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# The epitome of data paucity: Deep-sea habitats of the Southern Indian Ocean

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1 **The epitome of data paucity: deep-sea habitats of the Southern Indian Ocean**

2  
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29  
30 **Conflict of interest**

31 The authors declare no conflict of interest.

32  
33  
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44 **Abstract**

45

46 Vulnerable marine ecosystems (VMEs) are protected from bottom-fishing impacts in  
47 international waters by UN resolutions through Regional Fishery Management Organizations.  
48 VMEs include deep-sea benthic taxa whose life-history traits make them vulnerable to  
49 disturbance. Conservation measures for VMEs require regulatory frameworks informed by  
50 biodiversity maps. Here we evaluate biogeographic patterns of deep-sea benthic biodiversity  
51 of the Southern Indian Ocean to understand conservation avenues for the Southern Indian  
52 Ocean Fisheries Agreement (SIOFA) management organization. We synthesised knowledge  
53 on the distribution of benthic deep-sea taxa and explored the quality and quantity of available  
54 data. Next, we explored how taxa are structured into bioregions using biogeographical  
55 networks. We found astounding Wallacean and Linnaean shortfalls within SIOFA's  
56 management area, which is virtually devoid of distributional data. Across the entire area,  
57 results suggest that only 73% of the expected deep-sea taxa has been sampled, and most  
58 sampled cells appeared to be inadequately sampled. Yet, our bioregionalization analysis  
59 identified multiple bioregions, some only observed within SIOFA's area. The Wallacean and  
60 Linnean shortfalls are so important for VMEs that they severely impede to make adequate  
61 maps for conservation planning. Bioregionalization results suggest that SIOFA hosts a unique  
62 faunal composition that must be safeguarded. Predictive approaches to compensate for these  
63 shortfalls exist but will likely be insufficient and uncertain. Within SIOFA's area, there is no  
64 satisfying solution to cope with the data shortfalls. Yet, biodiversity maps are a global  
65 responsibility. This study makes a call to invest in biodiversity inventories in this world's  
66 region to promote informed policy-making decisions.

67

68 **Keywords**

69 Deep-sea habitats; Bioregionalization; Indian Ocean; Conservation; Fisheries; ABNJs

70

71

72 **Highlights**

- 73
- 74 • Bioregionalization of the Southern Indian Ocean using bipartite networks
  - 75 • Major Linnean and Wallacean shortfalls
  - 76 • Unknown extent of unique bioregions in offshore areas
  - 77 • Southern Indian Ocean systematically data-poor for benthic studies

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## 90 **Introduction**

91

92 The increasing appropriation of marine resources by human societies, termed “the blue  
93 acceleration”, is multiplying and intensifying pressures on the ocean (Jouffray et al., 2020).  
94 This holds especially true for the deep sea where cumulative impacts from fishing, potentially  
95 deep-sea mining, and climate change (Sweetman et al., 2017), will increase and new  
96 dynamics and threats will emerge (Halpern et al., 2019; O’Hara et al., 2021). In the deep sea,  
97 we find species such as cold-water corals and sponges with life-history traits (slow-growth,  
98 late-maturing and long-lived) that make them highly vulnerable against disturbance. These  
99 species, collectively known as indicator taxa of Vulnerable Marine Ecosystems (VMEs),  
100 have ecological and functional importance by enhancing biodiversity and providing habitat to  
101 other rare, threatened, or endangered species (FAO, 2009). Such roles confer VME taxa with  
102 conservation significance, and the United Nations require management measures that can  
103 include closing areas to fishing (UNGA, 2007). As a result, there is an increasing need to  
104 enforce conservation measures for deep-sea regions on a global scale, which in turn requires  
105 understanding species distributions across temporal and spatial scales (Lourie & Vincent,  
106 2004; Rice et al., 2011).

107

108 To support conservation and spatial management objectives for VMEs, it is fundamental to  
109 define the boundaries, extent, and connections of deep-sea regions with ecological,  
110 environmental, and biogeographic characteristics (Danovaro et al., 2009). However, this  
111 fundamental definition of deep-sea regions is compromised by the critical under-sampling of  
112 deep waters (Hughes et al., 2021; Menegotto & Rangel, 2018) that prevents resolving  
113 biogeographic patterns for deep-sea taxa, although there are efforts at regional (e.g., Summers  
114 & Watling, 2021) and global (e.g., Watling et al., 2013; Watling & Lapointe, 2022) scale for  
115 certain groups. The vastness, remoteness, and required technological complexities render  
116 deep-sea scientific exploration patchy, punctual, and rather costly. At a spatial resolution of 5  
117 km, Hughes et al. (2021) estimate the area of ocean sampled at 0.6% for all taxonomic groups  
118 between 1,000 and 1,800 m water depth and at less than 0.02 % for deeper waters. At depths  
119 between 1,000 and 1,800 m, certain groups like Cnidaria dominate the percentage of global  
120 records. Further to this sampling imbalance across depths, sampling bias prevails in the  
121 southern hemisphere (Menegotto & Rangel, 2018), underlining the inequity in scientific  
122 technological capacity needed for this realm. Accordingly, the deep sea is an environment  
123 that suffers systematically from taxonomic and geographical knowledge biases, also known  
124 as the Linnean (Brown & Lomolino, 1998) and Wallacean (Lomolino, 2004) shortfalls,  
125 respectively.

126

127 Linnean and Wallacean shortfalls for deep-sea vulnerable taxa are greatest in waters beyond  
128 national jurisdiction (hereafter, high seas), which cover 61% of ocean area and 73% of ocean  
129 volume (Costello et al., 2010). There, these taxa of groups of mainly suspension feeders, tend  
130 to occur on locations where currents are accelerated by kilometre-scale topographic features,  
131 such as the crest or rims of seamount summits and ridges (Rogers, 2018). However, although  
132 Linnean (i.e., most species remain undescribed; Cardoso et al., 2011) and Wallacean (i.e.,  
133 knowledge on species’ distribution is inadequate; Cardoso et al., 2011) are the most  
134 prominent knowledge gaps, in reality most deep-sea taxa endure other renowned shortfalls:  
135 Darwinian (phylogenetic relationships), Hutchinsonian (environmental tolerance), Prestonian  
136 (population in time and space), Raunkerian (species traits), and Eltonian (species  
137 interactions) (see Hortal et al., 2015 for a review on biodiversity shortfalls). For example, for

138 deep-sea octocorals of the Order Alcyonacea (Phylum Cnidaria), which can create single or  
139 multi-species aggregations known as coral gardens (Freiwald & Roberts, 2005; Rossi et al.,  
140 2017), the phylogeny has just become resolved and well supported to proceed with taxonomic  
141 revisions (McFadden et al., 2022). In addition, few studies have assessed the interaction  
142 behind octocoral species co-occurrence (e.g., Rakka et al., 2021), and baseline studies  
143 continue to shed light on life-history traits (e.g., Baillon et al., 2016; Rakka, Godinho, et al.,  
144 2021) and environmental tolerances (e.g., Rakka, Godinho, et al., 2021; Scanes et al., 2018)  
145 for a handful of species. Whilst we are steadily advancing our understanding of deep-sea  
146 species, habitats, and more generally VMEs, knowledge shortfalls on the high seas may  
147 hinder the application of conservation measures by managerial regulatory bodies, such as  
148 regional fisheries management organizations (RFMOs).

149  
150 In the Indian Ocean, the Southern Indian Ocean Fisheries Agreement (SIOFA) is the entity in  
151 charge of managing deep-sea fisheries on the high seas. As other RFMOs in other world's  
152 oceans, SIOFA must comply with international obligations towards the conservation of  
153 VMEs against potential impacts from deep-sea bottom fishing. In this regard, since its  
154 relatively recent establishment in 2012, SIOFA has initiated management efforts to protect  
155 VMEs by identifying a list of VME indicator taxa for Indian Ocean waters (CMM 2018/01).  
156 In addition, SIOFA has designated five interim benthic protected areas where bottom-fishing  
157 trawling is not permitted (CMM 2019/01) and is currently undertaking work to establish new  
158 interim protected areas. Situated over seamounts and ridges, the relevance of the existing  
159 protected areas for preserving VMEs is however unknown because it has not been studied:  
160 they were areas where only exploratory or no fishing had occurred. Considering that half of  
161 the estimated number of seamounts of the Indian Ocean fall in the high seas and about a  
162 quarter are deemed to be at fishable depths (i.e., with summit depths less than 1,500 m)  
163 (Yesson et al., 2011), further conservation measures will likely also focus on seamounts and  
164 ridges, where deep-sea fisheries develop around aggregations of resident fish (Clark et al.,  
165 2007; Kerry et al., 2022). To crown it all, the Southern Indian Ocean remains one of the least  
166 explored oceans in the world (Ingole & Koslow, 2005; Rogers & Taylor, 2012; Saraswat et  
167 al., 2022; Wafar et al., 2011).

168  
169 For SIOFA to develop a conservation plan, it requires to map biogeographical regions of  
170 VMEs in order to scientifically inform decision making. Biogeographical classifications, or  
171 bioregionalizations (Woolley et al., 2020), are the building blocks for the planning and  
172 implementation process of management measures and are highly connected to the  
173 development of marine protected areas (Rice et al., 2011). This is because bioregionalizations  
174 enable the identification of units that should be represented in a network, ensuring the  
175 protection of biogeographically unique areas and the development of a network that considers  
176 representativity, connectivity and replication of sites (Rice et al., 2011). Here, we compiled  
177 all the available distribution data on VME indicator taxa to map such regions and report on  
178 how problematic Linnean and Wallacean shortfalls are for VMEs on the high seas of the  
179 Southern Indian Ocean. We develop a bioregionalization, explore these knowledge shortfalls,  
180 and speculate on what are their impact and the possible avenues for VME conservation so  
181 that SIOFA meets their international management obligations.

## 182 **Materials and methods**

183

### 184 *Study area*

185

186 The Southern Indian Ocean Fisheries Agreement (SIOFA) covers the high seas (i.e., waters  
187 beyond national jurisdiction) of the Indian Ocean between the parallels 10° N and 45° S, and  
188 the meridians 30° E to 80° E, with the area east of 65° E to the equator outside their  
189 jurisdiction (Figure 1A). We extended the study area to encompass latitudes 13° N – 65° S  
190 and longitudes 20° E – 147° E.

191

192 The seabed of the Indian Ocean is geomorphologically complex. The Indian Ocean includes  
193 numerous mid-ocean ridges (some not active sites of seafloor spreading such as the Ninety-  
194 East Ridge, the Mascarene Ridge and the Chagos-Laccadive Ridge), seamounts, plateaus and  
195 rises, abyssal plains and trenches. Most of the geomorphological features fall within areas  
196 beyond national jurisdiction and are therefore within SIOFA's management area. Within  
197 SIOFA, the seafloor bathymetry ranges from as shallow as 1 m at Saya de Malha Bank to  
198 approximately 8,000 m in the abyssal plains, wherein the Southwest Indian Ocean Ridge and  
199 Broken Ridge summit between 1,000 m and 2,000 m, and the Central Indian Ridge, Southeast  
200 Indian Ridge and Ninety-East Ridge have generally deeper summits. With a mean peak  
201 summit at 2,250 m, there are 1,746 estimated seamounts in SIOFA (Yesson et al., 2011).

202

### 203 *Biological data*

204

205 The VME indicators list adopted by SIOFA (CMM 2018/01) at order, class, and phylum  
206 levels, includes the following categories of deep-sea (generally > 200 m) benthic taxa:  
207 Cnidaria (Gorgonacea, Anthoathecatae, Stylasteridae, Scleractinia, Antipatharia, Zoantharia,  
208 Actiniaria, Alcyonacea, Pennatulacea), Porifera (Hexactinellida, Demospongiae), Ascidiacea,  
209 Bryozoans, Brachiopoda, Pterobranchia, Serpulidae, Xenophyophora, Bathylasmatidae,  
210 Crinoidea (stalked species only), Euryalida, Cidaroida. We downloaded all occurrence  
211 records under these categories from the public databases the Ocean Biodiversity Information  
212 System (OBIS, <https://obis.org/>) (accessed on 10/11/2020 and 02/04/2021), the Global  
213 Biodiversity Information Facility (GBIF; <https://www.gbif.org/>) (accessed on 09/11/2020 and  
214 14/04/2021), NOAA's Deep-sea Corals Data Portal (<https://deepseacoraldata.noaa.gov/>)  
215 (accessed on 16/11/2020 and 09/04/2021), and Smithsonian Natural History Museum  
216 (<https://collections.nmnh.si.edu/>) (accessed on 16/11/2020). We also obtained occurrence  
217 records from SIOFA's observer programme, research campaigns led by the Muséum National  
218 d'Histoire Naturelle, and the published literature (Taylor & Rogers, 2017). We obtained  
219 records for the whole Southern Indian Ocean to account for ecological continuity, that is,  
220 SIOFA's management area and all exclusive economic zones bordering it (latitudes 13° N –  
221 65° S and longitudes 20° E – 147° E).

222 We applied verification procedures for taxonomic consistency, error detection, as well as  
223 evaluation of records in the environmental space. Specifically, we first checked species  
224 names against the most updated authority, the World Register of Marine Species (WoRMS,  
225 2021) for synonyms and fossil records. Secondly, we applied automatic error and outlier  
226 detection using the function clean-coordinates from the R package CoordinateCleaner version  
227 2.0-18 (Zizka et al., 2019). We tested for equal coordinates, coordinates over land using the  
228 Natural Earth data ocean shapefile version 4.1.0 ([www.naturalearthdata.com](http://www.naturalearthdata.com), accessed  
229 November 2020), and zero coordinates. Finally, we used the catalogue number and  
230 geographical coordinates to filter out potential duplicates across GBIF and OBIS.

231 Our download strategy incorporated numerous shallow water species in the dataset,  
232 particularly zooxanthellate corals (i.e., corals with photosynthetic algae) – however, only  
233 deep-sea species fall under the definition of VME indicator taxa. Although very few

234 zooxanthellate corals occur below 50 m (Cairns, 2007), using the typical definition of deep  
235 sea as waters below 200 m would exclude deep-water species that expand into shallower  
236 depths. Consequently, we aimed to integrate the ecology of taxa and the general definition of  
237 deep sea by applying several filters to exclude zooxanthellate corals and other strictly  
238 shallow-water taxa. First, we individually assessed the depth distribution of each species, and  
239 we kept a species if 90% of its records were below 200 m water depth. To assess the depth  
240 range of records, we relied on their original recorded depth as indicated in the sample record.  
241 In the cases where this information was not available, we used the General Bathymetric Chart  
242 of the Oceans (GEBCO, 2021) to assign depths. Second, we further filtered species known to  
243 be shallow water as we worked through with peer-reviewed deep-sea taxa lists (Cairns, 2017;  
244 Kocsis et al., 2018). Our filtered dataset of deep-sea VME indicator taxa comprised 1,997  
245 species (of which 1,312 had an observation date).

246

### 247 *Completeness of the inventory*

248 We investigated the accuracy and uncertainty of our consolidated occurrence dataset by  
249 calculating the completeness of our inventory based on a class of diversity measures known  
250 as Hill numbers (Hill, 1973). Hill numbers are defined as the effective number of equally  
251 abundant species and are parameterized by a diversity order “ $q$ ”. Hill numbers for order  
252  $q \geq 0$  include the species diversity measures species richness, Shannon diversity, and  
253 Simpson diversity as special cases of order  $q = 0$ ,  $q = 1$ , and  $q = 2$ , respectively. For  
254 incidence-based data, as here, this class of measures quantifies the effective number of  
255 equally frequent species. For  $q = 0$ , this measure reduces to species richness, and the  
256 measures of  $q = 1$  and  $q = 2$  can be interpreted respectively as the effective number of  
257 frequent and highly frequent species in an assemblage (Chao et al., 2014). As our objective is  
258 to detect biogeographical regions, completeness at orders  $q = 1$  and  $q = 2$  are particularly  
259 important. Biogeographical regions are based on the overlapping distribution of species, and  
260 therefore it is a requirement for bioregionalization methods to detect the majority of frequent  
261 and highly frequent species across a large number of sites throughout the study area.

262 We used the estimated sample completeness profile, which depicts completeness as a  
263 function of a diversity order  $q$  in a four-step integrated approach developed by Chao et al.  
264 (2020) that links the concepts of sample completeness and diversity. In practice, a  
265 completeness profile is plotted for all values of  $q$  from  $q=0$  to  $q=2$ , beyond which the profile  
266 generally stabilizes (Chao et al., 2020). A bootstrap method permits to obtain 95% confidence  
267 intervals. We computed the completeness estimators at  $q = 0$ ,  $q = 1$ , and  $q = 2$ , as described  
268 in Chao et al. (2020) (iNEXT.4steps R package; Chao & Hu, 2023). We estimated the sample  
269 completeness on a per-grid cell basis at resolutions ranging from  $1^\circ$  to  $5^\circ$ , because the quality  
270 of estimates of taxonomic richness is dependent on the spatial scale (extent and resolution) of  
271 the study (Soberón et al., 2007). We did not compute completeness indices for insufficiently  
272 sampled cells, which include cells that had less than 10 species, only singletons, or less than 3  
273 sampled sub-cells, but instead these were manually set to have zero completeness. Our  
274 evaluation of different resolutions revealed an equal completeness at orders  $q = 1$ , and  $q =$   
275  $2$ . However, coarser resolutions also aggregated species from different regions within a grid  
276 cell, ultimately blurring boundaries between regions (Lobo et al., 2018; Menegotto & Rangel,  
277 2018; Mora et al., 2008). We decided to work at a resolution of  $1^\circ$ , which was a compromise  
278 between completeness and the identification of boundaries between bioregions. Further  
279 details on the computation of the sample completeness profiles can be found in the  
280 Supplemental Material (section “1. Inventory completeness”).

281  
282 **Bioregionalization**

283  
284 We delineated biogeographical regions for VME taxa using bipartite biogeographical  
285 networks (Vilhena & Antonelli, 2015) with the hierarchical clustering algorithm Map  
286 Equation (Rosvall & Bergstrom, 2008). Bipartite biogeographical networks have been  
287 recommended to map biogeographical regions (Bloomfield et al., 2018; Edler et al., 2017;  
288 Rojas et al., 2017) and perform better in data-poor situations than similarity-based approaches  
289 (see Leroy et al., 2019, Appendix S2). A bipartite network represents the distribution of  
290 species across sites as a network of nodes, where each node is a species or a site. A network  
291 comprises nodes that can be connected to each other by links (or edges). Here, nodes  
292 represent grid cells and, separately, the species that occur in them, while edges link grid cell  
293 and species nodes indicating whether a species is present in a grid cell. The network is  
294 bipartite because each type of node, grid cell and species, cannot connect to another node of  
295 the same type; that is, species nodes can only connect to grid cell nodes and grid cell nodes  
296 can only connect to species nodes. Thus, a species can be found in several sites and a site can  
297 host several species. In this study, we divided the Southern Indian Ocean into a 1° latitude-  
298 longitude grid, created a species/grid cell contingency table of presence-absence and  
299 transformed it into a bipartite occurrence network (Vilhena & Antonelli, 2015).

300  
301 In order to detect biogeographical regions, we applied a community-detection algorithm to  
302 the network. Community-detection algorithms aim at grouping together nodes that have high  
303 intra- group but low inter- group connectivity, which correspond to the definition of  
304 biogeographical regions as regions of assemblages with distinct endemic taxa. This is  
305 achieved based on flows of information (Rosvall & Bergstrom, 2008). As a community  
306 detection algorithm, we chose “Map Equation” (Rosvall & Bergstrom, 2008), as it has been  
307 recommended in previous biogeographical works (Bloomfield et al., 2018; Edler et al., 2017;  
308 Rojas et al., 2017; Vilhena & Antonelli, 2015) and it features hierarchical clustering. We ran  
309 Map Equation with 1,000 trials to find the optimal clustering and we ran it with hierarchical  
310 clustering to test whether larger regions showed a nested hierarchy of subregions. We  
311 explored bioregions that had strictly more than ten occurrences as our focus was to detect the  
312 main biogeographical regions in SIOFA. We explored the biological significance of each  
313 bioregion by calculating metrics to characterise the bioregions in terms of endemism, the  
314 affinity ( $A_i$ , i.e., range in their region / total range of the region; the higher the value, the more  
315 widespread the species is in the region) and fidelity of a species to its bioregion ( $F_i$ , i.e., range  
316 in their bioregion / total range across all regions; the higher the value, the more exclusive the  
317 distribution range of the species is located in its associated region – a fidelity of 1 means that  
318 the species is endemic to its region) (Leroy, 2021). Fidelity, in particular, is useful to detect  
319 transition bioregions. Transition bioregions are located at the interface between multiple  
320 bioregions and are thus classified as distinct bioregions by Map Equation (Vilhena &  
321 Antonelli, 2015). A transition bioregion will not have high-fidelity species, as all species  
322 occurring therein will have their distribution spread over multiple bioregions. We also  
323 calculated the indicator value (*IndVal*) for each species in each region as  $A_i * F_i$  – the *IndVal*  
324 will have a high value for species that occupy most of their associated cluster (high affinity)  
325 and are not present in any other cluster (high fidelity). We created and analysed the networks  
326 using the R package “*biogeonetworks*” (Leroy, 2021).

327  
328 All analyses were conducted in R (R Core Team, 2021). The R code and data are available  
329 online in Zenodo (<https://doi.org/10.5281/zenodo.7704934>).



## 330 **Results**

331

### 332 *Linnean and Wallacean shortfalls*

333

334 Our compilation of VME occurrences showed that most of the Indian Ocean was unsampled  
335 and that the bulk of available records was distributed in coastal waters, i.e., outside SIOFA's  
336 management area (Figure 1A). At 1° spatial resolution, the observed richness per grid cell  
337 was very low with a median at 5 species approximately (Figure 1B) and sample completeness  
338 was nearly 0% for all diversity orders (Figure 1C). For adequately sampled cells (i.e., those  
339 that have more than two sample sub-cells of 0.01° spatial resolution, not only singletons, and  
340 strictly more than ten species), the sample completeness increased with diversity order  
341 (Figure 1D), suggesting that we had at least sampled most of the highly frequent species  
342 (q=2) in the inventory.

343

344 We highlighted this issue at all resolutions (Figure S1). The sample and diversity profiles  
345 revealed that, at all spatial resolutions, the inventory was incomplete for infrequent species  
346 (q=0), frequent species (q=1) and for highly frequent species (q=2) (Figure S1). The  
347 estimated sample completeness profiles increased with diversity order (q), implying that there  
348 was undetected diversity (Figure S1, panel (a)). Diversity as a function of sample size (Figure  
349 S1, panel (b)) and sample coverage (Figure S1, panel (d)) indicated that at increasing  
350 resolutions we would expect higher estimates and that any diversity estimates would be lower  
351 bounds given that the asymptotic estimator does not level off (Figure S1, panel (c)). Evenness  
352 among species was similar regardless of the resolution (Figure S1, panel (e)).

353

### 354 *Bioregions in the high seas of the Southern Indian Ocean*

355

356 We detected multiple bioregions structured in two hierarchical levels for VME indicator  
357 species in the Southern Indian Ocean. At the first level (i.e., largest regions with highest  
358 degree of endemism) there were four biogeographical regions (Figure 2A): an inshore and an  
359 offshore bioregion, and two bioregions representing the Southern Ocean at latitudes south of  
360 40°S mostly. The four bioregions are present within SIOFA's management area, where the  
361 offshore bioregion has most of its distribution. The four bioregions have distinct faunas, and a  
362 very high degree of endemism with bioregion 1 having the largest endemism (95.01%),  
363 followed by bioregion 2 (75.94%), 3 (64.60%) and 4 (64.15%) (Table 2). In addition, we  
364 found that all four bioregions had high fidelity species (Figure 3). The top indicator species  
365 for bioregion 1 were all corals from the order Scleractinia; for bioregion 2, indicators were  
366 mostly sponges; for bioregion 3, mostly tunicates; and for bioregion 4, mostly sponges (Table  
367 S1). We provide the full list of indicator species for bioregions in Supplemental File 1.

368

369 At the second level of hierarchy (i.e., subregions nested within the level 1 regions, with a  
370 lower degree of endemism), we found nine subregions with distinct geographic  
371 characteristics (Figure 2B). The large inshore bioregion differentiated into six subregions:  
372 one covering eastern South Africa; one subregion mostly north of 20°S, and four bioregions  
373 along the western coasts of Australia. The offshore bioregion revealed only one subregion  
374 and the Southern Ocean displayed two subregions. At this level, the lack of sufficient  
375 available data was reflected by sparse subregions occurrences in the SIOFA's management  
376 area. The endemism patterns varied by subregion, wherein subregion 1.1 (29.05%), 1.3  
377 (41.34%) and 2.1 (43.16%) have the largest endemism, followed by subregion 1.12  
378 (21.62%) and subregion 1.5 (17.65%) (Table 2). The fidelity of species to their subregion is  
379 less marked than at the first level, where in some cases there is a wide bimodal distribution,

380 reflecting species with distribution spreading across multiple subregions (Figure 3). Yet, all  
381 subregions had species with a high fidelity, suggesting that none of the subregions was a  
382 transition zone. The top indicator species for subregion 1.1 were all scleractinian corals; for  
383 subregion 1.2, mostly scleractinians too; subregion 1.3 was mostly characterised by bryozoa;  
384 subregion 1.5 by tunicates; subregion 1.12 by a mix of scleractinian, alcyonacean, and  
385 antipatharian corals, and actinians; subregion 1.23 by an equal mix of corals (alcyonacean,  
386 antipatharian, scleractinian and pennatulaceans) and sponges; subregion 2.1 in its majority by  
387 sponges of several orders; subregion 2.3 by basket stars and brachiopods; and subregion 3.1  
388 by a mix of tunicates, sponges and antipatharian corals (Table S2). We provide the full list of  
389 indicator species for subregions in Supplemental File 2.

390

## 391 **Discussion**

392

### 393 *Major Wallacean and Linnean shortfalls in the Southern Indian Ocean*

394

395 We found that VME taxa of the Southern Indian Ocean and, more specifically, within  
396 SIOFA's management area, are subject to an extreme version of the Wallacean and Linnean  
397 shortfalls (Cardoso et al., 2011). First, there was very little distributional data for VME  
398 indicator taxa (Wallacean shortfall), and the bulk of records was distributed in coastal waters  
399 within national jurisdiction, where survey effort is typically concentrated (Hughes et al.,  
400 2021). This first result is particularly worrisome as it suggests that SIOFA's management  
401 area has virtually no data at species level, making it extremely challenging to resolve the  
402 biogeographic patterns of VME indicator species.

403

404 Second, considering the large spatial scale over which we calculated the completeness of our  
405 inventory, this incompleteness constitutes a major Linnean shortfall (Cardoso et al., 2011).  
406 Our analysis on a per-grid cell basis revealed that the top 20% most adequately sampled cells  
407 had a median completeness of 55% at 1° spatial resolution, but this was repeatedly observed  
408 at all resolutions (Figure S2), which is an alarming insight into the incompleteness of our  
409 data. For comparison, marine fish inventories with a level of completeness above 80% are  
410 considered as good quality (Mora et al., 2008); freshwater fish inventories with a  
411 completeness above 78% are fair quality and those with > 90% completeness are good  
412 quality (Pelayo-Villamil et al., 2018). However, Fautin et al. (2013) propose that inventories  
413 70% complete are not well inventoried, after they examined the global distribution of the  
414 Order Actiniaria (Phylum Cnidaria) and statistically compared observed with theoretical  
415 completeness values. More recently, global marine benthic inventories have been quantified  
416 to be less than 80% complete in general, particularly in southern hemispheres and subtropical  
417 regions (Menegotto & Rangel, 2018). The fact that the percentage of undetected diversity for  
418 adequately sampled cells is 50% for all  $q$  diversity orders (i.e., for infrequent, frequent, and  
419 very highly frequent species) at all spatial resolutions (Figure S3) and that these cells were all  
420 in territorial waters (Figure S4) corroborate these geographic and taxonomic biases for VME  
421 taxa of the Southern Indian Ocean.

422

### 423 *Unique yet unknown bioregions*

424

425 Our bioregionalization analysis has two main implications. First, SIOFA's management area  
426 hosts several biogeographical regions both at the first and second level of the hierarchy. Such  
427 diversity suggests a decisive responsibility for this regional fisheries management  
428 organization to preserve deep-sea biodiversity. On one hand, the percentage of endemism is  
429 high for all regions (10% is proposed as the threshold to define a biogeographic region;

430 Briggs & Bowen, 2012) and comparable to the endemism of the Indian Ocean marine realms  
431 (Costello et al., 2017), which provides robustness to our findings. On the other hand, the  
432 completeness analyses suggest that, in grid cells that are not undersampled, the majority of  
433 frequent species have been recorded (Figure 1D) additionally suggesting that the  
434 biogeographical regions based on these cells are robust. Nonetheless, the bioregions will  
435 likely become better defined as new taxa are identified or existing data are added to  
436 biodiversity inventories. For now, the first-level bioregions appear to reveal differences in the  
437 species composition across different depth environments, observed in the distribution across  
438 the continental shelves and slopes and the deeper offshore areas (Figure 2A). The subregions,  
439 in contrast, have a marked geographic distribution (Figure 2B). The complex seafloor  
440 topography and oceanography of the Indian Ocean are likely to be playing a central role in  
441 structuring these subregions, such as for octocorals in the North Pacific (Summers &  
442 Watling, 2021) and anthozoans globally (Watling & Lapointe, 2022), but future research will  
443 need to adequately address the environmental drivers behind these biogeographic patterns.  
444 Deep-sea biodiversity provides a central role in provisioning services such as fisheries and  
445 biochemical compounds (Armstrong et al., 2012; Thurber et al., 2014), and biodiversity  
446 maintenance increases resilience after a disturbance (Danovaro et al., 2008); thus,  
447 maintaining such biodiversity should be a key management objective in the pursuit of  
448 sustainable use of resources by SIOFA.

449  
450 Second, data shortfalls, however, make it impossible to: (1) identify comprehensively the  
451 nested biogeographical regions within their management area, and (2) map them at a higher  
452 spatial resolution relevant for conservation decisions. In other words, neither we can resolve  
453 spatially finer biogeographic clusters at a scale that matches habitat complexity and fishing  
454 operating distances, nor understand the extent of clusters, or identify new ones, because most  
455 of the area lacks distributional data, especially in the easternmost side. Presently, there are  
456 only detailed descriptions of the habitats, biological communities, and oceanography for a  
457 few seamounts in the Southwest Indian Ocean Ridge (Hestetun et al., 2017; Pollard & Read,  
458 2017; Pratt et al., 2019; Read & Pollard, 2017; Rogers et al., 2017; Taylor & Rogers, 2017)  
459 as part of the IUCN Seamount Project (Rogers, 2012; Rogers et al., 2017) and MADRidge  
460 Project (Roberts et al., 2020). With such few information we are not able to make informative  
461 maps, nor make robust predictions that translate into fine-scale characterisation of habitats  
462 across SIOFA's management area. Therefore the only solution is to resort to using this  
463 information at a coarse spatial scale (1° spatial resolution) so that analyses can only provide a  
464 first signal (reflected in the lower endemism of some subregions) that multiple bioregions  
465 are expected to be found in the Southern Indian Ocean, but not useful for the finer grain  
466 resolution needed for conservation measures. Future work might include the exploration of  
467 predictive modelling as a first solution to tackle the lack of data.

468  
469 In light of the many unknowns, the precautionary approach will be instrumental for the  
470 designation of conservation management measures to meet UN Resolutions towards  
471 protection of deep-sea habitats in the SIOFA area. Yet, negotiations to reach an agreement in  
472 the implementation of conservation measures may result in internal divisions in RFMOs due  
473 to limited cooperation and coordination among their members. This has been previously  
474 observed for seamounts, for instance, where those falling in the areas of competence of  
475 RFMOs eventually are more heavily fished than seamounts outside areas of competence in  
476 the same ocean basin (Kerry et al., 2022).

477  
478 ***The absolute necessity of deep-sea biodiversity inventories***

479

480 The shortfalls we identified here corroborate previous global data-driven biogeographic  
481 analyses (Watling & Lapointe, 2022) and global habitat suitability maps of different groups  
482 of deep-sea habitat-forming taxa (stony corals, Tittensor et al., 2009; octocorals, Yesson et al.  
483 2012; black corals, Yesson et al. 2017; framework cold-water corals, Davies and Guinotte  
484 2011). These knowledge shortfalls imply that global biogeographic analyses and conservation  
485 of marine biodiversity are not truly global, a fact increasingly recognized in the literature  
486 (Lenoir et al., 2020). Given the unique composition and endemism of deep-sea ecosystems,  
487 and the increasing pressures on them due to the blue acceleration (Jouffray et al., 2020), we  
488 strongly urge the absolute necessity of investing in biodiversity inventories to start filling out  
489 these knowledge gaps. Although we advocate for this solution, we foresee that it will not  
490 change in the near future; hence, conservation decisions will have to rely on predictive  
491 modelling approaches in the short-term, which in turn will create an uncertain decision  
492 context.

493  
494 Predictive approaches are useful for marine ecosystem management in data-poor situations,  
495 but are not the panacea (Reiss et al., 2015; Ross & Howell, 2013). Indeed, predictive  
496 approaches require complex models whose adequacy for the implementation of management  
497 measures needs to be well-understood by model-builders and users (Guillera-Arroita et al.,  
498 2015). More importantly, they cannot address the fundamental and underlying key issue of  
499 missing data: models cannot predict incompletely sampled biodiversity or habitats, let alone  
500 unsampled biodiversity and habitats. For example, Stephenson et al. (2021) demonstrated the  
501 shortcomings of predictive models for informing the design of spatial management measures  
502 for VME taxa in the South Pacific, and urged for the need for better quality data, such as  
503 presence-absence and abundance. In addition, the applicability of predictive approaches for  
504 the management of these taxa is further challenged by disagreements specific to the definition  
505 of VMEs (Gros et al., 2022). Thus, despite the development of state-of-the-art predictive  
506 approaches for VME taxa designed to cope with their typical presence-only nature (Ardron et  
507 al., 2014), the high seas of the Southern Indian Ocean will still necessitate of exploration  
508 efforts and release of data to overcome the alarming observed data deficiency.

509  
510 Yet, detailed knowledge on the bathymetry and biodiversity of the Southern Indian Ocean  
511 exists for some areas on the high seas, through the fishing industry (e.g., Shotton, 2006;  
512 SIODFA, 2022). It will be critical that regional fisheries management organizations make  
513 information readily available just as international negotiations have agreed to a United  
514 Nations treaty on the conservation and sustainable use of biodiversity beyond national  
515 jurisdiction (the “BBNJ Treaty” or “UN High Seas Treaty”; UNGA, 2023). However, data  
516 mobilisation and digitisation of museum collections also constitute an important step in  
517 closing the gap of biodiversity synthesis to underpin conservation measures, more so in the  
518 realization of the post-2020 Global Biodiversity Framework (Orr et al., 2022). For now,  
519 conservation and management measures can be implemented in areas that benefit from  
520 existing data, building on a combination of key knowledge from RFMOs, bioregionalization  
521 schemes based on informed predictive approaches, and the precautionary approach. However,  
522 these areas are but snapshots of the deep-sea ecosystems and therefore it is unquestionable  
523 that much research exploration remains to be conducted to build comprehensive biodiversity  
524 inventories that serve to equip conservation managers with appropriate tools. In this respect,  
525 the recently proclaimed United Nations Decade of Ocean Science for Sustainable  
526 Development (2021 – 2030) might serve as a platform to catalyse opportunities and develop  
527 projects in the Southern Indian Ocean to ensure achieving sustainable management in line  
528 with international commitments (Sustainable Development Goals; UNGA, 2015).

529

530 The deep-sea community has paved the way with the development of a blueprint for a global  
531 deep-sea field programme that identifies and maps the needs and actions to achieve the  
532 objectives of the “Ocean Decade” (Howell et al., 2020). Similar as to the progress of the  
533 basin-wide Indian Ocean Observing System programme (IndOOS; Beal et al., 2020; Hermes  
534 et al., 2019), among them are identified the development of effective strategies that merge  
535 regional and basin-scale objectives, international coordination, capacity building, data sharing  
536 and, importantly, data release. These will be critical to finally put an end to the artificial  
537 empty maps that are systematically observed throughout the literature for this world’s ocean  
538 region.

539

540

541

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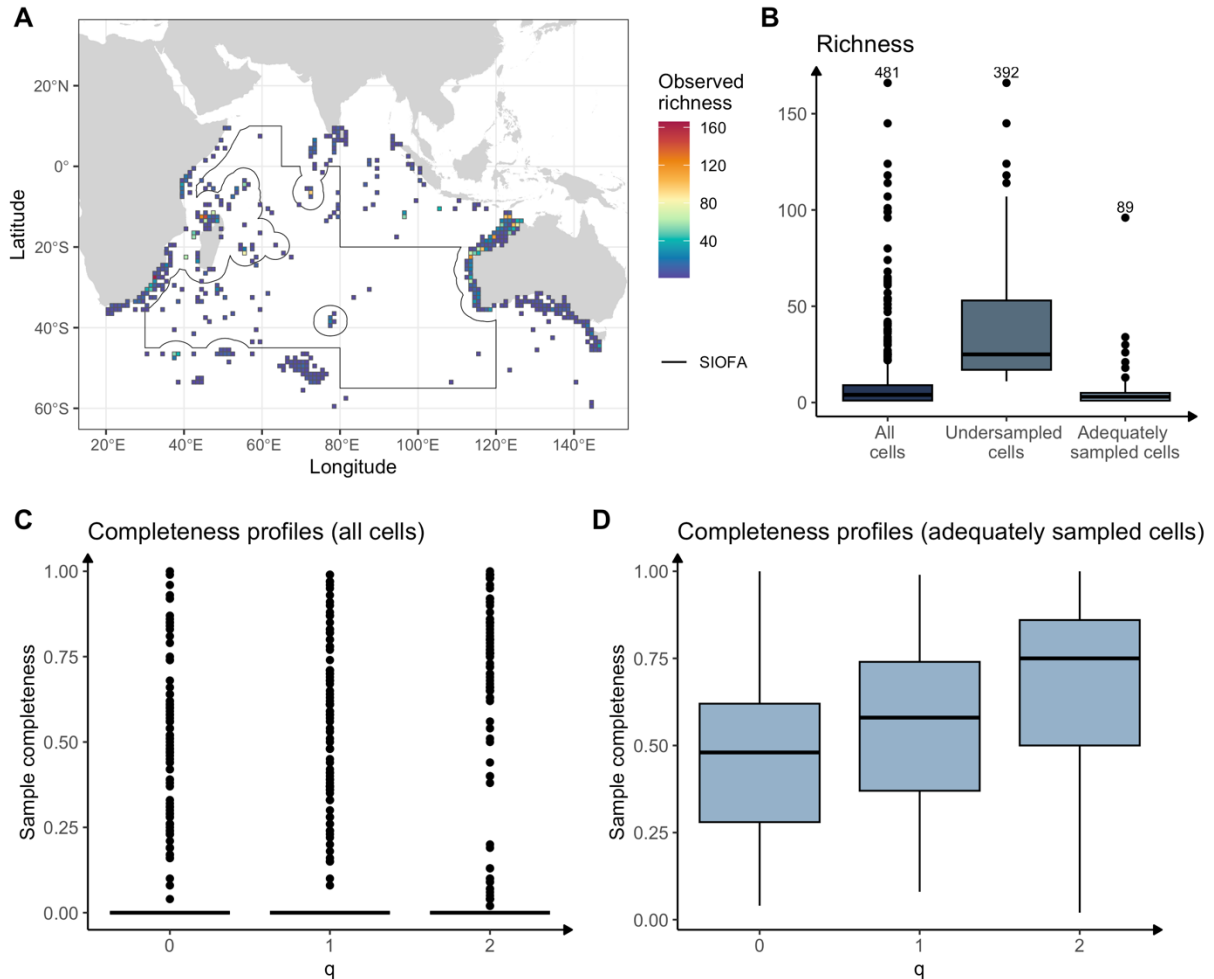
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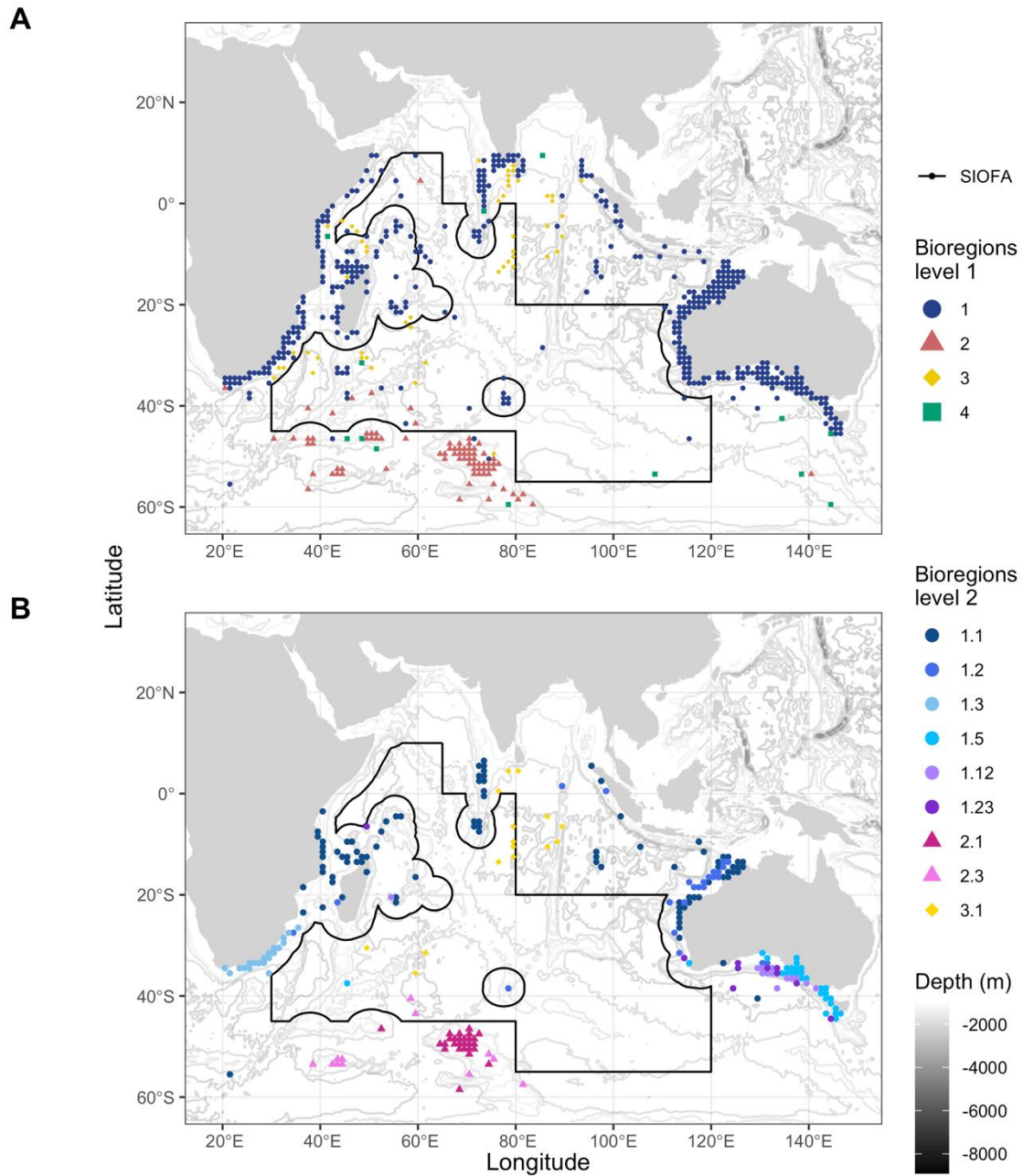
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884 Figure 1. (A) Distribution of observed richness in the study area at 1° latitude-longitude  
 885 spatial resolution. The black polygon represents SIOFA's management area. (B) Observed  
 886 richness calculated over different subsets of our data at 1° spatial resolution. (C) Sample  
 887 completeness profiles calculated for all cells, and (D) Sample completeness profiles  
 888 calculated for adequately sampled cells only, for all  $q$  diversity orders at 1° spatial resolution.  
 889 Undersampled cells are cells that had less than 10 species, only singletons, or less than 3  
 890 sampled sub-cells. Numbers over the boxplots indicate sample size (i.e., number of cells).  
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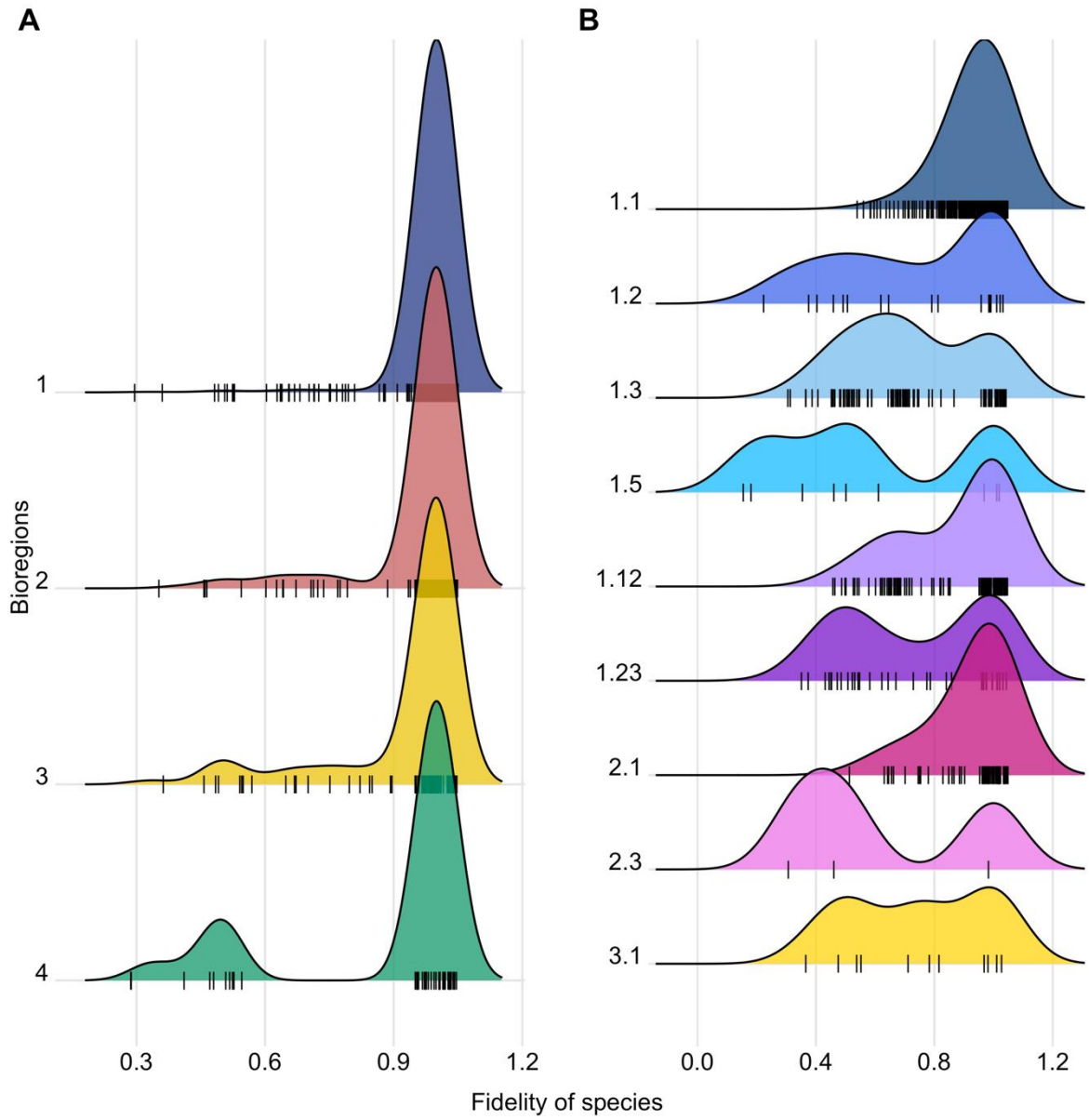
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894 Figure 2. Distribution of bioregions (A) and subregions (B) at 1° spatial resolution. There are  
 895 four bioregions at the first level: an inshore (1), an offshore (3), a Southern Ocean (2) and a  
 896 sparse (4) bioregion. At the second level, there were six subregions nested within bioregion 1  
 897 (prefix 1), two subregions in the Southern Ocean bioregion (prefix 2) and one in the offshore  
 898 bioregion (prefix 3). The black polygon denotes SIOFA's management area. Bathymetric  
 899 contours (every 1000 m) are shown for reference.  
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902 Figure 3. Distribution of fidelity values of species to their assigned first-level (A) and second-  
903 level (B) bioregions.



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918 Table 1. Number of species and endemism of each biogeographical region for the species-  
 919 based bioregionalization. Total richness refers to the total number of species found in a  
 920 bioregion. Assigned richness refers to taxa that the Map Equation algorithm has grouped into  
 921 the same bioregion (even if a species is assigned to a bioregion, its distribution can expand  
 922 into other bioregions). Endemic richness refers to taxa exclusively found in a bioregion.  
 923 Percentage of endemism refers to the endemic richness in a bioregion divided by the total  
 924 number of species in that bioregion. Percentage of species in the study area refers to the  
 925 number of assigned species to a bioregion divided by the total richness in the database.

| <b>Bioregion</b> | <b>Total richness</b> | <b>Assigned richness</b> | <b>Endemic richness</b> | <b>Percentage of endemism</b> | <b>Percentage of species in study area</b> |
|------------------|-----------------------|--------------------------|-------------------------|-------------------------------|--|
| <b>Level 1</b>   |                       |                          |                         |                               |  |
| <b>1</b>         | 1664                  | 1621                     | 1581                    | 95.01                         | 83.32                                      |
| <b>2</b>         | 212                   | 183                      | 161                     | 75.94                         | 10.62                                      |
| <b>3</b>         | 113                   | 93                       | 73                      | 64.60                         | 5.66                                       |
| <b>4</b>         | 53                    | 44                       | 34                      | 64.15                         | 2.65                                       |
| <b>Level 2</b>   |                       |                          |                         |                               |  |
| <b>1.1</b>       | 754                   | 416                      | 219                     | 29.05                         | 37.75                                      |
| <b>1.2</b>       | 206                   | 90                       | 27                      | 6.89                          | 10.32                                      |
| <b>1.3</b>       | 179                   | 119                      | 74                      | 41.34                         | 8.96                                       |
| <b>1.5</b>       | 95                    | 38                       | 15                      | 17.65                         | 4.76                                       |
| <b>1.12</b>      | 48                    | 18                       | 8                       | 21.62                         | 3.00                                       |
| <b>1.23</b>      | 22                    | 9                        | 3                       | 6.00                          | 1.10                                       |
| <b>2.1</b>       | 96                    | 60                       | 41                      | 43.16                         | 4.81                                       |
| <b>2.3</b>       | 8                     | 3                        | 1                       | 10.00                         | 0.40                                       |
| <b>3.1</b>       | 22                    | 11                       | 4                       | 9.09                          | 1.10                                       |

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