

# Ocean climate connectivity and the future range shifts of marine biodiversity.

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## Article

### Keywords:

**Posted Date:** January 6th, 2022

**DOI:** <https://doi.org/10.21203/rs.3.rs-1043050/v1>

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**Version of Record:** A version of this preprint was published at Communications Earth & Environment on October 14th, 2022. See the published version at <https://doi.org/10.1038/s43247-022-00569-5>.

1 **Title:** Ocean climate connectivity and the future range shifts of marine biodiversity.

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9  
10  
11 ***Abstract***

12 Shifting distribution to track suitable climate is a potential strategy for marine species to cope  
13 with ocean warming. Yet, the ability of species to successfully reach future climate analogs  
14 largely depends on the length of the paths that connect them, and on the exposure of these  
15 paths to extreme climates during this transition. Here, we evaluate marine climate  
16 connectivity for trajectories between climatic analogs on a global scale. We find that while  
17 movement between climatic analogs is more intense in the northern seas of the planet, they  
18 require longer trajectories to reach climatic analogs, with high climatic exposure to extreme  
19 conditions. On the contrary, the southern seas host areas that have closer climatic analogs,  
20 further subjected to a lower exposure to dissimilar climates. These patterns are mirrored in the  
21 connectivity properties of the global marine protected areas, highlighting sites which might  
22 fail to facilitate connectivity to future climates. Our results suggest that potential shifts  
23 between climatic analogs might be subjected to more limitations than those suggested by  
24 previous studies, with marine connectivity offering novel insights for the establishment of  
25 climate-wise conservation future networks.

26  
27 ***Main text***

28 Climate driven redistribution of marine biodiversity triggers the reorganization of ecosystems,  
29 alerting their functionality and the services they provide<sup>1,2</sup>. Factors such as the accelerating  
30 rate of ocean warming<sup>3</sup>, the novel climates<sup>4</sup> and the increased occurrence of marine  
31 heatwaves<sup>5,6</sup> force species to shift their range in order to maintain favorable environmental  
32 conditions<sup>7</sup>. Indeed, two third of the fish species in North Sea have shifted their distribution  
33 either by mean latitude or by depth from 1977 to 2001<sup>8</sup>. Similarly, multiple fish species in  
34 South East seas of Australia have exhibited major climate-related distribution shifts<sup>9</sup>.  
35 Evidence suggests that a poleward shift at the cooler edges is a key climate-driven response of  
36 an organism tracking the shifting isotherms<sup>10-12</sup>.

37 However, following a shifting climate is not feasible for all species. The limited ability to  
38 disperse at the rates of climate change and the extinction of suitable climate could result in  
39 inefficient shift responses. Hence, it is critical to quantify climate connectivity<sup>13</sup> for  
40 trajectories between sites with specific climatic conditions and sites that will feature these  
41 conditions in the future (hereafter called climatic analogs), contributing to species persistence  
42 in a changing planet. Former attempts to project climate trajectories that describe the shift of  
43 climate isotherm through time, were based on the delineation of single paths that minimize  
44 distance between climatic analogs<sup>14,15</sup>. However, these methods ignore the actual exposure to  
45 climatic differences along the routes, which could hinder species movement<sup>16</sup>. More recent  
46 studies accounted for climatic exposure between climatic analogs, by delineating paths that  
47 minimize the exposure to dissimilar climates during the studied period<sup>16,17</sup>. Nevertheless,

48 these studies only use climatic data for the first and the last periods, as they interpolate the  
49 intermediating climate with a linear function. While this approach accounts for temperature  
50 increments, it fails to incorporate the potential impact of extreme climatic events during the  
51 studied period. Therefore, generated outputs are likely to highlight climatic trajectories that  
52 are not actually suitable for minimizing climate exposure.

53 Here, we assess global marine climate connectivity by spatially delineating traverse sites of  
54 climate trajectories between current climate and their future climatic analogs. We used sea  
55 surface temperature data from historical and future projections of eleven models from  
56 Coupled Model Intercomparison Project phase 6 (CMIP6)<sup>18</sup>, interpolated to a common grid of  
57 1°x1° resolution. Future projections were based on the Shared Socioeconomic Pathways (SSP)  
58 5-8.5, which is considered the “business as usual” scenario, where greenhouse-gas emissions  
59 are relatively high<sup>19</sup>. The temporal interval covered a total of 150 years, from the mid of 20<sup>th</sup>  
60 century (1951), up to the end of 21<sup>st</sup> century (2100). To account for different dimensions of  
61 sea surface climatic conditions, we defined unique climates and identified climatic analogs by  
62 using a combination of nine bioclimatic variables. To delineate trajectories that connect  
63 climatic analogs while avoiding exposure to non-analogue conditions, we generated cost  
64 surfaces for all unique climates, indicating climatic dissimilarity. We created cost surfaces for  
65 all consecutive 30 five-year periods from 1951 to 2100, with the minimum cost per pixel over  
66 all periods used to produce the final cost surface. To highlight important areas which could  
67 facilitate movement between climatic analogs, areas with low velocity (i.e., distance to closest  
68 climatic analog), as well as areas with low climatic exposure through their trajectory to their  
69 climatic analog, we applied four metrics derived from circuit theory<sup>20</sup> and least-cost path  
70 analysis<sup>21</sup>. Eventually, we utilized the aforementioned metrics to evaluate the performance of  
71 marine protected areas (MPAs) in enhancing climate connectivity.

72 Our study showed that approximately 27% of the ocean pixels did not have a climatic analog,  
73 indicating that their unique climatic conditions would be lost by the end of the 21<sup>st</sup> century  
74 (Fig. 1). The majority of these pixels were found in northern seas, which are affected by high  
75 warming rates<sup>22,23</sup>. Still, the northern seas were mostly found to host climatic analogous  
76 conditions for other pixels. This finding is consistent with studies suggesting that species will  
77 have to move northward to meet their climatic conditions<sup>11,12</sup>. Approximately 18.6% of the  
78 pixels were projected to experience novel climates in the future, therefore they would not be  
79 able to host climatic conditions of the recent past. These pixels were found mostly in the  
80 tropics, likely to reflect the extreme climatic events of this zone<sup>24</sup>. About 4.2% of the ocean  
81 pixels were found to neither have a climatic analog nor being themselves a climatic analog for  
82 other climates in the future, with majority of them located within the tropics, in the area of the  
83 equatorial Pacific Ocean.

84 Across the seascape, pixels that could facilitate movement between climatic analogs were  
85 found to be spatially aggregated, covering extensive marine areas, but their extent and  
86 distribution varied among oceanic regions and latitudes (Fig. 2A). These areas, which could  
87 contribute to climate connectivity under projected shifts of ocean climate, were identified  
88 with the use of current flow at each ocean pixel<sup>20</sup>. This metric quantifies the probability that a  
89 trajectory between climatic analogs passes through a given pixel. Current flow was projected  
90 to be higher in northern areas ( $r_s = 0.70, p < 0.01$ ), with this latitudinal pattern maintained  
91 when performing the analysis at an ocean level ( $H = 19621, df = 6, p < 0.01$ ,  
92 Supplementary Figure 1) This pattern could be related to the higher warming rate of the  
93 north<sup>22,23</sup>. As the climate becomes warmer, the local climates are likely to have climatic

94 analogs in distant areas. To avoid passing through areas of very dissimilar climatic conditions,  
95 trajectories mostly pass through specific sites that minimize climatic exposure. In addition,  
96 the increased projected movement in the northern oceans is in line with the observed evidence  
97 on northward distribution shifts<sup>11,12</sup>, where species are expected to track warmer climates.  
98 Furthermore, the extended terrestrial masses in the north were constraining the trajectories  
99 between climatic analogs, eliminating potential routes. Indeed, the highest metric values were  
100 found at areas such as the Bering Sea, located between North America and Asia; Gibraltar,  
101 which connects Atlantic Ocean with Mediterranean Sea; and Baltic Sea in Scandinavia. These  
102 areas represent narrow passages, where only few alternative routes could exist.

103 Multiple sites near the equator were found to have high path density, a metric that quantifies  
104 the number of optimal routes that pass over a pixel<sup>17</sup> (Fig. 2B). Path density demonstrated no  
105 latitudinal pattern ( $r_s = -0.08, p < 0.01$ ) and was weakly correlated with current flow ( $r_s =$   
106  $0.17, p < 0.01$ ). As path density is based on optimal routes between climatic analogs, it could  
107 be a more representative metric for assessing connectivity potential for highly migratory  
108 species, while current flow accounts for multiple pathways, and could be more suitable for  
109 species with limited dispersal capacity<sup>20</sup>. Many notable differences between the two metrics  
110 were observed in specific marine regions (Fig. 2A-B, Supplementary Figures 1-2). For  
111 example, multiple sites in the Indian Ocean were found to have high path density, but  
112 relatively low current flow values. Still, marine regions such as the North Atlantic Ocean, as  
113 well as areas on narrow passages (e.g., Bering Sea, Gibraltar), were identified as important by  
114 both metrics. In addition, multiple sites hosted in the equatorial Pacific Ocean were found to  
115 facilitate little to no movement between climatic analogs by both metrics, mirroring the  
116 evidence on high warming rate of this ocean<sup>25</sup> that will likely impede species dispersal.

117 At the tropical and subtropical regions of the Western Atlantic Ocean, numerous pixels were  
118 found to have high velocity, but relatively low climatic exposure (Fig. 2C-D). While these  
119 sites had climatic analogs in distant areas, their trajectories would pass over sites with  
120 conditions close to optimal thermal ranges. The topographical barriers in this region are  
121 limited to the landmasses of South and Central America, providing multiple pathways  
122 towards climatic analogs. Nevertheless, for many tropical regions of the planet, the rate and  
123 magnitude of warming could result in novel climates, often exceeding thermal tolerance of  
124 species<sup>26,27</sup>, potentially eliminating connectivity process. While the metrics of velocity and  
125 climatic exposure do not incorporate any species-specific information, they imply that species  
126 that are more sensitive to climate change and have limited dispersal capacity may not be  
127 capable to track areas of analogous climatic conditions. Indeed, there is increasing evidence  
128 on widespread declines in marine tropical biodiversity<sup>28-30</sup>. Similarly, under future climate,  
129 projections reveal high rates of tropical species loss<sup>31,32</sup>, with sensitivity to thermal tolerance  
130 of species further controlling invasion rates<sup>31,33</sup>.

131 The physical barriers posed by the land masses at the northern marine regions of the planet,  
132 along with the higher warming rate of these areas<sup>22,23</sup> resulted in a latitudinal pattern in  
133 velocity ( $r_s = 0.59, p < 0.01$ ) and climatic exposure ( $r_s = 0.63, p < 0.01$ ) (Fig. 2C-D). The  
134 few pixels in Arctic Ocean that were found to have climatic analogs were identified to require  
135 longer ( $H = 6105.3, df = 6, p < 0.01$ , Supplementary Figure 3) and more exposed  
136 transitions ( $H = 7858.5, df = 6, p < 0.01$ , Supplementary Figure 4) compared to the other  
137 oceans. Changes in community composition at the Northern Hemisphere are projected to be  
138 large in the future<sup>33-35</sup>, as the local species are vulnerable to the high warming rate<sup>36</sup>. While  
139 there are northern sites with climatic analogs, some species are likely to be further challenged

140 by the reduced climatic connectivity. Indeed, species in North and Norwegian Seas are found  
141 to track their analogous climatic conditions faster, but this might not be the case for species in  
142 Barents Sea<sup>12</sup>, which is projected to be exposed to high warming<sup>36</sup>. On the contrary, pixels in  
143 Southern Hemisphere have lower velocity and climatic exposure values, indicative of less  
144 distant climatic analogs, passing through similar climates during the transition.  
145 Approximately 13.7% of the pixels with climatic analogs were found to have a climatic  
146 exposure value of zero, with the majority of them found in the Southern Hemisphere (Fig.  
147 2D). Still, tolerance of different marine organisms to warming and changes to productivity,  
148 along with sea ice characteristics and seasonal dynamics would further challenge their ability  
149 to track their suitable climatic conditions<sup>37</sup>. Indeed, species of great ecological significance in  
150 the Southern Hemisphere, such as Antarctic krill, are highly vulnerable to climate change and  
151 are forced to change their distributions<sup>38</sup>. Therefore, towards a climatic-smart conservation  
152 planning, information on species observations, potential responses, and climate redistribution  
153 patterns should be considered<sup>39,40</sup>.

154 The necessity of determining marine protected areas (MPAs) that could facilitate connectivity  
155 for climatic trajectories has been highlighted as a key challenge to improve conservation  
156 efficiency<sup>41</sup>. We identified MPAs with high current flow hosted in North Atlantic Ocean (Fig.  
157 4A), while MPAs near the equator had to have higher path density values (Fig. 4B). These  
158 two metrics were not correlated ( $r_s = 0.11, p = 0.15$ ), suggesting that MPAs with a high  
159 value on either metric could be considered as critical areas for facilitating species movement.  
160 The MPAs found in the Southern Hemisphere were subjected to lower velocity and climatic  
161 exposure values, indicative of relative shorter, less exposed paths (Fig. 4C-D). While MPAs  
162 have been designed to conserve marine biodiversity<sup>42</sup>, their selection and prioritization have  
163 been based on a snapshot of biological features, largely ignoring potential changes triggered  
164 by changing climate. It is therefore not surprising that an increasing amount of evidence  
165 questions their potential efficiency to mitigate threats posed by climate change<sup>43</sup>. Yet, MPAs  
166 in the Northern Hemisphere are subjected not only to increasing rates of warming, but also to  
167 climatic barriers in tracking shifting isotherms. The Post-2020 Framework of the Convention  
168 for Biological Diversity highlighted the need to increase the cover of protected areas of the  
169 planet to 30% by 2030<sup>44</sup>. Thus, the enlargement of the global network of marine protected  
170 areas is an ongoing process. As these new sites must however confront the challenges of  
171 climate change<sup>45</sup>, considering in prioritization processes sites which could facilitate species  
172 distributional shifts could offer a significant chance for enhancing the climatic resilience of  
173 the protected network of the future<sup>39,46</sup>.

174

## 175 *Conclusion*

176 With the aim to support conservation planning, a number of tools have been developed to  
177 project potential climate-driven shifts of species distribution. Ecological niche models<sup>47</sup>,  
178 metrics of the velocity of isotherm shifts<sup>15,48</sup>, and spatial patterns of future climate analogs<sup>16,49</sup>  
179 offer projections of future redistribution of biodiversity. There are now available numerous of  
180 such spatial trajectories which are used for assessments of conservation efficiency and policy  
181 recommendations<sup>39,50</sup>. Still, our results demonstrate that delineating the potential range shifts  
182 based solely on slots of climate (i.e., current and projected climatic niche, climate change  
183 velocity over distinct periods, climate analogs) largely ignores the inherent dynamics of  
184 seascape climate. For example, while the increased warming rate of the northern sea might

185 force local species to exhibit movements to capture favorable climatic conditions, our  
186 findings on distant analogs and extreme climate exposed paths connecting them question the  
187 ability of the species to successfully perform such movements. The framework presented here  
188 provides the foundation on which to explore the potential of the projected climate driven  
189 distribution shifts of marine organisms, under the dimension of climate connectivity. We thus  
190 call for future research perspectives to incorporate methods and outputs presented here  
191 towards providing a more comprehensive view of future range shifts.

192

## 193 **Methods**

### 194 *Climate data*

195 In order to assess global ocean climate, we combined daily data on historical and future  
196 temperature projections of 11 ocean surface temperature models (Supplementary Table 1)  
197 from Coupled Model Intercomparison Project phase 6 (CMIP6)<sup>18</sup>. The time period studied  
198 here covered a total of 150 years, starting from the mid of 20<sup>th</sup> century (1951) up to the end of  
199 21<sup>st</sup> century (2100). The yearly datasets were further divided 30 five-year periods (hereafter  
200 called periods). Future projections are based on the Shared Socioeconomic Pathways (SSP) 5-  
201 8.5, which is considered the “business as usual” scenario, where greenhouse-gas emissions  
202 are relatively high<sup>19</sup>.

203

### 204 *Bioclimatic variables*

205 For each period, we calculated a total of 9 bioclimatic variables, which express seasonal  
206 trends and extreme temperature values (Supplementary Table 2). These variables are  
207 calculated by inputting minimum and maximum monthly temperature data. To obtain this  
208 input, for each model, we used the daily data to calculate the minimum and maximum  
209 monthly data per year. For each period, we calculated mean minimum and maximum monthly  
210 temperatures. Next, to combine all models, we extracted the mean minimum and maximum  
211 monthly data per period. This process resulted in 24 climatic layers per period (i.e., 12 for  
212 minimum and 12 for maximum monthly data), interpolated to a common grid of 1°x1°  
213 resolution.

214 To reduce the number of variables, while maintaining their information, we performed a  
215 principal component analysis. We reduced the bioclimatic variables to two principal  
216 components (hereafter *PC1* and *PC2*, Supplementary Figure 5), which explained the 93.3% of  
217 the original variables’ variance. Following this process, we generated a total of 60 climate  
218 layers (i.e., two principal components for each period).

219

### 220 *Defining climates*

221 The values of the two principal components were scaled based on the minimum and  
222 maximum values of the first period (i.e., 1951-1955), using the following formula<sup>17</sup>:

223

$$PC'_i = 1 + 99 * \frac{PC_i - \min\{PC_1\}}{\{PC_1\} - \min\{PC_1\}}$$

224

(Eq. 1)

225 Where  $PC_i$  denotes a principal component for the period  $i$ . Using this formula, values of a  
 226 principal component in the first period are scaled in the range of [1,100], while other periods  
 227 can have values out of this range, indicative of novel climates. In order to classify the values  
 228 of a principal component, we created two sets of bins, one per component. Their centers are  
 229 integer values, with width of  $\pm 0.5$ , covering all their scaled values. In our study, there were  
 230 116 bins for  $PC1$  and 104 bins for  $PC2$ , resulting in 12064 possible combinations. These bin  
 231 combinations were used to define climate. We identified 2780 different climates in the first  
 232 period.

233

### 234 *Climatic analogs and their connections*

235 We consider that a pixel has a climatic analog if its climate in the first period (i.e., 1951-  
 236 1955) was observed in the last period (i.e., period 30; 2096-2100), either on the same or on a  
 237 different pixel. To quantify the exposure of trajectories between climatic analogs to dissimilar  
 238 climates, we constructed cost surfaces. Following Carroll et al. (2018)<sup>17</sup>, cost surfaces indicate  
 239 the climatic dissimilarity of the seascape for a given climate (i.e., difference in  $PC1$  and  $PC2$   
 240 values). For each unique climate, we constructed 30 cost surfaces (one per period). The total  
 241 cost for the pixel  $k$  is given by this formula:

$$242 \quad \text{cost}(k) = 1 + p * |PC1 - PC1(k)| + p * |PC2 - PC2(k)|$$

243

(Eq. 2)

244 Where  $PC1$ ,  $PC2$  denote the  $PC$  values of the specific climate,  $PC1(k)$ ,  $PC2(k)$  denote the  
 245  $PC$  values of the pixel  $k$ , and  $p$  is the dissimilarity penalty. In our case,  $p = 2^{16,17}$ , indicating  
 246 that a unit of difference between the scaled  $PC$  values increases the cost by 2. The final  
 247 climate cost surface, which integrates all periods, is derived as the minimum cost per pixel  
 248 from all periods.

249

### 250 *Connectivity metrics*

251 In order to quantify climate connectivity, we used four metrics. The first two metrics are  
 252 called current flow<sup>20</sup> and path density<sup>17</sup>, and evaluate a pixel based on the extent to which it  
 253 facilitates movement between climatic analogs. Current flow is a metric derived from circuit  
 254 theory, which quantifies the probability that a trajectory between climatic analogs passes  
 255 through it. Path density<sup>17</sup> is based on least-cost path algorithm<sup>21</sup> and measures the number of  
 256 trajectories that cross a pixel. The key difference between the two metrics is that for current  
 257 flow estimation we assume that an individual is moving randomly, based on climatic  
 258 dissimilarity, while path density we account only for the trajectories that minimize the  
 259 climatic exposure (i.e., least-cost paths<sup>21</sup>). In essence, path density accounts for specific  
 260 trajectories where the individual moves with prior knowledge of the climates, and thus  
 261 traverses through the seascape while minimizing climatic exposure. Current flow, given the  
 262 limited knowledge of the seascape, quantifies the movement towards all climatic analog  
 263 pixels. Conversely, path density accounts only the trajectories of a pixel to their climatic  
 264 analog with the minimum cumulative cost (i.e., the minimum climatic exposure).

265 The other two metrics used here are called minimum exposure distance (MED)<sup>16</sup> and  
266 minimum cumulative exposure (MCE)<sup>16</sup>, which indicate the effort required from an individual  
267 (i.e., species) to reach the climatic analog. These two metrics are available only for pixels  
268 with climatic analogs. To calculate these metrics for a given pixel, we first extract the  
269 trajectory to its climatic analog that minimizes climatic exposure by using the least-cost path  
270 algorithm<sup>21</sup>. MED quantifies velocity, defined as the extracted trajectory's length. MCE is a  
271 complimentary metric which quantifies the exposure to dissimilar climates during this  
272 transition. In case a pixel has multiple climatic analogs, the values maintained are the ones  
273 obtained from the trajectory with the least climatic exposure.

274

275 *MPAs*

276 We obtained MPA data from World Database of Protected Areas (UNEP-WCMC, IUCN  
277 2021)<sup>51</sup>, transformed in a grid of 1°x1° resolution. Each MPA was evaluated with the metrics  
278 described above (i.e., current flow, path density, MED and MCE). Each MPA metric received  
279 a value equal to the median metric value of the pixels that cover the MPA. For this purpose,  
280 we maintained only MPAs that consisted of 10 or more pixels. We selected this threshold to  
281 ensure that the evaluated MPAs have a substantial area to derive a robust estimation of the  
282 metrics. For the MED and MCE metrics, we accounted only the pixels with climatic analogs.

283

## 284 **Acknowledgments**

285 PP was supported by the Hellenic Foundation for Research and Innovation (HFRI) under the  
286 HFRI PhD Fellowship grand (Fellowship Number: 1018). VA, AD and ADM were supported  
287 from the European Union's Horizon 2000 research and innovation programme under grand  
288 agreement No 869300 "FutureMARES".

289

## 290 **Authors' contributions**

291 ADM and PP conceived the ideas and designed the methodology. PP led the analysis and  
292 coding. VA and AD contributed to ecological knowledge and statistical analyses. All authors  
293 contributed critically to the drafts and gave final approval for publication.

294

## 295 **Competing Interests statement**

296 The authors declare that they have no conflicts of interest.

297

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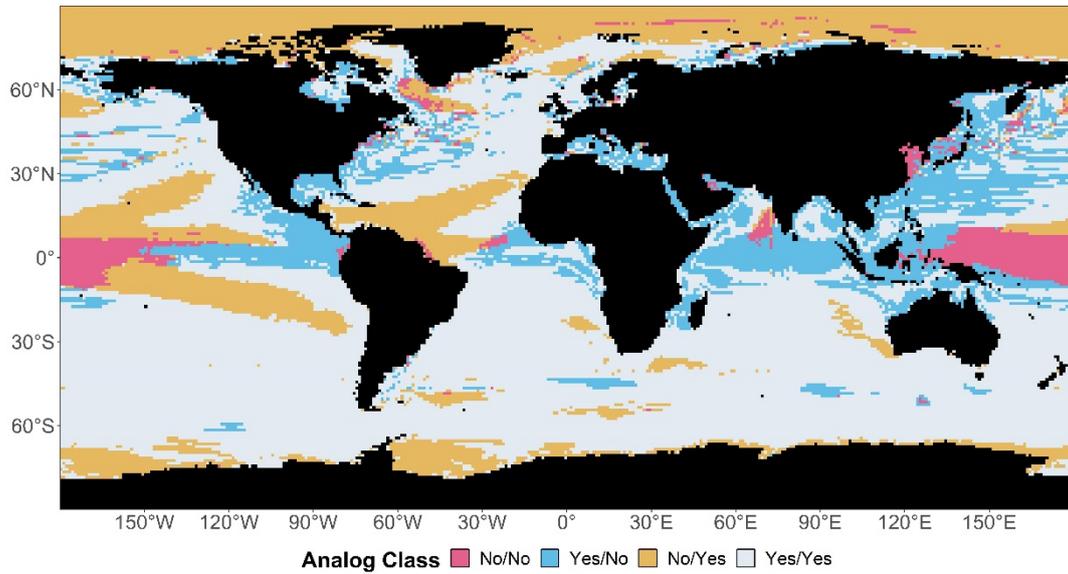
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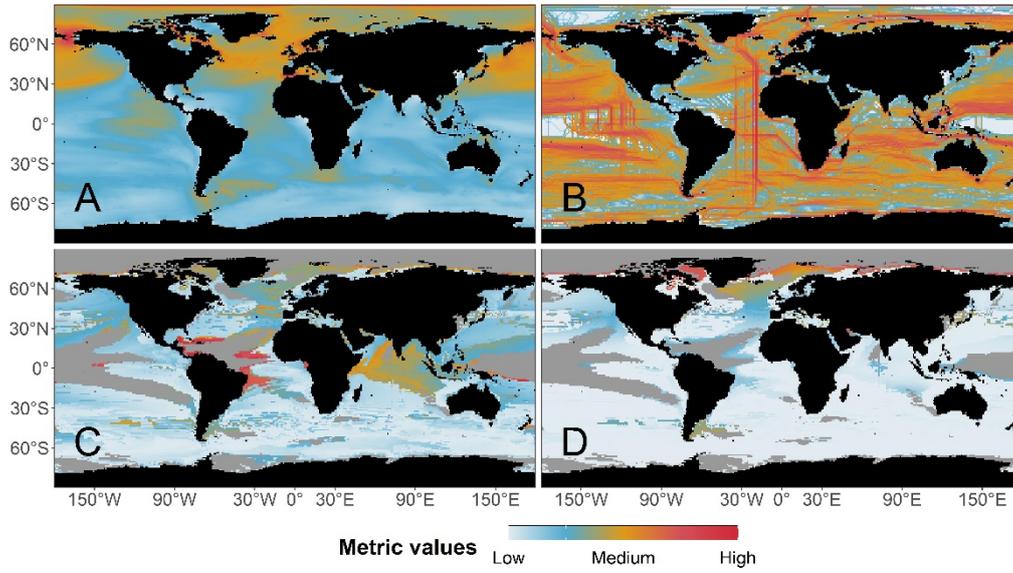
426 **Figures**



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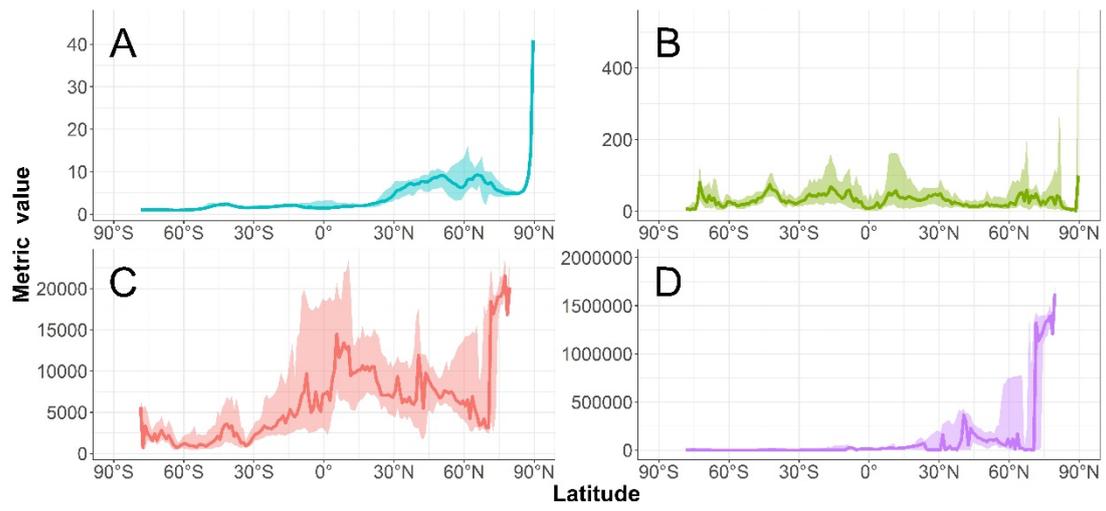
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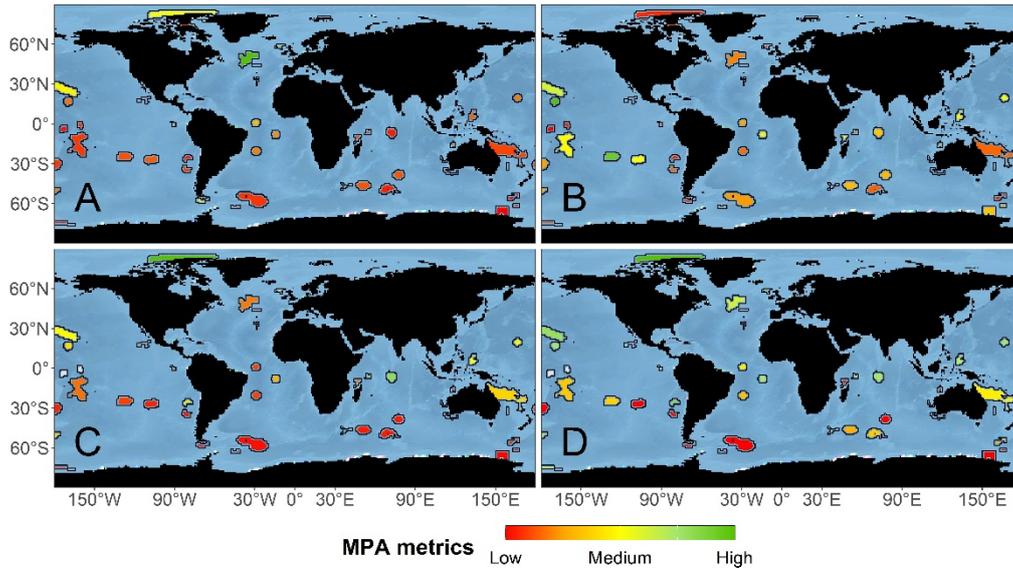
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