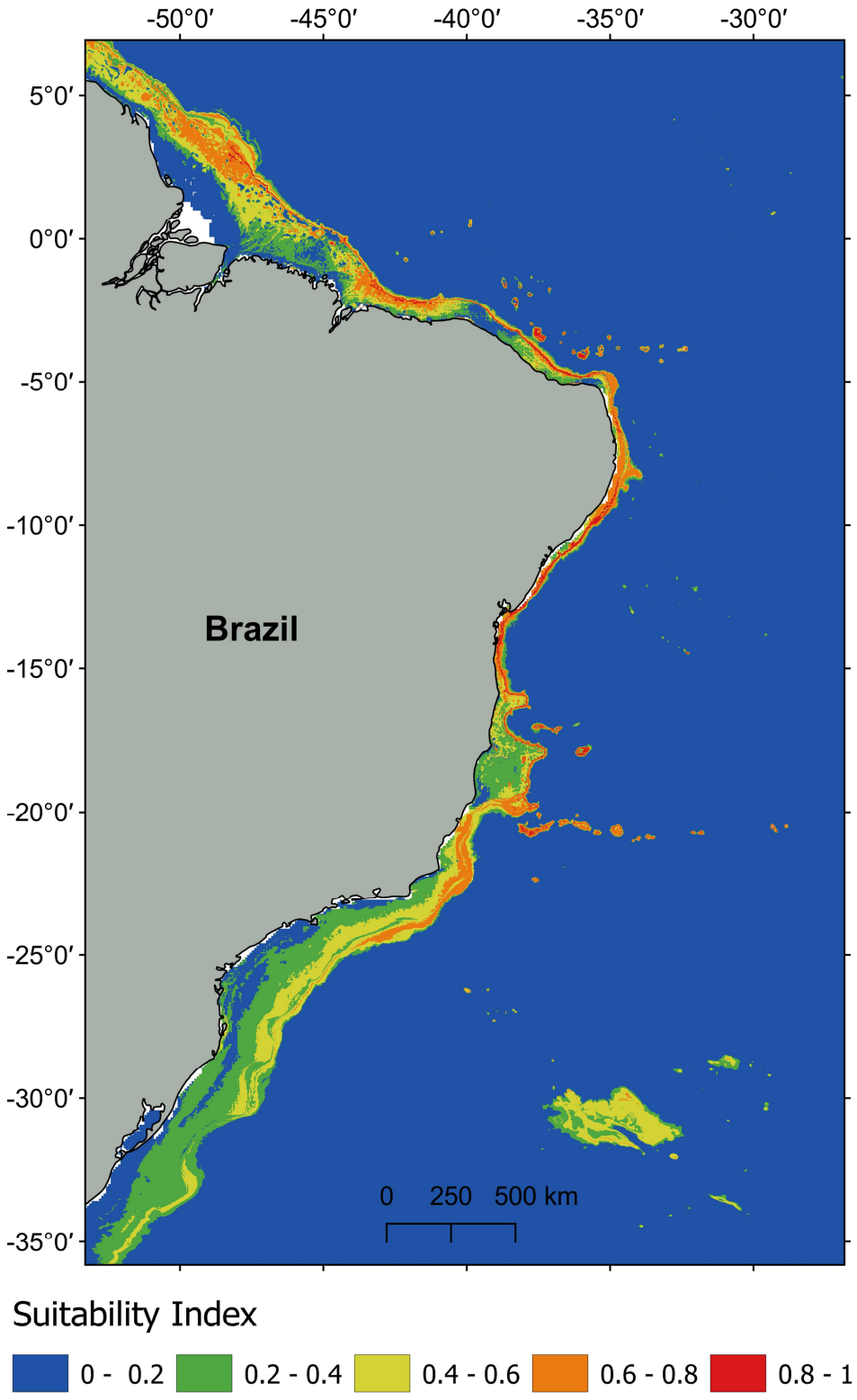

Figure 1. Habitat suitability prediction for Octocorallia in the southwest Atlantic Ocean. The legend indicates the habitat suitability index from 0 to 1 as the maximum suitable pixels.

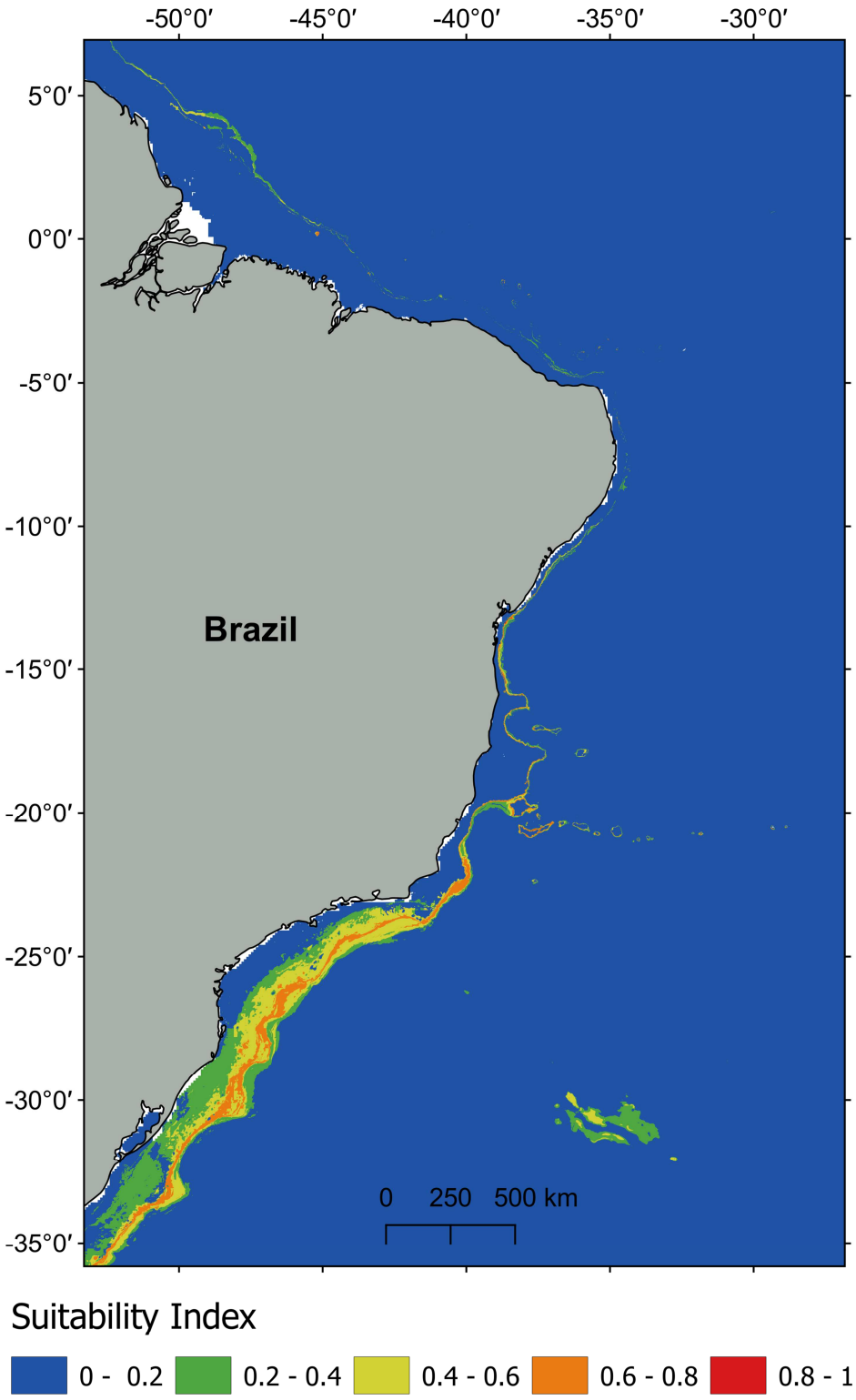

Figure 2. Habitat suitability prediction for Scleractinia in the Brazilian continental margin. The legend indicates the habitat suitability index from 0 to 1 as the maximum suitable pixels.

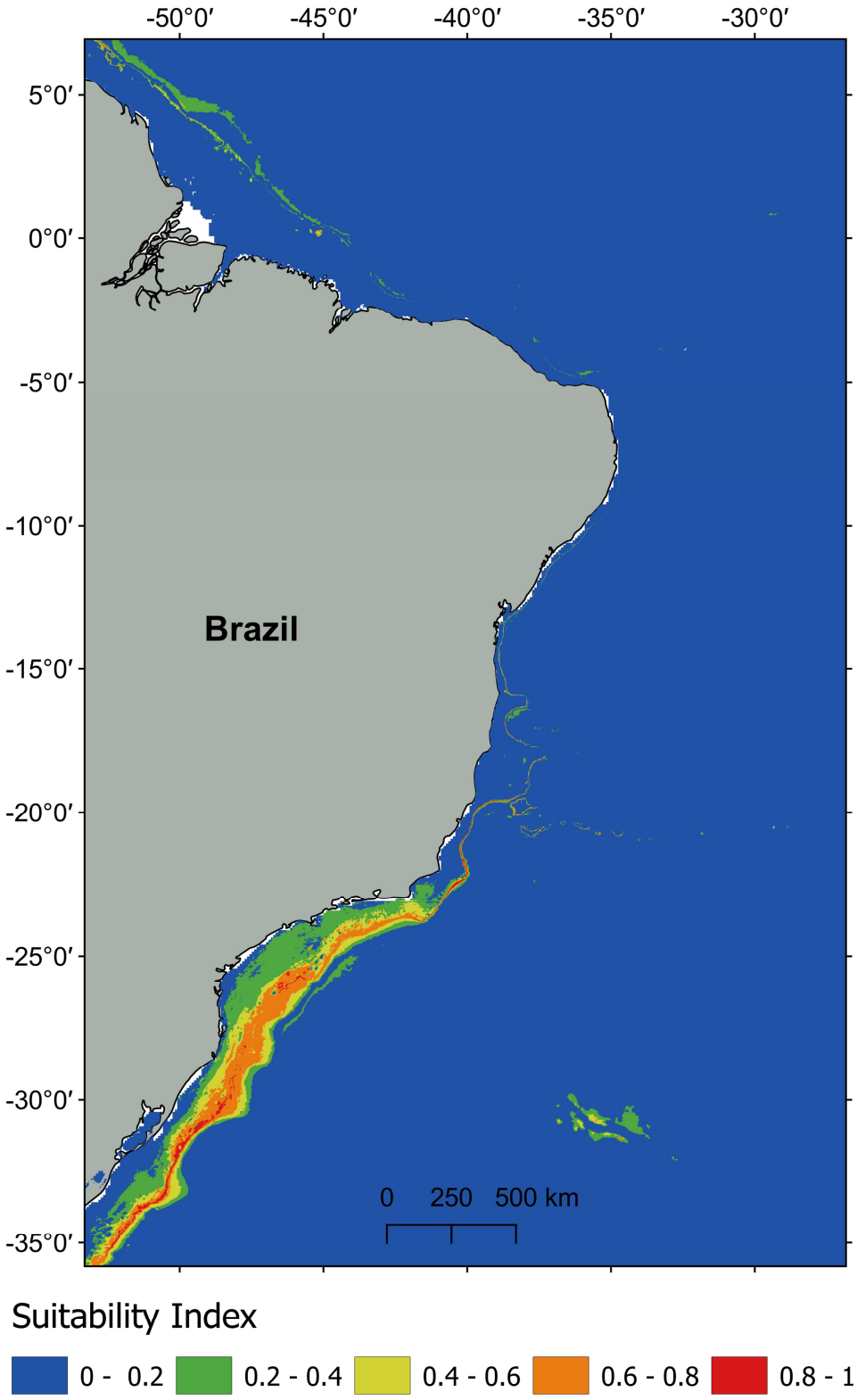

Figure 3. Habitat suitability prediction for *Cladocora debilis* in the Brazilian continental margin. The legend indicates the habitat suitability index from 0 to 1 as the maximum suitable pixels.

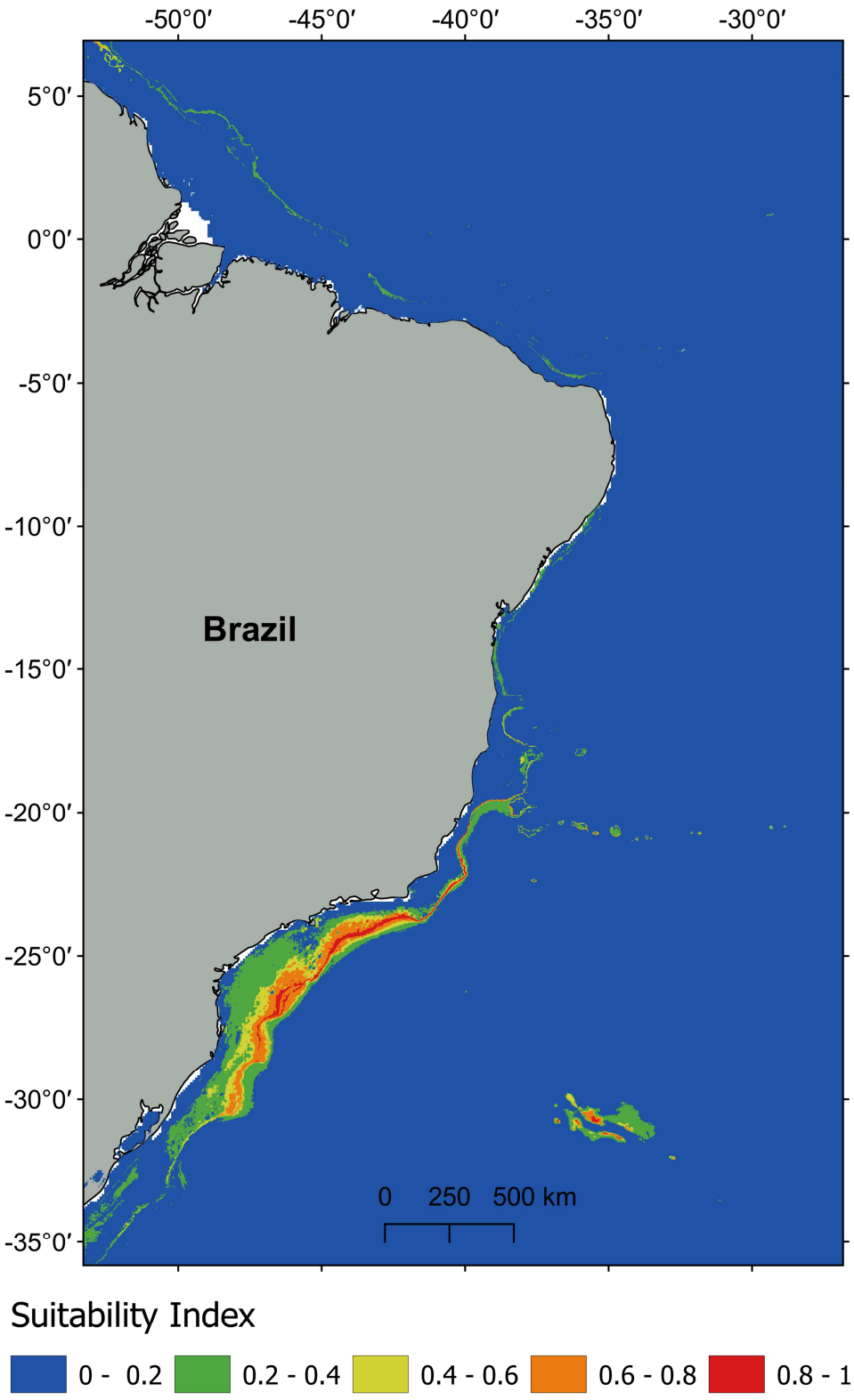

Figure 4. Habitat suitability prediction for *Deltocyathus* spp. in the Brazilian continental margin. The legend indicates the habitat suitability index from 0 to 1 as the maximum suitable pixels.

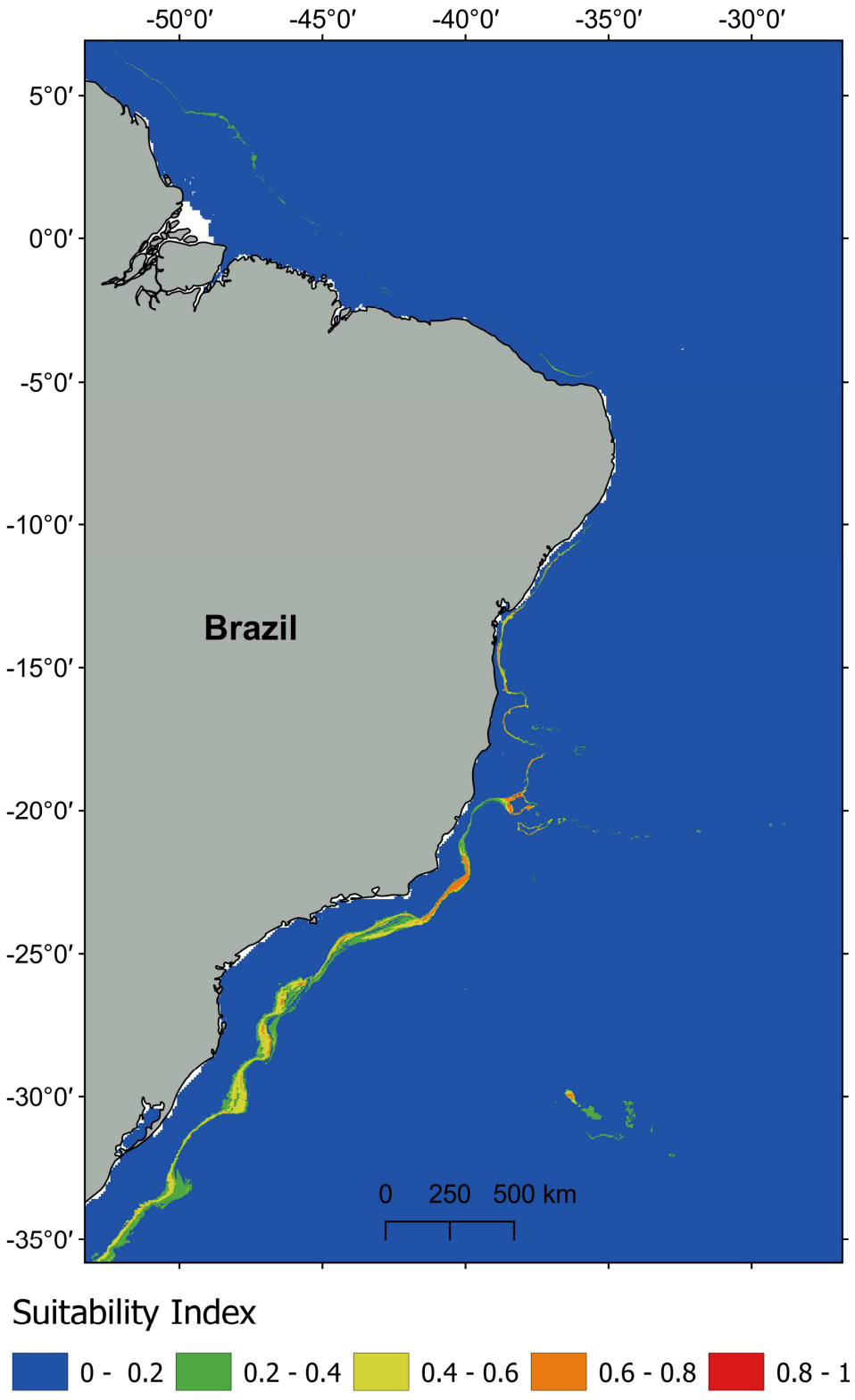

Figure 5. Habitat suitability prediction for *Lophelia pertusa* in the Brazilian continental margin. The legend indicates the habitat suitability index from 0 to 1 as the maximum suitable pixels.

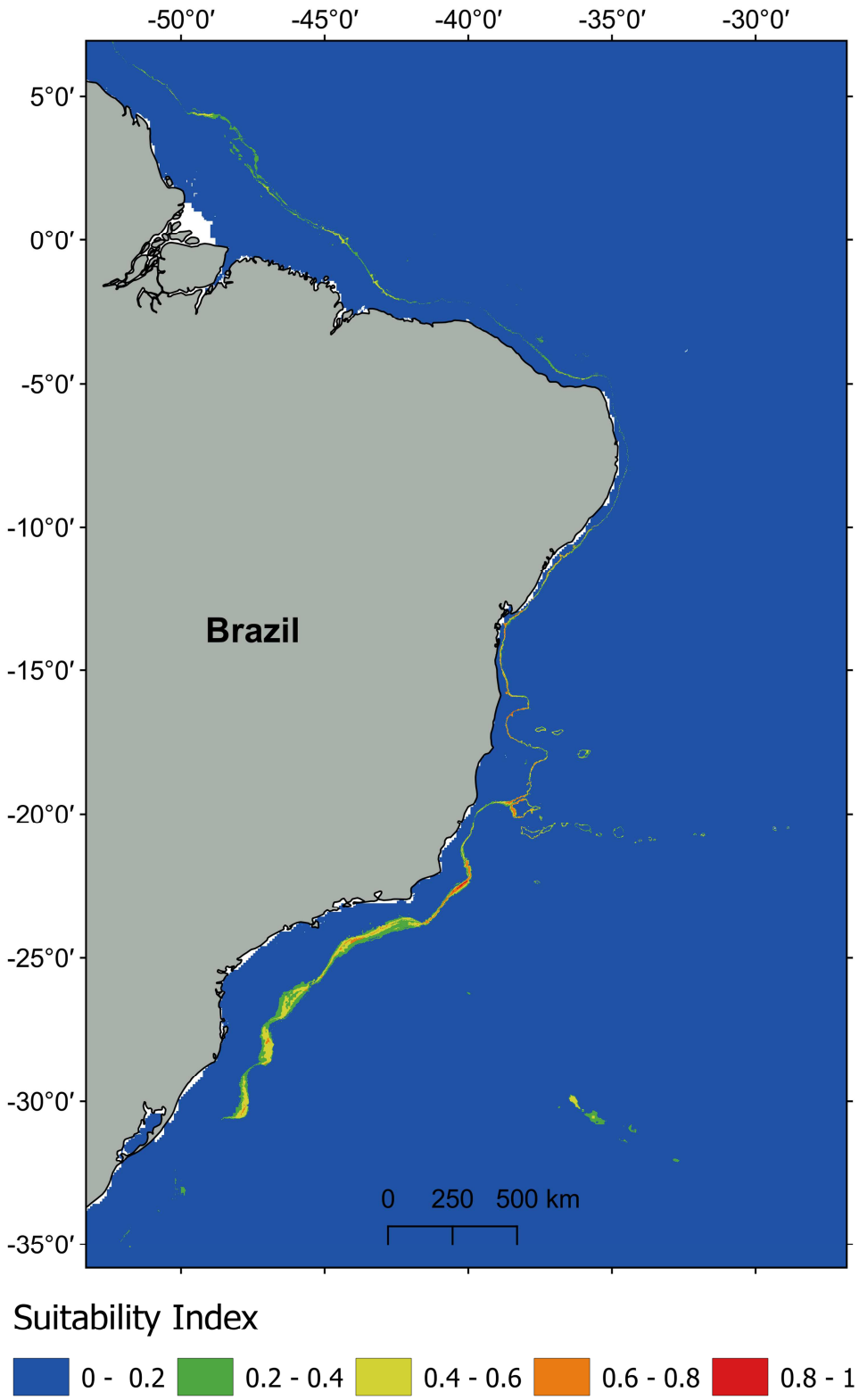

Figure 6. Habitat suitability prediction for *Madrepora oculata* in the Brazilian continental margin. The legend indicates the habitat suitability index from 0 to 1 as the maximum suitable pixels.

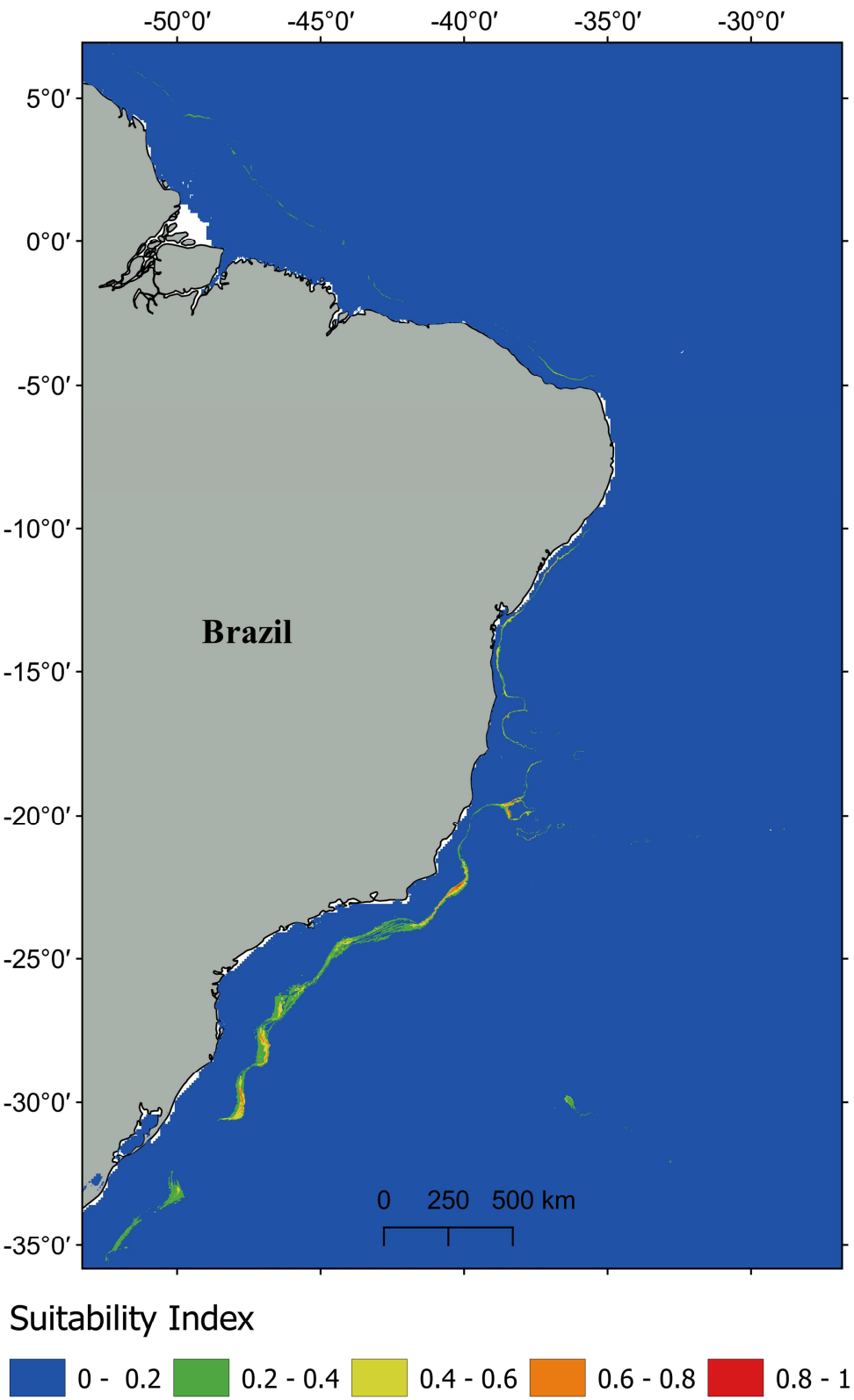

Figure 7. Habitat suitability prediction for *Enallopsammia rostrata* in the Brazilian continental margin. The legend indicates the habitat suitability index from 0 to 1 as the maximum suitable pixels.

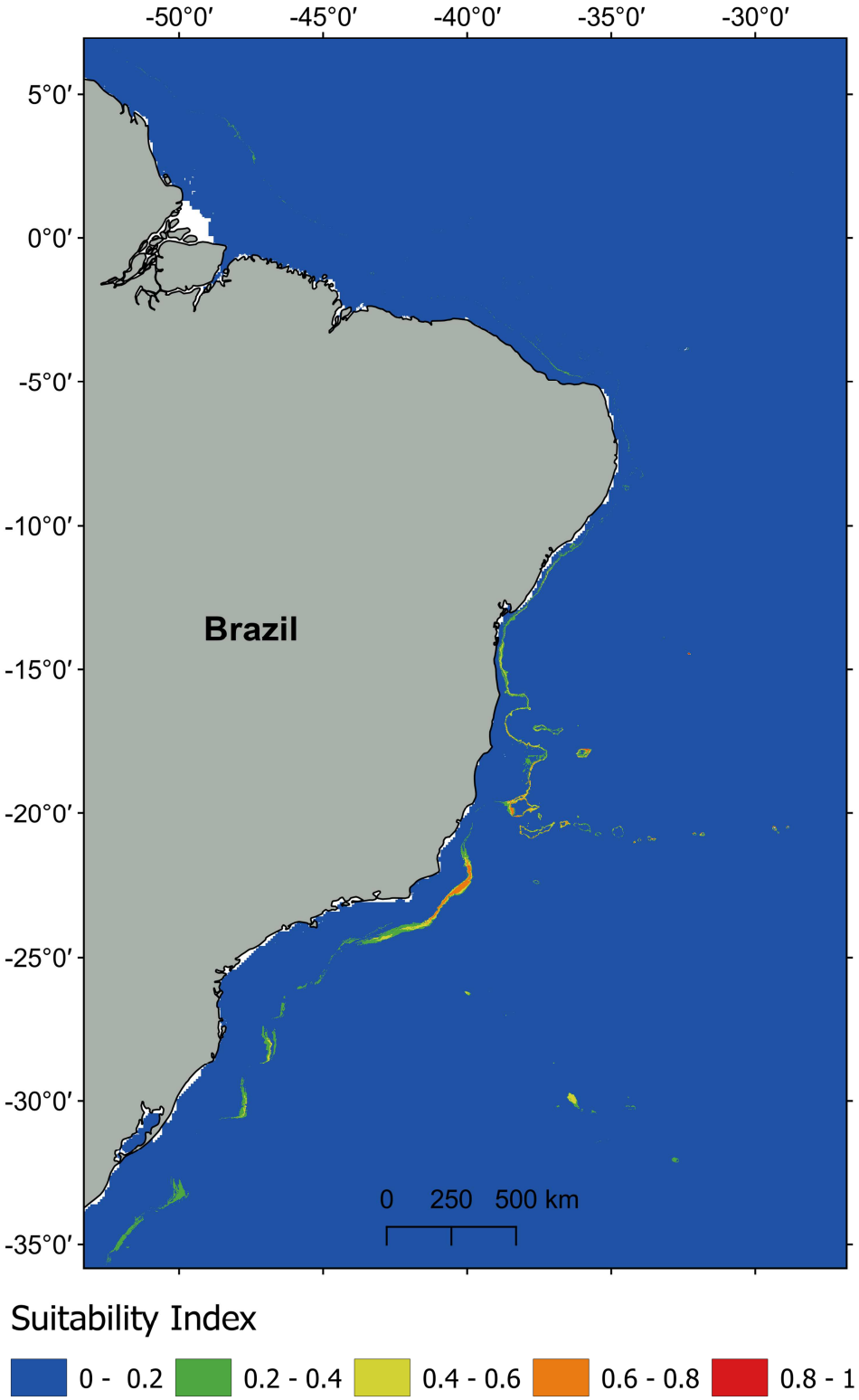

Figure 8. Habitat suitability prediction for *Solenosmilia variabilis* in the Brazilian continental margin. The legend indicates the habitat suitability index from 0 to 1 as the maximum suitable pixels.

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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
Order Scleractinia	396	1147	259
Subclass Octocorallia	151		60
Species			
Cladocora debilis	57		54
***Deltocyathus* spp.**	36		33
Enallopsammia rostrata	8	222	33
Lophelia pertusa	77	342	75
Madrepora oculata	21	97	29
Solenosmilia variabilis	26	486	72

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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
CARB	Aragonite saturation state	arag_orr	Orr et al. (2005)	Ω_{ARAG}
	Aragonite saturation state	arag_stein	Steinacher et al. (2009)	Ω_{ARAG}
	Calcite saturation state	cal_orr	Orr et al. (2005)	Ω_{CALC}
	Calcite saturation state	cal_stein	Steinacher et al.(2009)	Ω_{CALC}
BATH	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)	-
HYDRO	Current velocity	regfl	Carton et al. (2005)	$m\ s^{-1}$
	Vertical current velocity	verfl	Carton et al. (2005)	$m\ s^{-1}$
PROD	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)	$g\ C\ m^{-2}\ y^{-1}$
OXY	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)	$ml\ l^{-1}$
CHEM	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

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	Silicate	sil	Garcia et al. (2006)	µmol l^{-1}
TEMP	Temperature	temp	Boyer et al. (2005)	ºC

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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*
CARB	arag_orr	**0.9525**	0.9248	**0.9671**	**0.953**	**0.9612**	**0.9624**	**0.9586**	**0.9604**
	arag_stein	0.9562	0.9233	0.9691	0.9234	0.9588	0.9427	0.9757	0.9135
	cal_orr	0.9579	**0.9269**	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	**0.9664**	**0.9311**	**0.9737**	**0.9659**	**0.9913**	**0.9877**	**0.9951**	**0.9885**
	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
	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
HY	regfl	**0.8705**	**0.9231**	**0.9187**	**0.7648**	**0.9422**	**0.8762**	**0.9566**	**0.8705**
	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	**0.9369**	**0.8621**	**0.9662**	**0.9555**	**0.9878**	**0.9727**	**0.9931**	**0.978**
	vgpmean	0.8439	0.809	0.9544	0.8389	0.9449	0.8847	0.9706	0.8819
OXY	aoxu	0.8195	0.8954	**0.9126**	0.677	0.6107	0.7846	0.6575	0.6625
	disso2	**0.8913**	**0.939**	0.8654	**0.8969**	**0.9083**	**0.9375**	**0.9671**	**0.9477**
	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

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CHEM	nit	0.8281	0.8829	0.8761	0.7474	0.5964	0.8172	0.6385	0.6625
	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	**0.9445**
	sil	**0.9145**	**0.9273**	**0.9422**	**0.8868**	**0.9312**	**0.9158**	**0.9782**	0.8753
TEMP	temp	**0.9618**	**0.9309**	**0.9678**	**0.953**	**0.9855**	**0.9825**	**0.9951**	**0.9776**

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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.

	Scleractinia	*Octocorallia*	*C. debilis*	*L. pertusa*	*M. oculata*	*S. variabilis*	*E. rostrata*	*Deltocyathus* spp.
AUC								
calc-orr		**0.9403**						
arag-orr	**0.9457**		**0.9694**	**0.9565**	**0.9543**	0.9671	**0.9403**	**0.9683**
srtm30	**0.9518**	**0.9492**	**0.9784**	**0.9882**	**0.9812**	**0.9877**	**0.9493**	**0.9595**
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	**0.9748**	0.8326	0.9434
diso2	0.8941	0.9206		0.934	0.8869	0.9431	0.9206	0.8913
aoxu			0.8877					
sil	0.8864	0.8639	0.9358	0.9088	0.9527		0.8639	0.9484
sal						**0.9905**		
temp	**0.9424**	**0.9281**	**0.9698**	**0.98**	**0.9761**	0.969	**0.9281**	**0.9635**

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

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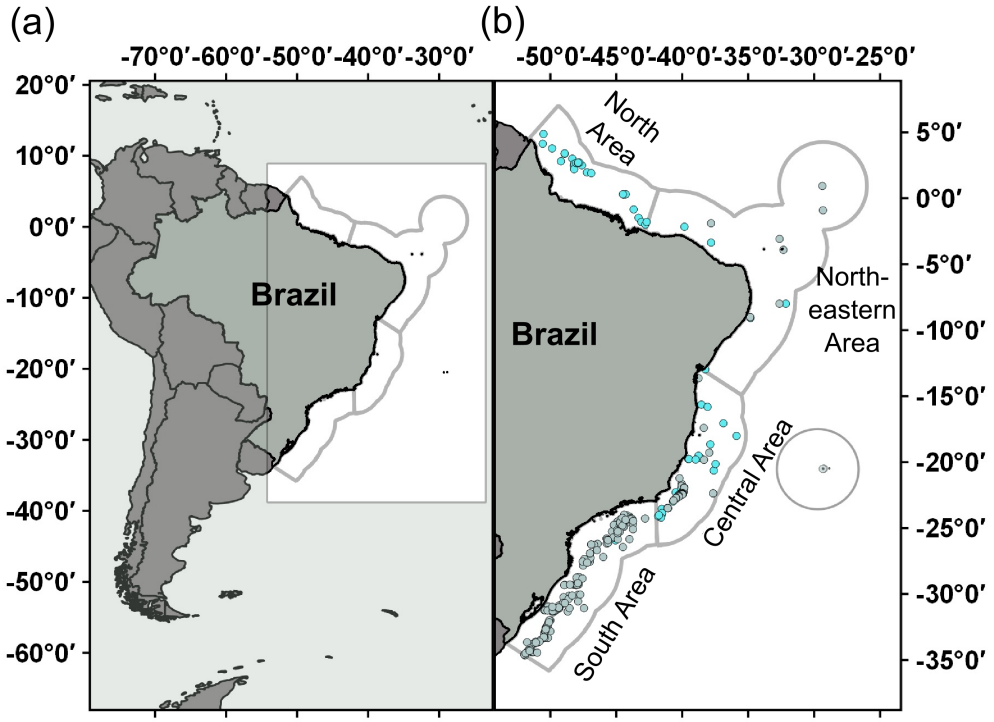

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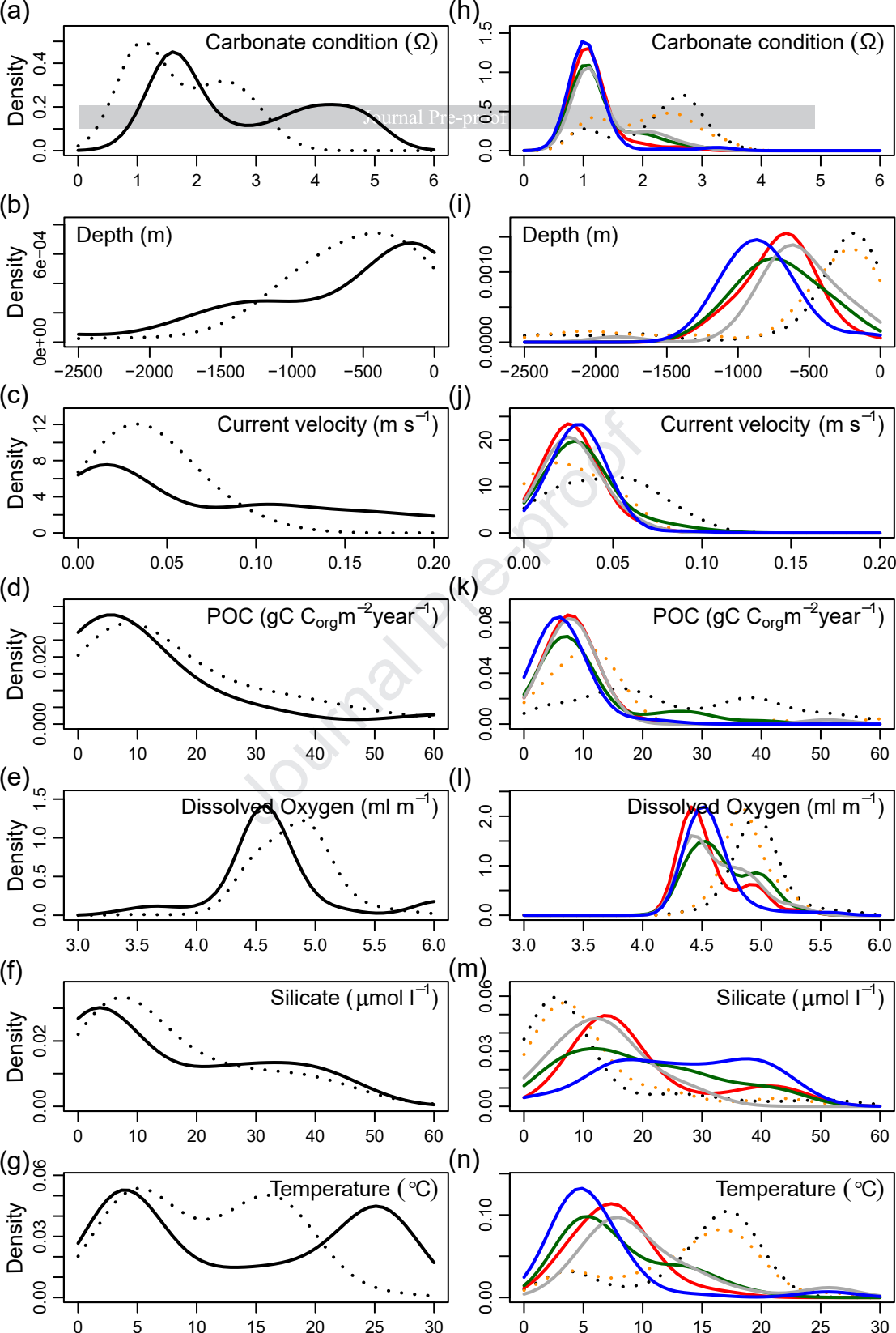

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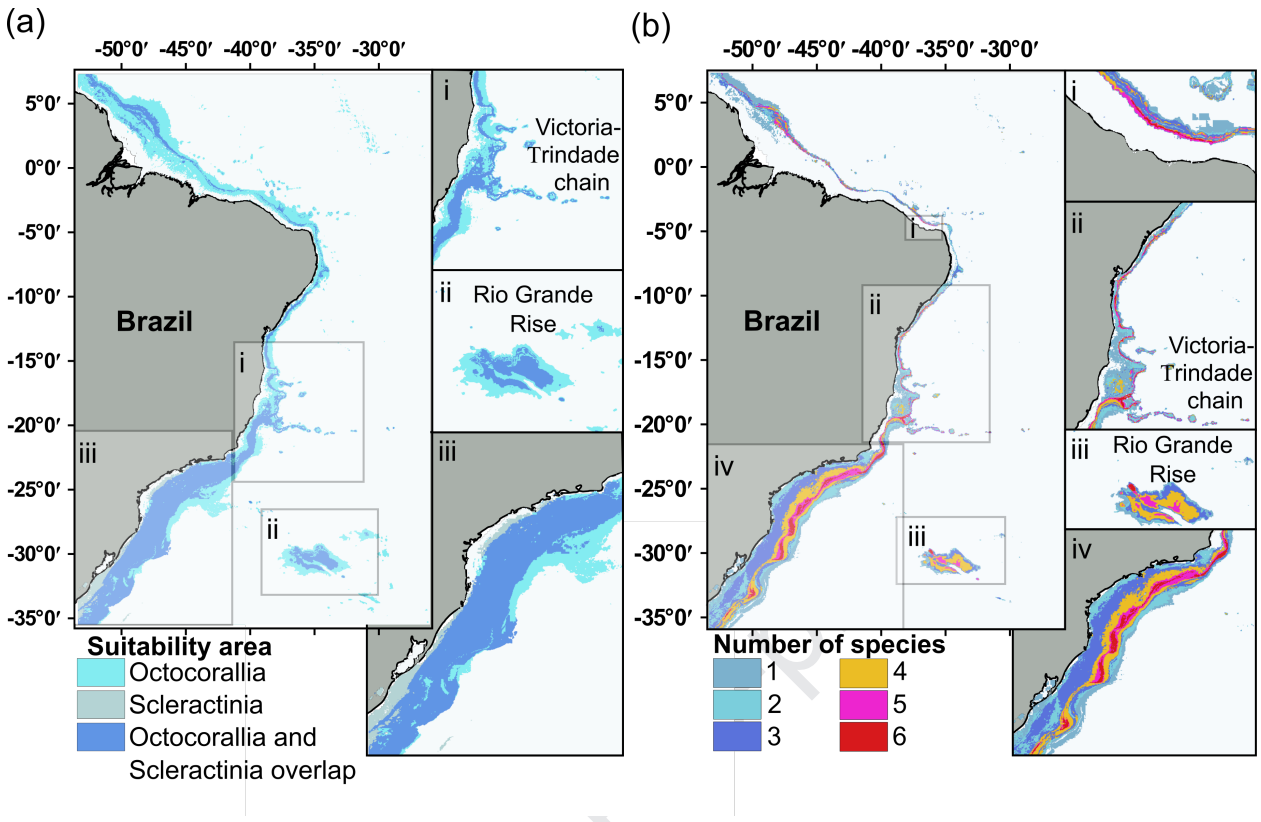
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Brazil
i
ii
iii
Victoria-Trindade chain
Rio Grande Rise
Suitability area
Octocorallia
Scleractinia
Octocorallia and Scleractinia overlap
(b)
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-30°0′
-35°0′
Brazil
i
ii
iii
iv
Victoria-Trindade chain
Rio Grande Rise
Number of species
1
2
3
4
5
6

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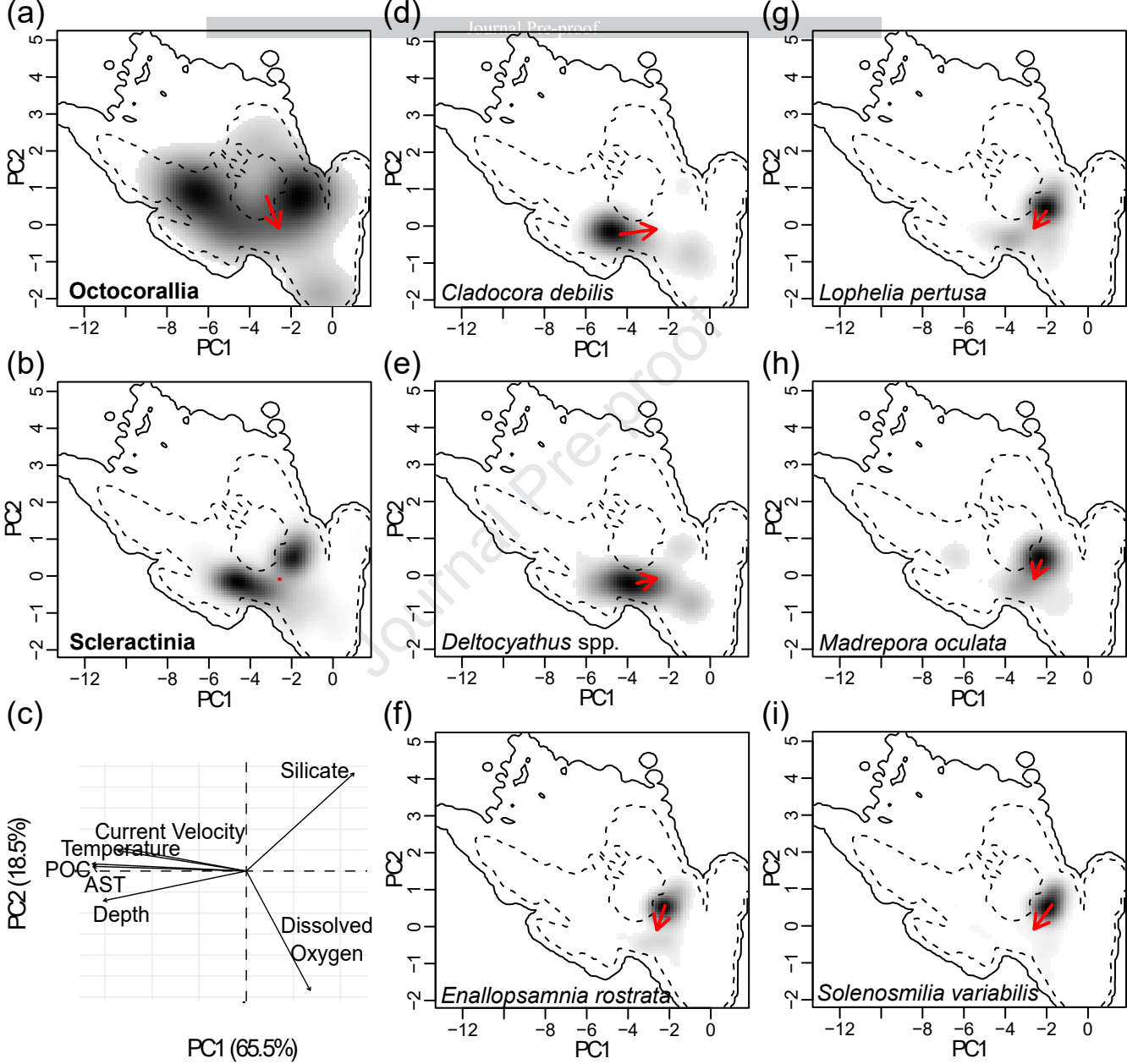

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HIGHLIGHTS

- 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.

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The authors declare that there is no conflict of interest.

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