The effect of climate change on the distribution of a tropical zoanthid (*Palythoa caribaeorum*) and its ecological implications

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Palythoa caribaeorum, a sea mat coral, is a zoanthid often dominant in shallow rocky environments along the west coast of the Atlantic Ocean, from the tropics to the subtropics. This species has high environmental tolerance and is a good space competitor in reef environments. Considering current and future scenarios in the global climate regime, this study aimed to model and analyze the distribution of *P. caribaeorum*, generating maps of potential distribution for the present and year 2100. The distribution was modeled using maximum entropy (Maxent) based on 327 occurrence sites retrieved from the literature. Calcite concentration, maximum chlorophyll-a concentration, salinity, pH, and temperature range yielded a model with the smallest Akaike information criterion (2649.8), and were used in the present and future distribution model. Data from the HadGEM2-ES climate model were used to generate the projections for the year 2100. The present distribution of *P. caribaeorum*shows that parts of the Brazilian coast, Caribbean Sea, and Florida are suitable regions for the species, as they are characterized by high salinity and pH and small temperature variation. An expansion of the species' distribution was forecast northward under mild climate scenarios, while a decrease of suitable areas was forecast in the south. In the climate scenario with the most intense changes, *P. caribaeorum*would lose one-half of its suitable habitats, including the northernmost and southernmost areas of its distribution. The Caribbean Sea and northeastern Brazil, as well as other places under the influence of coastal upwellings, may serve as potential havens for this species.

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16 **Abstract**

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18 *Palythoa caribaeorum*, a sea mat coral, is a zoanthid often dominant in shallow rocky

19 environments along the west coast of the Atlantic Ocean, from the tropics to the subtropics. This

20 species has high environmental tolerance and is a good space competitor in reef environments.

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22 and analyze the distribution of *P. caribaeorum*, generating maps of potential distribution for the

23 present and year 2100. The distribution was modeled using maximum entropy (Maxent) based on

24 327 occurrence sites retrieved from the literature. Calcite concentration, maximum chlorophyll-

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26 information criterion (2649.8), and were used in the present and future distribution model. Data

27 from the HadGEM2-ES climate model were used to generate the projections for the year 2100.

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29 Sea, and Florida are suitable regions for the species, as they are characterized by high salinity

30 and pH and small temperature variation. An expansion of the species' distribution was forecast

31 northward under mild climate scenarios, while a decrease of suitable areas was forecast in the

32 south. In the climate scenario with the most intense changes, *P. caribaeorum* would lose one-half

33 of its suitable habitats, including the northernmost and southernmost areas of its distribution. The

34 Caribbean Sea and northeastern Brazil, as well as other places under the influence of coastal

35 upwellings, may serve as potential havens for this species.

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40   **1. Introduction**

41

42   *Palythoa caribaeorum* (Duchassaing & Michelotti, 1860) is a sessile colonial anthozoan

43   common along the west coast of the Atlantic Ocean (Kemp et al., 2006). This ~~sea mat~~ species

44   can be found from Florida in the US (Kemp et al., 2006) to Arvoredo Island in Brazil (Bouzon,

45   Brandini & Rocha, 2012), as well as around many oceanic islands in the Atlantic, such as

46   Bermuda (Lesser et al., 1990) and the São Pedro e São Paulo archipelago (Edwards & Lubbock,

47   1983). Its distribution is not limited to the western side of the Atlantic Ocean, however; with

48   records in Cape Verde islands (Reimer, Hirose & Wirtz, 2010). This broad geographic

49   distribution is possible because *P. caribaeorum* has a great tolerance to a wide range of

50   environmental conditions (Sebens, 1982). Although studies on *P. caribaeorum* larvae are

51   lacking, it is expected that its biology would be similar to its sister species, *Palythoa turbeculosa*

52   (Esper 1791), which has ~~zoanthellae~~ larvae with planktonic habits and a larval stage up to 170

53   days long (Polak et al., 2011; Ryland, 1997).

54   It is found on hard bottom environments, from the intertidal zone to depths up to 12

55   meters (Sebens, 1982), where it can be dominant (Monteiro et al., 2008). Colonies have a mat

56   format usually occupy large areas along the substratum (Sebens, 1982; Acosta, 2001; Silva et al.,

57   2015). The animal's color varies from yellow and brown to bronze, easily identifiable in the field

58   (Fig. 1a).

59   *P. caribaeorum* is a mixotrophic organism, hosting symbiotic dinoflagellates

60   (*Symbiodinium*) inside its tissues (Sebens, 1977; Suchanek & Green, 1981) and feeding on

61   planktonic organisms, which contributes to the energy flux from plankton to benthic

62   environments (Sorokin, 1991; Santana et al., 2015). Few studies have highlighted the importance

63   of *P. caribaeorum* in association with other invertebrates (Pérez, Vila-Nova & Santos, 2005),

64   reef dynamics (Silva et al., 2015), or the enrichment of the bottom fish community (Mendonça-

65   Neto et al., 2008). However, a study conducted in the Todos os Santos Bay in Brazil (Cruz et al.,

66   2015b) showed that the increased abundance of *Palythoa* spp. decreased habitat heterogeneity,

67   and consequently the richness of fish and benthic organisms, changing the local trophic structure

68   in that region.

69   *P. caribaeorum* is capable of overgrowing and thus adversely affecting the growth and

70   recruitment of several organisms (Suchanek & Green, 1981; Castro et al., 2012), such as hard

71   corals, hydrocorals, and other zoanthids, showing great efficiency competing for space. *P.*

72   *caribaeorum* also has a fast growth rate estimated to vary between 0.04-0.15 mm per day

73   (Bastidas &Bone, 1996; Silva et al., 2015). In general, zoanthids can dominate in areas where the

74   environmental factors make it difficult for the settlement of scleractinian corals (Fautin, 1988;

75   Cruz et al., 2015a), often becoming important as the main benthic component (Mendonça-Neto

76   et al., 2008) and nursery habitat for other invertebrates (Pérez, Vila-Nova & Santos, 2005).

77   Suchanek and Green (1981) and Sebens (1982) claimed that predation does not seem to be an

78   ecological element controlling the distribution and abundance of *P. caribaeorum,* probably due

79   to defense strategies related to nematocysts and palytoxin that are found in the animal's tissue

80   (Hines & Pawlik, 2011). However, Stampar et al. (2007) report a case of a Hawksbill turtle,

81   *Eretmochelys imbricata*, preying colonies of P. caribaeorum in southeastern Brazil.

82   Regarding its ecological role, investigating the current and future distribution of *P.*

83   *caribaeorum* will yield a prognosis of areas likely to experience changes in their benthic

84 communities because of the presence or absence of *P. caribaeorum*. Assessing how species and

85 biological systems are affected by climate changes as well as the generation of forecast models

86 are increasingly needed by decision makers and environmental managers (Gutt et al., 2012).

87   Species distribution models (SDM) are largely used in ecology, biogeography, and

88 conservation biology to help solve practical problems in these fields (Guisan & Thuiller, 2005;

89 Elith et al., 2011; Acosta et al., 2016). One of the main assumptions of SDM is that the

90 environment is in equilibrium with its species, whose distribution is determined by

91 environmental variability (Araújo & Pearson, 2005), excluding biological interactions, dispersion

92 barriers, and fast or small-scale environmental disturbances (De Marco, Diniz-Filho & Bini,

93 2008). Temporal and climatic variations also interfere in the modeling, and environmental data

94 must be gathered from the same period in which the species was recorded, making it difficult to

95 acquire large amounts of data for mobile organisms. In this scenario, *P. caribaeorum* is a good

96 candidate for the use of SDM.

97   The accelerating rates of environmental changes pose a challenge to most organisms

98 living in shallow waters throughout the world's oceans. At a global scale, between 1971 and

99 2010, the warming rate of the oceans' surface waters reached 0.13°C per decade (IPCC, 2014).

100 Since 1950, coastal regions with high evaporation rates are becoming saltier; and for the same

101 period, the pH of surface waters has decreased by 0.1 (IPCC, 2014). The forecast for the year

102 2050 shows a redistribution of marine organisms as a function of the increase in temperature.

103 This redistribution is expected to be toward mid-latitude zones, increasing species richness in

104 these areas while decreasing richness in the tropics due to extinction, migration, and reduction in

105 genetic diversity (Fields et al., 1993). However, it is still unknown for sure how the effects of

106   climate change, at the population level, will affect the environment at large ecological scales

107   (Harley et al., 2006; Thomas et al., 2017).

108   This study aimed to investigate and model the distribution of *P. caribaeorum* along the

109   western coast of the Atlantic Ocean, generating potential distribution maps for the present and

110   the year 2100 based on forecast climate models. The maps were used to characterize the species'

111   habitat and identify areas where suitability was retained, lost, or gained for *P. caribaeorum* over

112   time and under different climate scenarios.

113

114   **2.   Materials and Methods**

115

116   *2.1. Study area*

117   The study area comprised the western Atlantic Ocean (from -42.5º to 42.5º latitude),

118   between 2 meters of altitude and 100 meters of depth (Fig. 1b), hence extending beyond the

119   current known distribution of *P. caribaeorum*. The oceanographic features of this region are

120   influenced by the South Equatorial Current, from the east, which is divided into two components:

121   northward (North Brazil Current) and southward along the coast (Brazil Current). The North

122   Brazil Current flows toward the northwest, passing by the Caribbean Sea, Yucatan Channel, and

123   Gulf of Mexico before merging with the Antilles Current in the Florida Strait to form the Gulf

124   Stream, which flows toward Europe. Due to the strong tropical component, the region between

125   20ºS and 30ºN is strongly influenced by waters heated in equatorial regions (Ekman, 1953). In

126   contrast, regions closer to the boundaries of this study are influenced by both tropical and colder

127   currents, such as the Slopewater Current from the Labrador Current in the north (Churchill &

128   Berger, 1998) and the Malvinas Current in the south (Talley et al., 2011). The study region is

129   also influenced by large river discharges, mainly from the La Plata, Amazon, Orinoco,

130   Mississippi, and Saint Lawrence rivers (Fig. 1b).

131

132   *2.2. Biological data mining and filtering*

133   An extensive literature review was performed to obtain the largest possible number of

134   studies with occurrence data for *P. caribaeorum* (Supporting information 1). Occurrence data

135   recorded by the authors of this study and from global databases, such as WORMS, OBIS, and

136   GBIF, were also used, totaling 327 occurrence points for the species. The three identified

137   synonyms (Reimer, 2015)—*Palythoa caribaea* Duerden, 1898, *Palythoa caribbaea* Goreau,

138   1959, and *Palythoa caribdea* Carballeira et al., 1998—were included.

139   Occurrence points found on land or at depths deeper than 100 meters were automatically

140   excluded, as were those localized in freshwater environments. Because sampled areas and

141   methodologies varied among study sites, only one occurrence per pixel (5 arcminutes), based on

142   the environmental variables dataset, was kept for analysis (Elith & Leathwick, 2009). This point

143   was placed in the middle of each pixel, disregarding the exact occurrence point. After that, to

144   avoid bias originating from densely sampled sites, the geographic filter "OccurrenceThinner"

145   version 1.04 (Verbruggen, 2012), with thresholds of 0.5 and 1, was used, resulting in the final

146   dataset.

147

148   *2.3. Selecting environmental variables, the RM value, and the running Maxent*

149   Environmental and bathymetric data, with resolutions of 5 and 1 arcminute, were

150   obtained from the Bio-Oracle (Tyberghein et al., 2012) dataset and the ETOPO1 Global Relief

151   Model, respectively (Amante & Eakins, 2009). Twenty-seven layers of environmental data and

152   their transformations available on the Bio-Oracle dataset were used in the analyses (Table 1).

153   Each layer was cropped using ArcGIS 10.2 to only include areas within 2 meters ~~of~~ altitude and

154   100 meters ~~of~~ depth.

155   The habitat modeling was done using the Maxent 3.3.3 program (Phillips, Anderson &

156   Schapire, 2006). Maxent has the advantage of using only occurrence points, instead of

157   occurrence and absence/pseudo-absence, considering the lack of this type of data, especially for

158   marine organisms. Maxent also demonstrates good performance identifying suitable habitats

159   (Phillips, Anderson & Schapire, 2006; Reiss et al., 2011; Meißner et al., 2014) and predicting

160   novel distributions for species (Costa et al., 2012; Acosta et al., 2016) when compared with other

161   software.

162   All the features available in Maxent were used during the modeling (standard set up). To

163   choose the environmental variables and the regulation multiplier (Rm) value, the

164   "MaxentVariableSelection" package (Jueterbock, 2016) for R 3.3.1 (R Core Team, 2015) was

165   used, with a contribution threshold of 4% and Pearson's correlation coefficient of 0.9. A series of

166   runs were conducted, varying the Rm from 0.5 to 10 with increments of 0.5, and were then

167   assessed using the Akaike Information Criterion (AIC). The environmental variables and Rm of

168   the model with a lower AIC were used to run the final Maxent model. The AIC tends to choose

169   models that sort the most important variables, as well as models that better estimate

170   environmental suitability (Warren et al., 2014), and therefore behave better when projected onto

171   novel climate scenarios than models chosen using the Area Under the Receiver Operator Curve

172   (AUC) value (Warren & Seifert, 2011). The AIC selects the optimal and most parsimonious

173   model, taking into account its complexity (Bozdogan, 1987). Thirty percent of the data were

174   randomly sampled to test the model along each of the 100 replicates, resulting in an average for

175   all replicates. In all the analyses, 10,000 random points were used as the background along the

176   whole study area.

177

178   *2.4. Climate model data*

179   Data from the HadGEM2-ES model (Collins et al., 2011) retrieved from the Coupled

180   Model Intercomparison Project (CMIP5) were used on the projections for the year 2100 under

181   three different Representative Concentration Pathway (RCP) climate scenarios: low, middle, and

182   high radiative forcing of 2.6, 4.5, and 8.5 W/m², respectively (Van Vuuren et al., 2011). The

183   RCPs are related to retention of energy by the Earth's surface due to accumulation of greenhouse

184   gases from human activities, therefore higher numbers represent a greater anthropogenic impact

185   on our biosphere. The HadGEM2-ES climate model was freely available and provided outputs of

186   the main interest variables and high resolution in tropical areas under the RCP climate scenarios.

187   When there were no available data for the projections, the layers were kept unchanged. NetCDF

188   files from the climate model were interpolated using the bilinear interpolation "interp2" of

189   Matlab 7.14, and were then cropped and converted to ASC format.

190

191   *Projecting the results onto maps*

192   Maps were generated using the cumulative likelihood of species occurrence obtained

193   from Maxent, which can be interpreted as the sum of the relative occurrence rate of the species in

194   one pixel and other pixels with the same or lower values of the relative occurrence rate (ROR).

195   This type of output is best for drawing species distribution boundaries for different climate

196   scenarios (Merow, Smith & Silander, 2013) and also has a better visual presentation. For the

197   binary maps, the threshold equal to the maximum sensitivity plus specificity (max SSS) was

198   chosen to detect suitable habitats for *P. caribaeorum*. This threshold improves the distinction

199   between occurrence and absence sites, as well as between occurrence and background, also

200   selecting the same threshold for both occurrence-only and occurrence-absence models (Liu,

201   Newell & White, 2015).

202   Because *P. caribaeorum* is distributed along coastal zones, the final results were cropped

203   to depths up to 30 meters, better defining its real habitat. The map of the Marine Ecoregions of

204   the World (Spalding et al., 2007) was used as a reference for the results and discussion of

205   specific areas (Fig. 2).

206

207   **3. Results**

208

209   After ~~the~~ filtering, 135 occurrence points of *P. caribaeorum* were kept for the analyses

210   (Fig. 2). The model with a lower AIC (2649.8) presented an *Rm* of 3.5 and showed good

211   performance defining occurrence and absence sites for *P. caribaeorum* (AUC = 0.860 ± 0.023)

212   (Swets, 1988). The difference between the test AUC and the train AUC yielded a value of 0.015,

213   showing that the model was not over-adjusted and is transferable to novel climate scenarios

214   (Jueterbock et al., 2016; Warren & Seifert, 2011).

215   The environmental variables that contributed the most to the model were salinity

216   (47.9%), concentration of calcite (21%), maximum concentration of chlorophyll-a (13.3%), pH

217   (9.2%), and temperature range (8.5%), and were therefore kept in the model (Table 1). The

218   habitat of *P. caribaeorum* is characterized by salinity values higher than 34, a maximum

219   chlorophyll-a concentration from 0 to 28 mg/m³, a pH higher than 7.85, and temperature

220   variation up to 10ºC, although these intervals become much narrower when variable correlations

221   are considered. For calcite, the model pointed to a modulating influence, as no minimum or

222   maximum values were indicated.

223   The output of the HadGEM2-ES climate model for salinity, pH, and temperature (used to

224   calculate temperature range) was used to project the SDM model to novel scenarios for the year

225   2100, while calcite and chlorophyll-a were kept constant. A max SSS equal to 25.97 was used as

226   a threshold to infer suitable areas, thus identifying the potential distribution of the species.

227   Five hundred forty eight square kilometers were characterized as currently suitable for *P.*

228   *caribaeorum* (Fig. 3). Under the RCP 2.6 scenario (Fig. 4), the southern range of *P. caribaeorum*

229   distribution would lose suitability, as would the Caribbean, Bermudan, and Floridian regions;

230   however, the total suitable area is close to the one observed for the present: 492,000 km². An

231   increase in suitable areas in the Guianan, Amazonian, Bahamian, and Caribbean regions was also

232   observed, but the biggest change occurred in the northern part of its distribution, in the northern

233   Gulf of Mexico and along the Carolinian and Virginian regions. In these areas, the potential

234   distribution of the species reached almost as far north as Chesapeake Bay. The southernmost area

235   capable of retaining suitability for the species was near Cape Frio, in southeastern Brazil.

236   Not much differently, the projection under RCP 4.5 (Fig. 5) also shows that part of the

237   Brazilian coast would lose habitat suitability, only remaining suitable around the Abrolhos Bank

238   and in northeastern Brazil. In the north, the species' potential distribution is similar to the 2.6

239   scenario, only presenting smaller suitable areas in those regions, 470,000 km² in total.

240   Under the scenario with the higher anthropogenic impact, RCP 8.5 (Fig. 6), almost the

241   entire potential distribution for *P. caribaeorum* along the Brazilian coast would be lost, including

242   the northeast region. Under RCP 8.5, the anthozoan would also lose suitable habitats in regions

243   around Florida, the northern Gulf of Mexico, and the eastern and western Caribbean.

244   Overall, for this climate scenario, only one-half of the suitable areas seen in the present,

245   around 275,000 km², ~~was~~ characterized as a potential habitat for the species, comprising the

246   southern, western, and southwestern Caribbean, the southern Gulf of Mexico, and the Bahamian,

247   Greater Antilles, and eastern Brazil regions. Nevertheless, under the RCP 8.5 scenario, there

248   would be an increase in suitable areas in the southwestern Caribbean, along Nicaragua's coast,

249   similar to the RCP 4.5 forecast (Fig. 5).

250   To demonstrate the most important regions for the species, a map of the intersection of all

251   suitable areas under any climate scenarios for the year 2100 was made (Fig. 7). Figure 7 shows

252   that the northern part of the map (from 0° northward) would have much more significance for the

253   potential distribution of *P. caribaeorum* than the southern part. The suitable areas comprise six

254   ecoregions in the north (southern, southwestern, and western Caribbean, southern Gulf of

255   Mexico, and Bahamian and Greater Antilles regions) against only two in the south (northeastern

256   and eastern Brazil).

257
258   **4. Discussion**

259

260   *4.1. Environmental variables and* P. caribaeorum*'s habitat*

261   The variables selected to model *P. caribaeorum's* habitat suitability are in line with those

262   used in studies about environmental controls for other anthozoans. For instance, temperature and

263   salinity are two of the most important factors shaping the growth of modern reefs (Wood, 1993).

264   Temperature is also related to coral (Hoegh-Guldberg, 1999; Hughes et al., 2003; Villamizar et

265   al., 2008) and *P. caribaeorum* bleaching (Kemp et al., 2006). Variation in salinity may induce

266   osmotic stress and can alter the zonation of zoanthids, including *P. caribaeorum* (Sebens, 1982).

267   Changes in chlorophyll-a concentrations can also play a role in the distribution of *P.*

268 *caribaeorum* due to its heterotrophic nutrition and dependency on the water column productivity,

269 unlike most coral reef species ~~dependent~~ solely on autotrophy and therefore, clear oligotrophic

270 waters. This species also seems to be affected by lower pH (Kroeker et al., 2013), which is

271 another consequence of global environmental changes (Okazaki et al., 2017).

272   When the projection of the habitat suitability of *P. caribaeorum* for the present (Fig. 3) is

273 compared with the map of the biggest river discharges in the study area (Fig. 1), it becomes

274 evident that salinity has a major influence on the distribution of this species. Salinity had a

275 higher contribution to the model, sometimes reducing habitat suitability even when the values of

276 other variables, like temperature and chlorophyll-a, were adequate for the species. Freshwater

277 discharges from rivers are also an important source of calcite for oceans; however, calcite is 100

278 times more soluble in seawater than in freshwater (Libes, 2009), so high concentrations of this

279 mineral are not limited to river-influenced regions. In fact, regarding only calcite, habitat

280 suitability is positively correlated with its concentration, possibly because calcite concentration

281 also indicates other important biogeochemical controls.

282   The maximum concentration of chlorophyll-a presented a distribution pattern similar to

283 calcite and was also strongly affected by coastal processes, mainly big river discharges, which

284 fertilize the sea and enhance primary production. From satellite data, chlorophyll-a cannot be

285 distinguished from dissolved organic matter (DOM) without an algorithm specific to each region

286 (Ali et al., 2016; Liew et al., 2001; Vazyulya et al., 2014). Away from river discharges,

287 chlorophyll-a can be re-suspended back into the water column by wind, currents, and waves, and

288 is therefore correlated with suspended sediment (Walsh, Dieterle & Esaias, 1987). The values of

289 chlorophyll-a data used in this study are relative to its maximum concentration over several

290 years. Hence, it is likely that these values are the sum of all processes listed above: river

291   discharge, new production, and re-suspension. *P. caribaeorum* inhabits coastal regions with high

292   chlorophyll-a concentrations, but when these concentrations are related to river discharge, the

293   regions lose habitat suitability due to lower salinity and pH values. This can indicate that despite

294   the low salinity, chlorophyll-a and turbidity can be important factors for the species' niche. This

295   information corroborates previous studies (Segal & Castro, 2011; Steiner et al., 2015), which

296   suggested that low salinity was an exclusion factor for *P. caribaeorum*. However, it is difficult to

297   decouple the influence of variables related to water quality from demands related more to depth

298   and substrate in coastal areas, as both are intrinsically linked in continental shores. For instance,

299   *P. caribaeorum* is quite abundant around remote oceanic islands where eutrophication, turbidity,

300   and other processes typical of continental shores are not present. However, *P. caribaeorum*

301   seems to be more common in regions influenced by coastal processes with high turbidity along

302   the Brazilian coast (Cruz, personal observation).

303   Similar to calcite and chlorophyll-a, pH has a strong coastal component related to

304   salinity, especially around the Amazonian river mouth, where pH drops below 7, and in the

305   Virginian and Carolinian regions, where values exceed 8.25—both regions are devoid of the

306   anthozoan. Regarding pH alone, a habitat with a pH over 7.85 is considered suitable, but due to

307   correlations with the other variables, the habitat of *P. caribaeorum* is constrained to a pH

308   between 8.05 and 8.25.

309   Lastly, temperature range seems to influence the species in a typical latitudinal fashion,

310   presenting higher values in the northernmost and southernmost regions of the study area due to

311   the intrusion of colder waters onto the continental shelf at higher latitudes. Although *P.*

312   *caribaeorum* exhibits high tolerance to changes in temperature and water properties in tide pool

313   environments (Bastidas & Bone, 1996) and in southeastern Brazil (Bouzon, Brandini & Rocha,

314   2012), extreme variations in temperature and decreases in salinity caused by rain can cause

315   mortality (Sebens, 1977). For current environmental conditions, the latitudes 30º North and 30º

316   South can be recognized as limits to the distribution of this organism, mainly due to the

317   temperature range: between 9ºC and 13ºC in the south and 13ºC and 24ºC in the north. In these

318   regions, salinity reaches a value of 34, with high seasonal variation (Piola et al., 2000;

319   Rasmussen, ~~Gawarkiewicz & Owens,~~ 2005).

320

321   *4.2. Present distribution of P. caribaeorum*

322   There are regions characterized as potential habitats for *P. caribaeorum* that have no

323   record of the species (Fig. 2 and 3). This indicates either a lack of adequate sampling effort in the

324   Guianan, Greater Antilles, Bahamian, and western and southwestern Caribbean regions, the

325   absence of proper substrata, or other conditions not considered in the present modeling.

326   In general, the region between Florida and the Yucatan Peninsula, with the exception of

327   Flower Garden Banks off the coast of Texas (Tester et al., 2013), is characterized by the absence

328   of coral reefs due to low temperatures during winter and high rainfall (Longhurst, 2007). In

329   shallow areas in the northern Gulf of Mexico previously dominated by corals and sponges,

330   changes in temperature and an increase in river discharge were followed by a community shift

331   around 2005, and these areas are now dominated by algae (DeBose et al., 2013). This

332   information corroborates our model predictions for *P. caribaeorum* in that region, strongly

333   influenced by the Mississippi River Delta.

334   Using Briggs and Bowen's (2012) classification, it is evident that all of *P. caribaeorum's*

335   current potential habitat is within warm marine provinces, characterizing the species' distribution

336   as tropical. However, the limits of its distribution are close to warm-temperate and cold

337   provinces, which are characterized as marginal parts of the distribution. Studying reef

338   communities located at higher latitudes can improve our knowledge of how this species will be

339   affected during environmental and climatic changes (Thomas et al., 2017); thus, examining *P.*

340   *caribaeorum's* distribution in these regions is extremely important.

341

342   *4.3 Palythoa caribaeorum's response to climate change in the year 2100*

343   According to the RCP 2.6 climate scenario for the year 2100, there would be an increase

344   in salinity of 2.5 in the northern Gulf of Mexico, Virginian, and Carolinian regions, in turn

345   increasing habitat suitability for *P. caribaeorum* (Fig. 4). Along the southeastern Brazilian coast,

346   salinity would drop by 0.3, sufficient to become an unsuitable area for the species. Changes

347   would also be seen in the plume of the Amazon river, influencing adjacent coastal regions to a

348   lesser degree.

349   Values of pH in the year 2100 would drop for all regions, which is one of the factors that

350   could exclude *P. caribaeorum*. Since the anthozoan response to changes in pH is related to

351   salinity, its northernmost distribution should increase due to a weaker influence of rivers and a

352   decline in the temperature range under the RCP 2.6 scenario. On the other hand, decreases in

353   salinity and pH and more intense temperature fluctuations in the southeast and east of Brazil

354   would result in a loss of suitable areas, except along the coast of Cape Frio in southeastern

355   Brazil. This result may be associated with upwelling in this region (Castro et al., 2006), which

356   modifies water characteristics and reduces the frequency of osmotic and thermal stress on the

357   species (Hu & Guillemin, 2016), making that region more suitable for the animal. The same

358   process seems to occur along the coast of Colombia, as seen for coral species in that region

359   (Chollet, Mumby & Cortés, 2010). The Colombian coast is very important for *P. caribaeorum*

360   since it would remain a suitable habitat under any climate scenario (Fig. 7).

361   The same trend observed under the RCP 2.6 scenario occurs in the RCP 4.5 scenario,

362   with an increase in potential habitat in the northernmost range of its distribution (Fig. 5).

363   However, for this scenario, *P. caribaeorum* would also lose habitat in the south, including

364   around Cape Frio. ~~Differently,~~ other areas, such as the continental shelf of the Yucatan

365   Peninsula, would gain suitable zones in the RCP 4.5 scenario, due to higher salinity values and

366   lower temperature variations. For regions experiencing a loss of suitable areas, such as the

367   northeastern Brazil and Amazonian regions, the drop in pH values, salinity, and an increase in

368   the temperature range would be responsible.

369   As expected, the climate scenario with the strongest anthropogenic impact, RCP 8.5,

370   presented the smallest suitable area for the species (Fig. 6). Although it presented smaller

371   temperature fluctuations compared to other scenarios, in the RCP 8.5 scenario *P. caribaeorum*

372   would lose potential habitats in both the northernmost and southernmost ranges of its

373   distribution, without any gain in suitable areas due to a drastic decrease in salinity and pH values.

374   Freshwater intrusions from the La Plata and Amazon rivers would influence the species' habitat

375   along the Brazilian shelf, restricting its distribution to northeastern Brazil. Similarly, the

376   Mississippi River plume would decrease the adequacy for the species in the north. In general,

377   when looking at changes in salinity, pH, and temperature for any climate scenario, the variations

378   are more intense in the north and south via the intrusion of polar and temperate currents into the

379   continental shelf. These differences alter the habitat of *P. caribaeorum* and are more prominent

380   in the Southern Hemisphere.

381   Regions such as the southern, southwestern, and western Caribbean, the southern Gulf of

382   Mexico, the Bahamas, the Greater Antilles, and northeastern and eastern Brazil would retain

383   suitable areas for the species under any climate scenario (Fig. 7), identifying them as refuges for

384   the species under adverse environmental conditions (Haffer, 1969). Except for the Brazilian

385   coast, all of these regions are within the Caribbean Province, which is considered the center of

386   ~~biodivesity~~ in the Atlantic Ocean (Rocha et al., 2008; Briggs & Bowen, 2013). Under intense

387   climate stress, it is likely that both *P. caribaeorum* and other invertebrate organisms will have

388   their distributions restricted toward this diversity-gathering hotspot in the Atlantic Ocean.

389   The difference in suitable areas between the Northern and Southern Hemispheres

390   suggests asymmetrical species distribution, with the Northern Hemisphere containing larger

391   suitable habitats. This may result from differences in the oceanographic conditions of both

392   basins. In contrast to other oceans, the Atlantic Ocean presents a net flux of superficial water

393   transport to the north, with the Labrador Current being much weaker than the Malvinas Current;

394   therefore, its principal component is toward the north (Onken, 1994). This occurs mainly because

395   of thermohaline circulation and wind, both of which are likely to be altered by climate change

396   (IPCC, 2014), in turn helping to remodel the distribution of marine organisms, as predicted in

397   this study.

398

399   *4.4 Likely changes in reef communities*

400   Studies have shown that *P. caribaeorum* coexists with many other organisms, especially

401   algae such as *Caulerpa racemosa* var. *peltata*, *Bryopsis* spp. (Magalhães et al., 2015),

402   *Sargassum, Halimeda, Laurencia, Dictyota, Dictyopteris*, *Ulva,* and coralline algae (Steiner et

403   al., 2015). Macroalgae are common in coral reefs, sometimes dominating the community and

404   competing for space with corals (Tanner, 1995; Bruno et al., 2009). The disappearance of *P.*

405   *caribaeorum* from many Brazilian reefs in the Abrolhos Bank would imply a change in the reef

406   communities. It is possible that with the vanishing of *P. caribaeorum*, colonization of the

407   available space would first be by algae, most likely cyanobacteria, due to their fast growth rate,

408   especially in nutrient-poor environments (Villaça & Pitombo, 1997). However, the composition

409   of the new community will depend on multiple factors, from changes in recruitment rates,

410   growth, and mortality to changes in nutrient concentrations and herbivory (Littler, Littler &

411   Taylor, 1983; Sandin & McNamara, 2012); community resilience is another factor (Roff &

412   Mumby, 2012).

413   Regarding the colonization of new areas by *P. caribaeorum*, the temperate region of the

414   northwestern Atlantic would see its suitable area increased under RCP 2.6 and 4.5, around Cape

415   Hatteras and Chesapeake Bay. Zoanthids have the potential to disperse to great distances due to

416   their long larval stage (Ryland et al., 2000; Polak et al., 2011) and asexual reproduction (Acosta,

417   Sammarco & Duarte, 2005), alongside their potential to raft on floating objects and boats (Santos

418   et al., 2016). Thus, it is possible that the colonization of *P. caribaeorum* in the northwestern

419   Atlantic would occur under these climate scenarios for hard bottom environments.

420   Nicaragua's coast, which is part of the southwestern Caribbean region, was particularly

421   important for the species due to the increase in potential habitat area under RCP 4.5 and 8.5 (Fig.

422   5 and 6). Few studies were conducted about the benthic community in that region, which

423   presents high coverage of algae of the genera *Dictyota* and *Padina*, corals such as *Orbicella*

424   *annularis*, *Agaricia* spp., *Porites* spp., *Acropora palmata*, and *Millepora alcicornis,* and lower

425   coverage of sponge and soft corals (Kramer et al., 2000). The same study discusses the

426   likelihood of a phase shift in the coming years due to natural disturbances and climate change.

427   Phase shifts from reef-building corals to zoanthids were previously reported in the western

428   Atlantic (Cruz et al., 2015a), where they reduced fish diversity associated with the reefs (Cruz et

429   al., 2015b), and have the potential to adversely affect regional fisheries and tourism, which are

430   main income sources for the local populatio.

431   Although it was assumed in this work, it is not expected that all individuals will be

432   affected in the same way by climate change. It is known that, at smaller scales, differences

433   between symbiont algae (Kemp et al., 2006), as well as the anthozoan's plasticity (Costa et al.,

434   2011), can result in distinct outcomes for different populations under climate change. Average

435   and maximum temperatures had small contributions to the model and were not considered here;

436   however, it is known that surface waters are likely to experience an increase in temperature,

437   especially in tropical areas (IPCC, 2014). The ability to endure such changes will also play a role

438   in *P. caribaeorum's* distribution. The authors highlight here the importance of future

439   experimental work on temperature stress on key organisms, such as *P. caribaeorum,* to better

440   understand the future of tropical reef communities.

441   It is possible that, due to the scale of the problem, some local variations were not

442   accounted for, such as the discharge of small rivers around the Gulf of Mexico region. Smaller

443   scales and regional studies should use higher resolution data for this matter. Sea level rise can

444   modify wave stress atop coral reefs, favoring the colonization of *P. caribaeorum* over other

445   organisms, including ~~sea mat corals~~ (Rabelo et al., 2015). This effect was not considered in this

446   study because the IPCC forecast for sea level rise did not surpass 0.8 meters, which is smaller

447   than the error of the bathymetric data used in this work.

448

449   **5. Conclusions**

450

451 The present habitat of *P. caribaeorum* can be characterized by high salinity values, marine

452 pH, and a small to moderate range of temperature in coastal and shallow environments. The

453 species' current distribution in the western Atlantic Ocean is restricted to warm provinces,

454 identifying it as a coastal and warm-water species, together with shallow water corals. According

455 to this study, this organism's potential distribution is likely to change by the year 2100. It is

456 possible that, under low to mild anthropogenic impacts (RCP 2.6 and 4.5), the species'

457 distribution will be extended northward and will face a decrease of suitable habitat in the

458 southernmost range of its distribution under any climate scenario. Under the scenario with the

459 highest anthropogenic impacts (RCP 8.5), novel suitable areas poleward were not predicted, and

460 only one-half of its potential habitat area would be retained when compared to the present. Under

461 any climate scenario, the Caribbean Sea remained suitable for the species, characterizing this

462 region as a possible refuge. Upwelling regions, such as Cape Frio and northern Colombia, could

463 provide a refuge for this species as well, diminishing the local impacts of climate changes.

464 Although community changes were discussed according to the available literature, biological and

465 oceanographic processes not considered in this study may play an important role in the outcome

466 of these changes.

467

468

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470

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476

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744

Figure 1

Study area and major currents and rivers.

Underwater picture of (a) a *Palythoa caribaeorum* colony and (b) the study area (gray) with main rivers (black), adapted from the map "World Major Rivers" from ESRI; the schema of the main cold surface currents (gray) and warm surface currents (black) is adapted from Talley et al. (2011). Photo credit: Leonardo Durante.
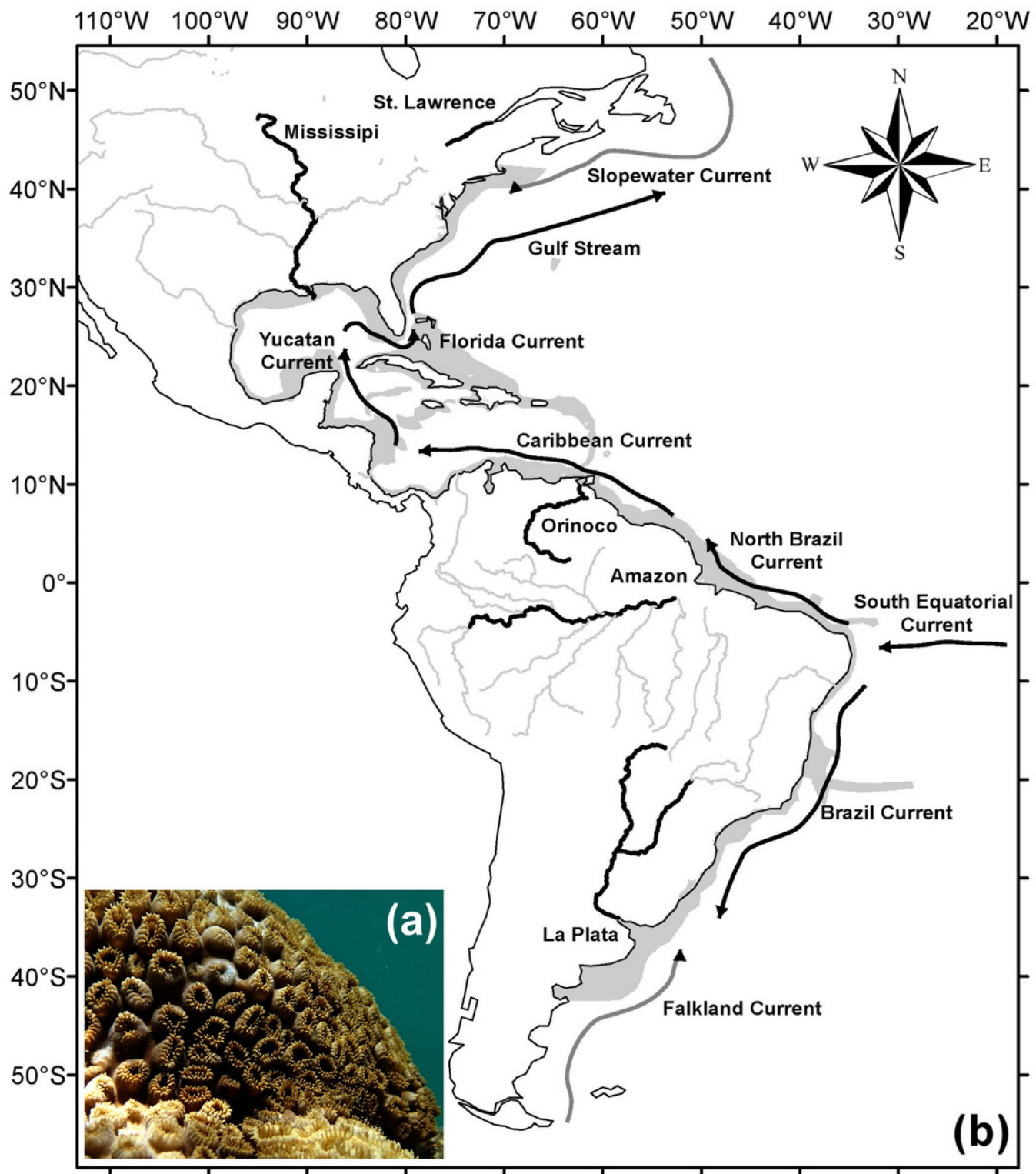
Figure 2

Occurrence points and Marine Ecoregions included in the study area

Study area and occurrence points of *P. caribaeorum* after filtering, with the Marine

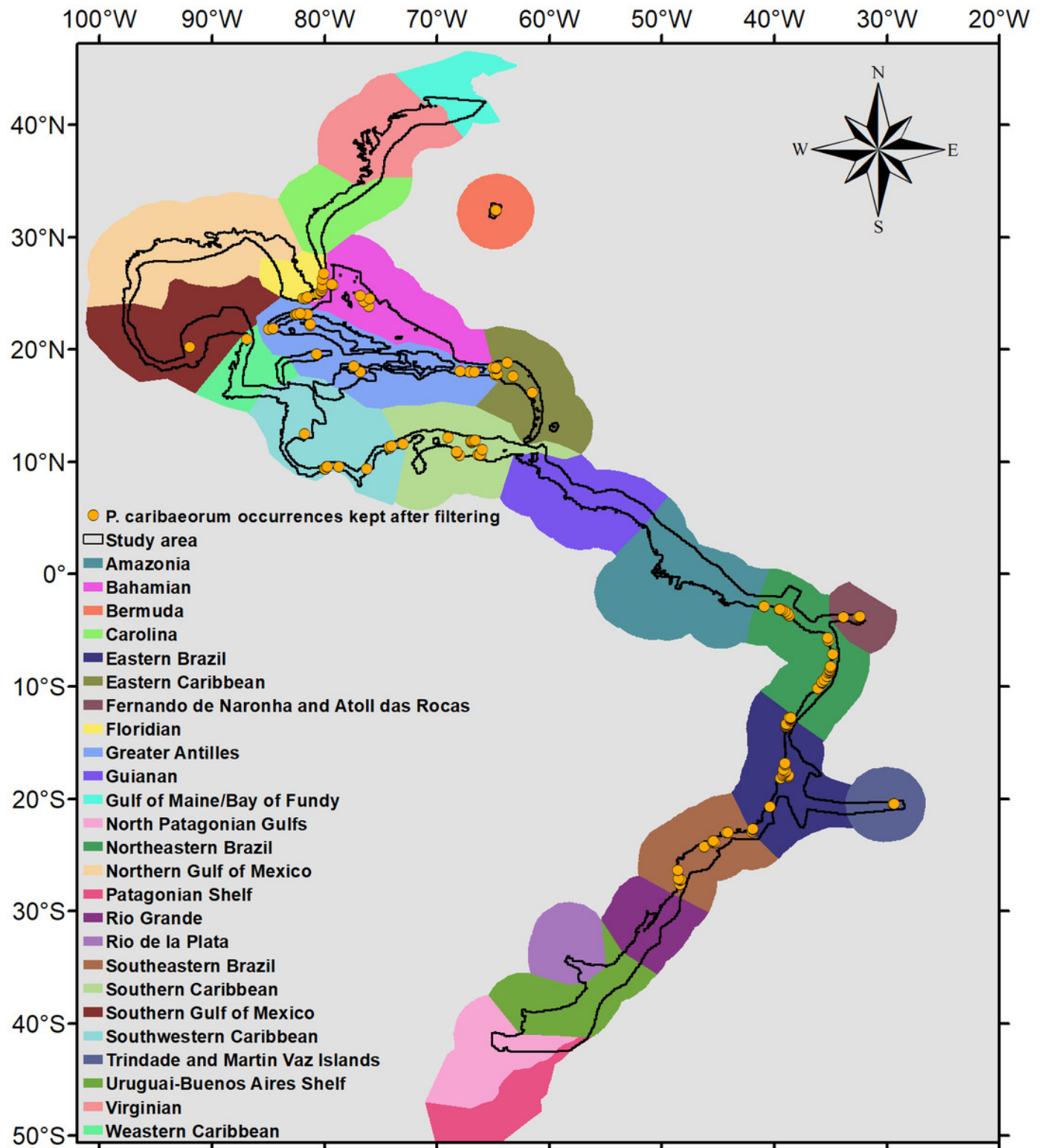Ecoregions of the World as a reference (Spalding et al., 2007).

Legend:
- ● P. caribaeorum occurrences kept after filtering
- ▢ Study area
- Amazonia
- Bahamian
- Bermuda
- Carolina
- Eastern Brazil
- Eastern Caribbean
- Fernando de Naronha and Atoll das Rocas
- Floridian
- Greater Antilles
- Guianan
- Gulf of Maine/Bay of Fundy
- North Patagonian Gulfs
- Northeastern Brazil
- Northern Gulf of Mexico
- Patagonian Shelf
- Rio Grande
- Rio de la Plata
- Southeastern Brazil
- Southern Caribbean
- Southern Gulf of Mexico
- Southwestern Caribbean
- Trindade and Martin Vaz Islands
- Uruguai-Buenos Aires Shelf
- Virginian
- Weastern Caribbean

Figure 3

Suitable habitat for *P. caribaeorum* in the present

Details for (a) southeastern Brazil, (b) southern Gulf of Mexico, (c) southwestern Caribbean, (d) southern Caribbean, and (e) Floridian regions.
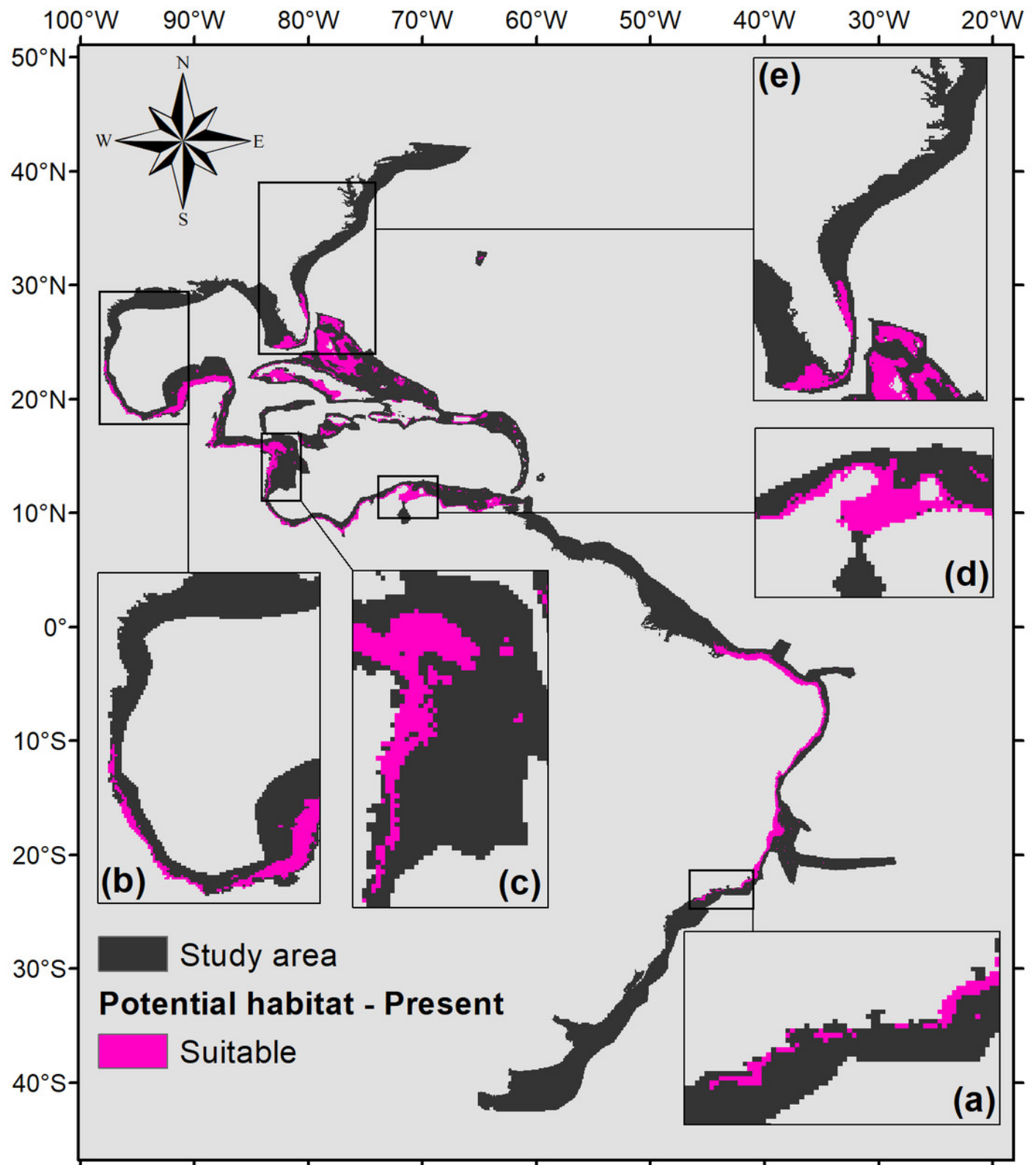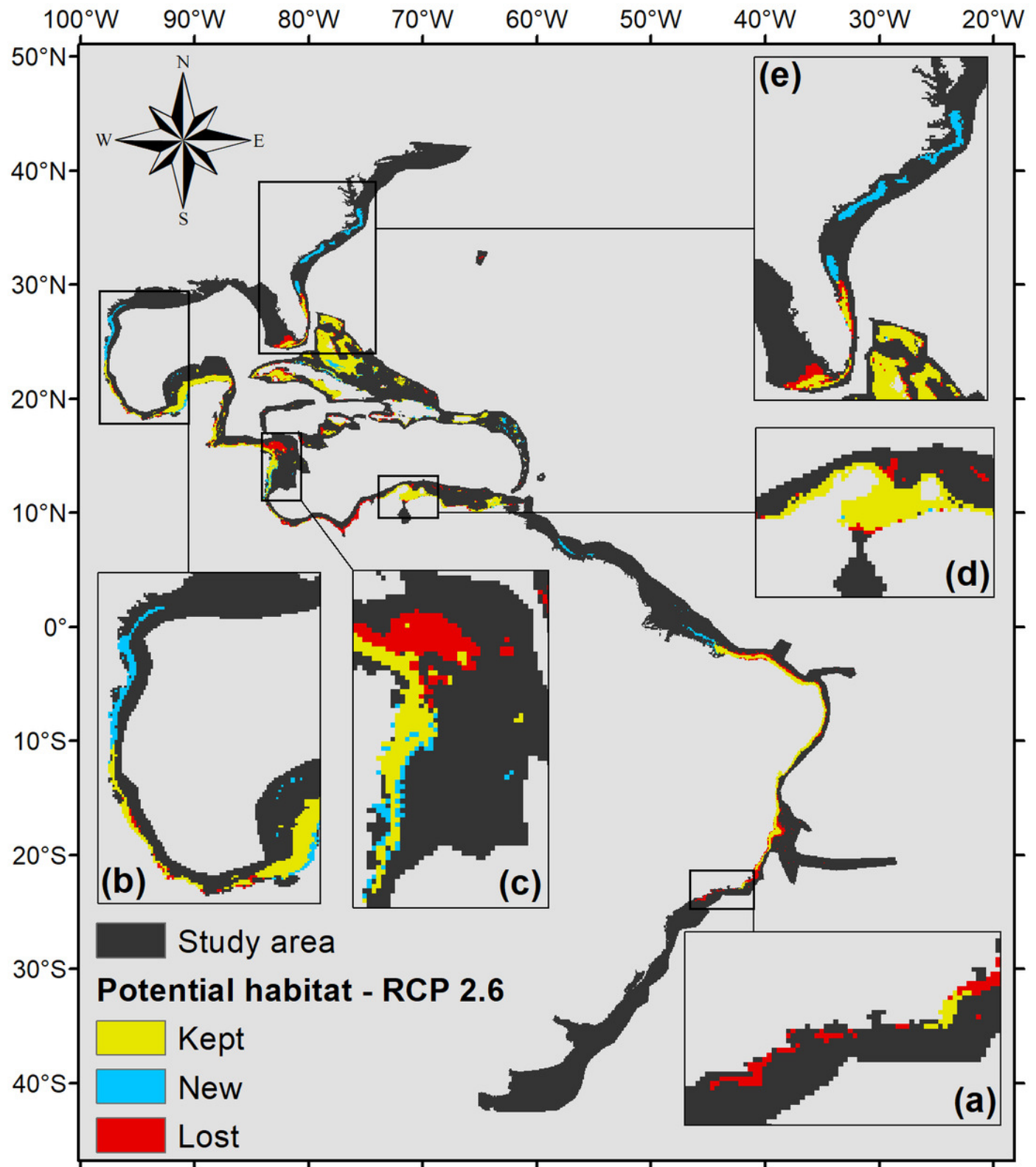
Figure 4

Suitable habitat for *P. caribaeorum* for the year 2100 under the RCP 2.6 climate scenario

Suitable habitat for *P. caribaeorum* for the year 2100 under the RCP 2.6 climate scenario, which includes regions with retained, new, and lost suitability compared with the present. Details for (a) southeastern Brazil, (b) southern Gulf of Mexico, (c) southwestern Caribbean, (d) southern Caribbean, and (e) Floridian regions.
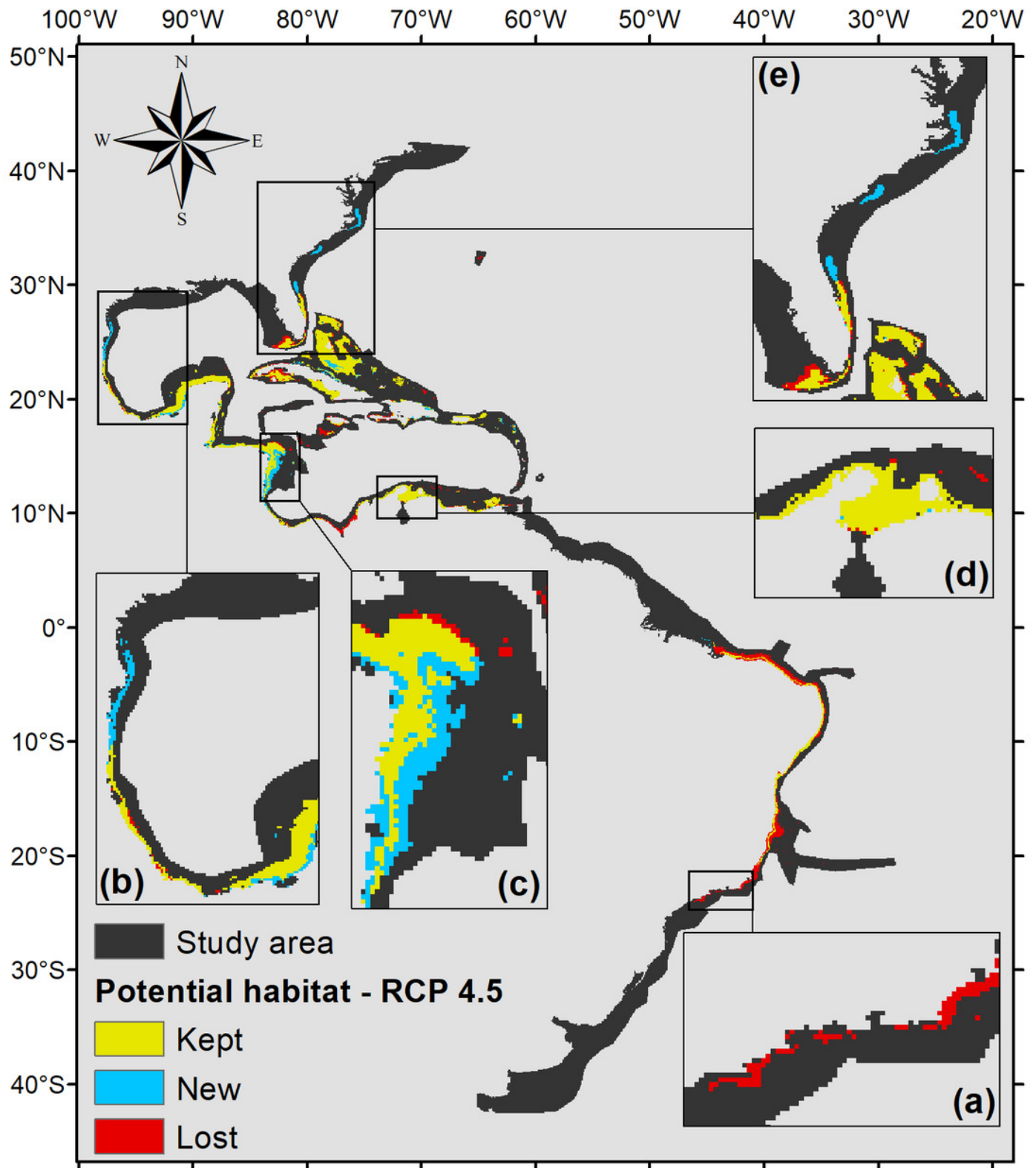
Figure 5

Habitat suitability map for *P. caribaeorum* in the year 2100 under the RCP 4.5 climate scenario.

The map includes regions with retained, new, and lost suitability compared with the present.

Details for (a) southeastern Brazil, (b) southern Gulf of Mexico, (c) southwestern Caribbean,

(d) southern Caribbean, and (e) Floridian regions.

Figure 6

Habitat suitability map for *P. caribaeorum* in the year 2100 under the RCP 8.5 climate
scenario.

The map includes regions with retained, new, and lost suitability compared with the present.

Details for (a) southeastern Brazil, (b) southern Gulf of Mexico, (c) southwestern Caribbean,

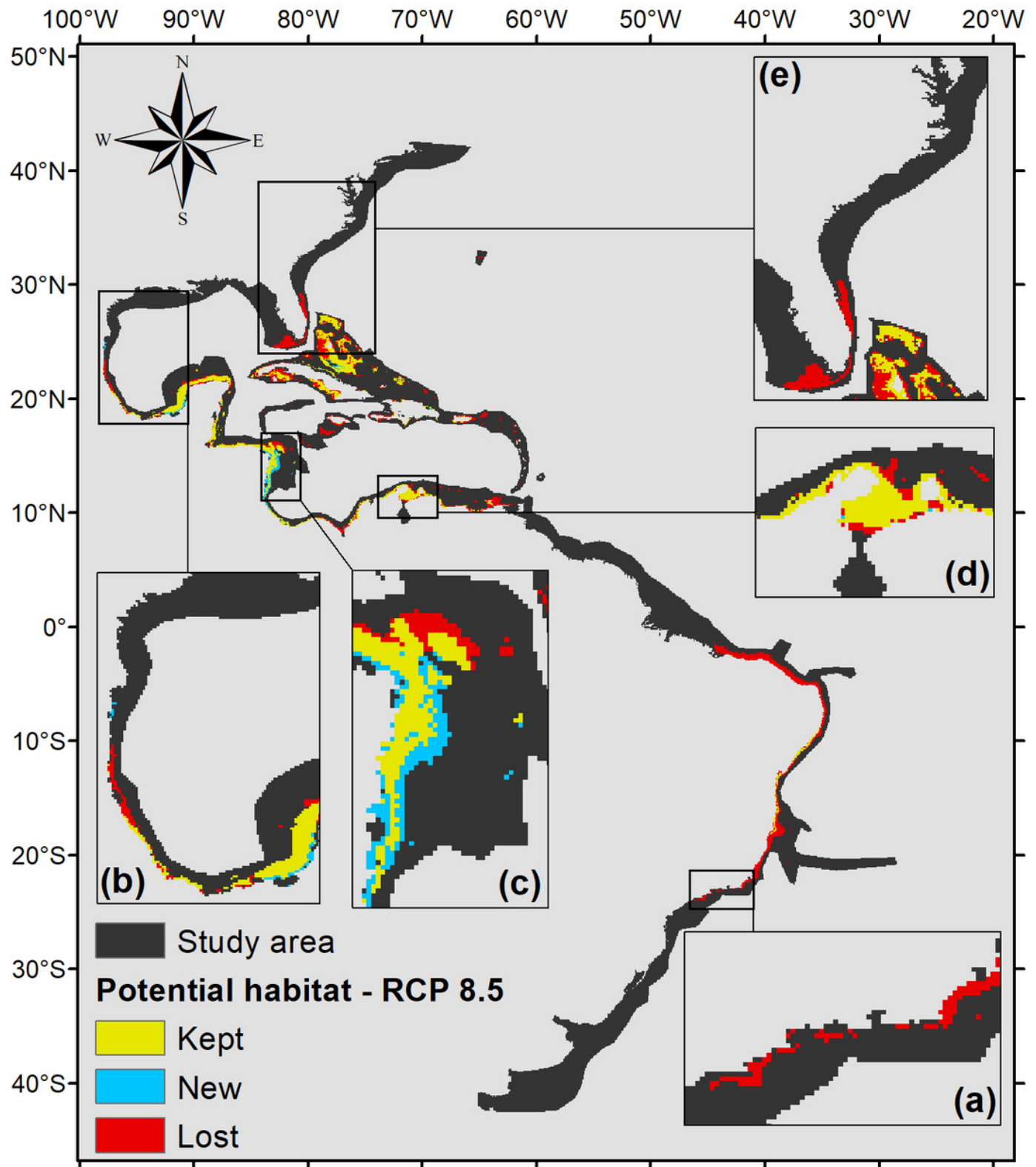(d) southern Caribbean, and (e) Floridian regions.

Figure 7

Map of potential habitat for *P. caribaeorum* in the year 2100 under any climate scenario (pink)

Details for (a) southeastern Brazil, (b) southern Gulf of Mexico, (c) southwestern Caribbean,
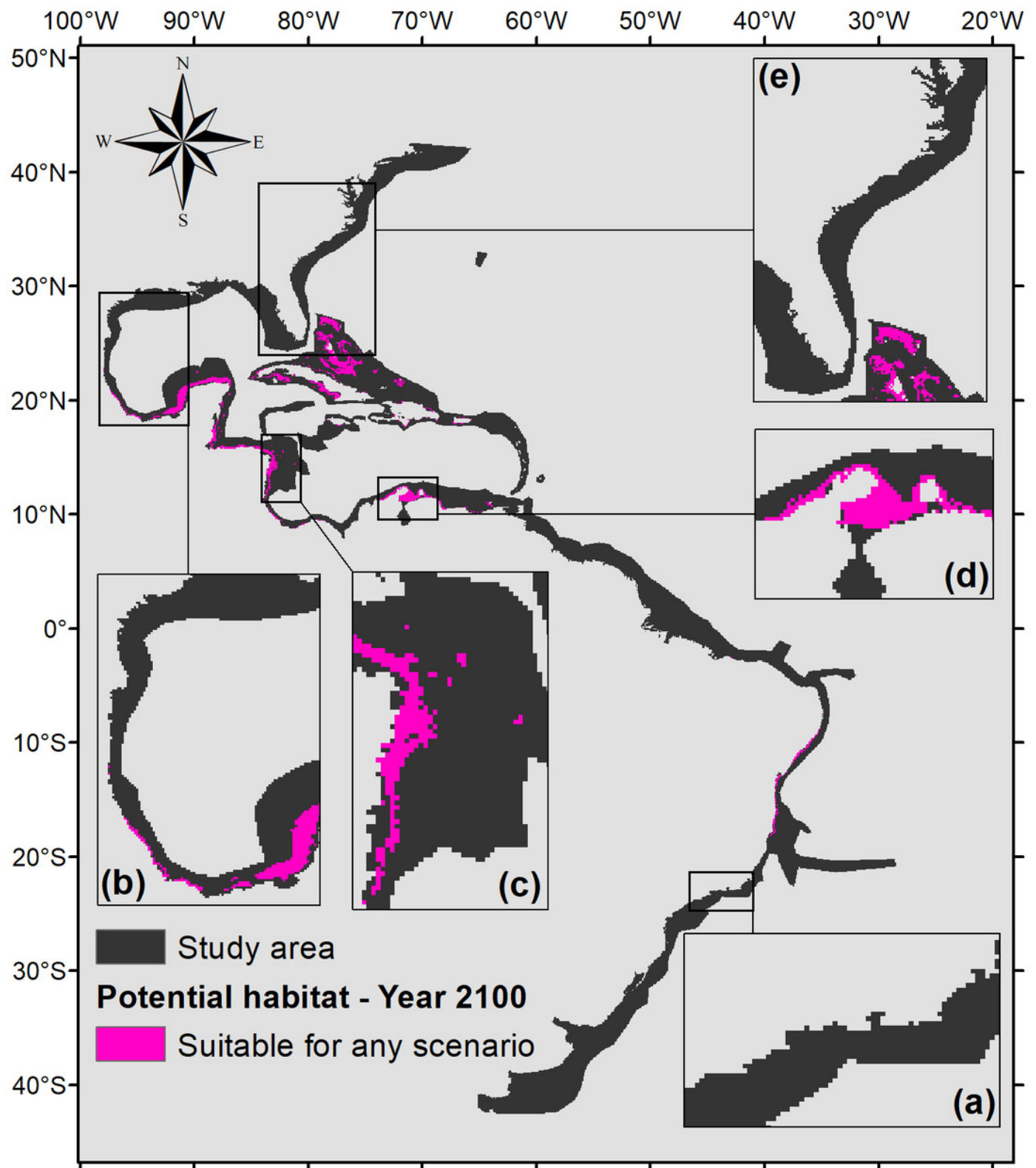
(d) southern Caribbean, and (e) Floridian regions.

Table 1(on next page)

Details about the variables retrieve from Bio-Oracle dataset and the layers kept in the final distribution model for *P. caribaeorum*.

Variables	Unit	Measurement	Measurement transformations	Number of layers	Kept in the final model
Calcite concentration	mol/m³	Remote sensor	Average	1	Average concentration
Chlorophyll-a concentration	mg/m³	Remote sensor	Average, minimum, maximum and range	4	Maximum concentration
Cloud coverage	%	Remote sensor	Average, minimum and maximum	3	-
Difusive atenuation coeficient (490 nm)	1/m	Remote sensor	Average, minimum and maximum	3	-
Photosynthetic available radiation	Einstein/m²/day	Remote sensor	Average and maximum	2	-
Air temperature above sea surface	°C	Remote sensor	Average, minimum, maximum and range	4	-
Sea surface temperature	°C	Remote sensor	Average, minimum, maximum and range	4	Range
Dissolved oxygen	ml/l	In situ	Diva interpolation	1	-
Nitrate	µmol/l	In situ	Diva interpolation	1	-
pH	-	In situ	Diva interpolation	1	Diva interpolation
Phosphate	µmol/l	In situ	Diva interpolation	1	-
Salinity	PSU	In situ	Diva interpolation	1	Diva interpolation
Silicate	µmol/l	In situ	Diva interpolation	1	-

1

2   Table 1: Details about the variables retrieve from Bio-Oracle dataset and the layers kept in the final distribution model for *P.*

3   *caribaeorum.*