

Modeling impacts of climate change on the potential habitat of an endangered Brazilian endemic coral: discussion about deep sea refugia

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Abstract

Climate and environmental changes are determinant for coral distribution and their very existence. Effects of such changes on distribution can be predicted through ecological niche models, anticipating suitable habitats for subsistence of species. *Mussismilia harttii* is one of the most widespread Brazilian endemic reef building corals, and in increasing risk of extinction. The ecological niche models were used through the maximal entropy approach to determine the potential present and future habitats for *M. harttii*, estimating suitable habitat losses and gains at the end of the 21st century. For this purpose, records published in the last 20 years and current and future environmental variables were correlated. The models were evaluated through the Area Under the Operational Curve of the Receiver, using the AUC values and additionally AUCratio, a new approach using independent occurrence data. Both approaches showed that the models performed satisfactorily in predicting areas of potential habitat for the species. The results showed that the area to the south of the São Francisco River is the most suitable for the current habitat of the species, and that nitrate was the most influential variable for the models. Simultaneously, the salinity and temperature exerted greater influence for the models in future scenarios, in which current northernmost and southernmost limits of the potential habitats shifted towards deeper regions, so these deeper sites may serve as a refugia for the species in global warming scenarios. Coral communities at such depths would be less susceptible to the impacts of climate change on temperature and salinity. However, deep sea is not free from human impacts and measures to protect deeper ecosystems should be prioritized in environmental policy for Brazilian marine conservation.

Introduction

Coral reefs are one of the most valuable ecosystems on earth [1] providing a number of ecological services [2], such as shelter for associated fishes [3] and crustaceans [4, 5, 6, 7], also serving as substrate for coralline algae [8, 9]. Stable water

conditions are determinant for the maintenance of living corals on reefs [10]. However, effects of climate changes put at least 50 % of shallow-water species in critical risk of extinction in the next 20 years [11, 12].

In the Southwestern Atlantic, coastal reef communities occur along of 3000 km of the Brazilian coastline [13], showing high endemism of reef-building species [14]. Four of those species belong to the genus *Mussismilia*, commonly known as brain-corals [15, 16, 17]. Although molecular assessments on *Mussismilia* are still rare [18], the distinctiveness between species is well established, allowing rapid identification on field [15]. The genus has at least two species in risk of extinction: *M. braziliensis* and *M. harttii* [19]. The first is restricted to shallow reefs of Bahia State and Abrolhos reefs, whereas the latter is found from the coast of Ceará to Espírito Santo States (from -3.822 to -40.583 latitud), commonly at depths of 2 - 6 m, and isolated records of up to 80 m [20].

Mussismilia harttii shows the lowest coverage percentages among its congeners [21], currently with populations in severe decline [19]. However, its conservation status at the IUCN (International Union for Conservation of Nature) database is still regarded as “Data Deficient” (DD). In contrast, the “Red Book of the Brazilian Fauna Threatened with Extinction” (2014, 2018), classifies the species as EN (Endangered) [19].

The distribution of marine organisms, such as corals, is determined by interactions of physical, chemical and biological factors [22]. Based on that, Ecological Niche Models (ENMs) approaches can provide information on the potential distribution of species within specific study areas [23]. ENMs associates environmental or spatial data to a set of distributional informations, such as distribution records [24], to outline the environmental conditions in which a given species may occur [25] indicating the most suitable areas for its occurrence [26, 27]. These models have been broadly applied to: prevent marine bioinvasions [28], conservation management planning [29], and especially to studies on climate changes [30, 31], predicting possible shifts on geographical distributions of key species [32].

The ENM also can be used to calculate the relative adequacy of a given habitat occupied by a species and to estimate changes in such suitability over time [33]. In the present study, we applied ENMs to generate maps of Current Potential Habitat (CPH) and Future Potential Habitat (FPH) for *M. harttii* at the end of the 21st century. These maps indicate potentially suitable areas and estimate habitat gains and losses in the

different climatic scenarios projected. The projections will serve as tools for management plans and reef conservation in the southwest Atlantic reefs.

Materials and methods

Study area

The studied area comprises the Brazilian Exclusive Economic Zone - EEZ, in which *M. harttii* potentially occurs, from the intertidal zone to 100 m deep [34], based on all current records of its distribution [35, 36]. The study area also includes the priority areas for conservation according the Brazilian Ministry of the Environment (Portaria N° 19, of March 9, 2016 - ICMBio) (Fig 1).

Fig 1. Map of the study area and occurrence records. Study area (Brazilian EEZ up 100 m), priority area for conservation of *M. harttii* and filtered occurrence data (one point in each pixel of 1km²).

Occurrence records

An extensive search was made in specialized literature through academic indexing portals using the terms "Mussismilia", "harttii", "Brazil", and "Brasil", with publications containing precise geographic information (latitude, longitude and/or maps). Records of occurrence without georeferenced data were not used in the analyzes. These publication records were used to discuss the suitable area provided by the models. The search focused on records of *M. harttii* in the last two decades, avoiding the temporal decay in the quality of presence data due to the inherent dynamism of natural systems [37]. Sometimes, these data may be influenced by drastic phenomena, such as the local extinction of species [38] or changes in its distribution and abundance patterns [39]. Sampling bias on occurrence data are also common in areas of greater accessibility (more studied) because of regional interests [40]. This may reduce the model's ability to predict the spatial data independence [41]. Alternatively, simple rarefaction method was used to reduce the autocorrelation of such points of occurrence,

using SDMtoolbox v.2.2 [42], in which they were filtered (Fig 1), reducing data to only one point per pixel of 1km², which was selected for modeling.

Species data collected *in situ*, from reefs located in the States of Paraíba, Pernambuco, Alagoas, Bahia, as well as independent species presence data, were not used during the modeling process, but *a posteriori* to evaluate the model [43].

Selection of environmental layers

The environmental characterization variables provided by Bio-oracle available online (www.bio-oracle.org) were used. This global database provides current *in situ* and satellite-based oceanic information [22]. Bio-oracle also provides future variables based on the projections made by the International Panel on Climate Change (IPCC) for 2100 [44], in scenarios with different levels of greenhouse gas concentration (Representative Concentration Pathways - RCPs) [45]. These variables were cut to the extent of our study area [46] and re-sampled for the 30 arc seconds resolution (~ 1 km), as it is more indicated in local scale studies [47] and also due to low dispersal efficiency of the species.

The number of variables used may depend on the number of occurrence records [48], and when there are few records, such as endemic or threatened species, a small number of variables may be sufficient [49]. In order to generate the CPH map, 12 uncorrelated variables (Table 1) were selected through Pearson correlation matrix [50] with $r < 0.8$ (S1 Appendix), all ecologically or physiologically relevant [40].

The projections of the IPCC for the year of 2100, developed by different research groups [51, 52], provide likely ranges of global temperature in future scenarios for population, economic growth and carbon use. These projections, called Representative Concentration Pathways (RCPs) [44], were used to model the *M. harttii* FPH in three different scenarios: decrease in emissions (RCP 2.6), stabilization of emissions (RCP 4.5) and increase in emissions (RCP 8.5) [53, 54, 55].

Modeling process approach

The maximum entropy approach MaxEnt v. 3.3.3 [56, 57, 58] was used to model the potential distribution of *M. harttii*. MaxEnt is one of the most widely used algorithms for ENMs [59], because it presents consistent predictive performance

compared to other algorithms [60], especially when the number of occurrence points is low [43, 61].

Table 1. Details about the 12 Bio-Oracle variables used in the modeling process.

Remotely sensed data	Variable	Sensor	Temporal range	Original spatial resolution	Unit
	Calcite.mean	Aqua-MODIS §	2002-2009	5 arc min (9.2 km)	mol / m ³
	Diffuse attenuation.max	Aqua-MODIS §	2002-2009	5 arc min (9.2 km)	m ⁻¹
	Temperature.max	Aqua-MODIS §	2002-2009	5 arc min (9.2 km)	° C
	Photosynthetically available radiation.max	SeaWiF§	1997-2009	5 arc min (9.2 km)	Einstein / m ² / day
	Chlorophyll.range	Aqua-MODIS §	2002-2009	5 arc min (9.2 km)	mg / m ³
	Primary productivity.max	PISCES	2002-2009	5 arc min (9.2 km)	g / m ⁻³ / day ⁻¹
	Present.surface.phytoplankton.min	PISCES	2002-2009	5 arc min (9.2 km)	mmol / m ⁻³
	Current velocity.min	ORAP	2002-2009	5 arc min (9.2 km)	m / s ⁻¹
In situ measured oceanographic data	Variable	Database	Temporal range	Number of data points	Unit
	Salinity.max	World Ocean database 2009 †	1961-2009	532377	PSS
	Dissolves oxigen.min	World Ocean database 2009 †	1898-2009	540582	ml / l
	Nitrate.max	World Ocean database 2009 †	1928-2009	189530	µmol / l
	pH	World Ocean database 2009 †	1910-2007	117833	-

Table 1. Information on data searching and acquisition, and data availability of the 12 Bio-Oracle variables used in the modeling process, highlighting the five variables used to generate the Current Potential Habitat (CPH) model for *Mussismilia harttii*.

In the first step, we used relevant non-correlated variables and the filtered points of occurrence (Fig 1). The algorithm was calibrated using standard parameters [62], 1 % fixed omission threshold [63], 75 % of the records of occurrence for training and 25 % for test [64] (S2 Appendix), bootstrap (100 replicates) and maximum background number (5000). The Jackknife function of MaxEnt [65] was used to identify the percentage of contribution for each variable. In the second step, the five variables with the highest percentage of contribution (Table 1), the same points of occurrence and the same calibration of the MaxEnt were used to generate the CPH map.

To design the *M. harttii* FPH in the three future scenarios, MaxEnt was calibrated with the same parameters of steps 1 and 2, and also with: mean temperature, salinity and current velocity for the year 2100.

Suitability area

Based on threshold values, the continuous maps of CPH and FPH were transformed into binary maps of suitability or probability [66], in which pixels are classified as "adaptive / presence" and "non-adaptive / absence"[43].

Evaluation of the models

The Area Under the Receiver Operating Curve (AUC-ROC) is the most common metric to evaluate the accuracy of models [67]. AUC values ≤ 0.5 indicate that the model failed to perform better than random expectations, whereas values close to 1 indicate a good performance of the model [68]. In practice, the AUC-ROC is calculated based on a series of trapezoids [69], with the curve essentially "connecting the points" representing the different thresholds of the prediction [70]. This approach is used when input data is partitioned, in this case into training and test data [71]. When biotic data are divided into presence and absence (background), the AUC measures the discriminatory ability of the model to correctly predict the origin of these data if randomly selected [43].

Although the use of AUC-ROC for model evaluation is not questioned herein [72], we additionally used the partial ROC (AUCratio), an independent cutoff threshold metric where significant values are above 1 [73]. The AUCratio is a ratio between the predicted model AUC and null expectation [70] that a model generated with random data does not have a better prediction than the models generated with the input data

[74]. We calculated the ratio of AUC_{random} (at level of 0.5) and the AUC_{actual} (calibrating 5% of omission and 500 bootstrap interactions) using the predicted distribution model [68] and independent occurrence records (S3 Appendix), through the package "ntbox" v.0.2.5.3 for Rstudio [75], to ensure greater robustness in model analysis [76].

Results

One hundred and fifteen occurrence points were used for the modeling, of which 87 for training and 28 for testing and for external validation 24 points of occurrence were used. The variables with highest percentages of contribution and used to model CPH were, respectively: maximum nitrate (44.9 %); mean calcite (25.9 %); maximum salinity (21.3 %); maximum diffuse attenuation (5.8 %); and maximum temperature (2 %).

The maximum training sensitivity plus specificity logistic threshold used to generate the binary maps maximized the sensitivity and specificity of the model [77]. This threshold is best suited for studies on rare or endangered species [74], as it reduces the over-prediction rate and selects only areas with high environmental suitability [43]. The thresholds of CPH (0.1391) and FPH (RCP 2.6- 0.1872, RCP 4.5- 0.1606 and RCP 8.5- 0.1702) show that a random prediction in a fraction of the same area does not have a better prediction than the points used in the test step [74].

The CPH of *M. harttii* represents a suitable area corresponding to 0.0418 % of the study area (Fig 2; Table 2). The sites north of the São Francisco River shows a smaller suitability (25,7 %) (Figs 2 a and b; Table 2), whereas the largest suitable areas are concentrated southwards of the São Francisco River (74,3 %) (Figs 2 c, d and e; Table 2). The AUC (S4 Appendix) and AUCratio (S5 Appendix) of the model were 0.979 and 1.934446, respectively.

Fig 2. Map of Current Potential Habitat (CPH) of *Mussismilia harttii*. Highlighted figures (a, b, c, d, e) show concentrations of the highest number of suitable areas: a) Rio Grande do Norte and Paraíba States; b) Pernambuco and Alagoas States; c) north of Bahia State; d) south of Bahia State; and e) Espírito Santo State.

Table 2. Areas of suitable habitats

Model	North area	South area	Total area	New areas (km ²)		Lost areas (km ²)		Kept areas (km ²)	
	(km ²)	(km ²)		North	South	North	South	North	South
CPH	7951.5	22943.8	30895.3						
RCP 2.6	11720.8	38712.4	50433.2	8731.7	17403.5	962.4	5634.4	2989.1	21309.1
RCP 4.5	13375.1	42987.6	56362.7	10132.1	20735.7	708.5	4691.5	3243	22252
RCP 8.5	13581.3	43086.6	56667.9	10298.3	21545.7	668.4	5402.5	3283	21540.9

Table 2. Values of current potential habitat areas (CPH) and future potential habitat areas for *Mussismilia harttii* in three different scenarios of climatic projections for the year 2100 (RCP 2.6, 4.5, 8.5); including the new, lost and kept areas in each region, north and south of the São Francisco River.

The three future distribution scenarios for *M. harttii* (RCP 2.6, RCP 4.5 and RCP 8.5) were characterized by an increase of suitable areas for the persistence of the species (67 - 88 %) (Table 2), but there was a significant reduction of suitable areas at the southern end of the distribution, at the Espírito Santo State (Figs 3, 4 and 5e). In all scenarios of FPH the salinity was the variable with the greatest contribution to the models (> 80 %), followed by temperature (~ 13 %) and current velocity (< 5 %).

In a scenario of reduction of greenhouse gas emissions (RCP 2.6), the FPH of *M. harttii* represents a suitable area corresponding to 0.0805 % of the study area (Fig 3) (increasing 67 % of the CPH). The north of the São Francisco River shows a smaller area (23,2 %) (Figs 3a and b; Table 2), whereas the largest suitable areas are also concentrated to the south of the São Francisco River (76,8 %) (Figs 3c, d and e; Table 2). The AUC (S6 Appendix) and AUCratio (S7 Appendix) of the model were 0.975 and 1.914904, respectively.

Fig 3. Map of Future Potential Habitat (FPH) of *Mussismilia harttii* in a scenario of reduction of greenhouse gas emissions (RCP 2.6) in the year 2100. FPH includes regions with kept, new, and lost suitability compared with the present (CPH). Highlighted figures (a, b, c, d, e) show concentrations of the highest number of suitable areas. a) Rio Grande do Norte and Paraíba States; b) Pernambuco and Alagoas States; c) north of Bahia State; d) south of Bahia State; and e) Espírito Santo State.

In a scenario in which the emissions of greenhouse gases stabilize (RCP 4.5), the FPH of *M. harttii* represents a suitable area corresponding to 0.0881 % of the study area (Fig 4; Table 2) (increasing 87 % of the CPH). As with the previous scenarios, the sites northwards of the São Francisco River have a smaller suitable area (23.7 %) (Figs 4a and b; Table 2), while the largest areas of adequacy are concentrated southwards of the São Francisco River (76.3 %) (Figs 4c, d and e; Table 2). The AUC (S8 Appendix) and AUCratio (S9 Appendix) of the model were 0.973 and 1.912065, respectively.

Fig 4. Map of Future Potential Habitat (FPH) of *Mussismilia harttii* in a scenario of reduction of greenhouse gas emissions (RCP 4.5) in the year 2100. FPH includes regions with kept, new, and lost suitability compared with the present (CPH). Highlighted figures (a, b, c, d, e) show concentrations of the highest number of suitable areas. a) Rio Grande do Norte and Paraíba States; b) Pernambuco and Alagoas States; c) north of Bahia State; d) south of Bahia State; and e) Espírito Santo State.

In a scenario with increased greenhouse gas emissions (RCP 8.5), the FPH of *M. harttii* represents a suitable area corresponding to 0.0876 % of the study area (Fig 5; Table 2) (increasing 88 % of the CPH). The sites north of the São Francisco River again shows a smaller area (23.9 %) (Figs 5a and b; Table 2), whereas the largest suitable areas are concentrated southwards of the São Francisco River (76,1 %) (Figs 5c, d and e; Table 2). The AUC (S10 Appendix) and AUCratio (S11 Appendix) of the model were 0.973 and 1.911017, respectively.

Both current and future suitability areas for *M. harttii* are mostly within the Preservation Area for this species, with exception of Todos os Santos Bay, Bahia State (Figs 2, 3,4 and 5c). The three scenarios of future (year 2100) distribution of the species showed bathymetric expansion towards deeper areas, with a latitudinal restriction by the

loss of suitable areas in the northernmost and southernmost limits of its distribution. (Figs 3, 4 and 5; Table 2).

Fig 5. Map of Future Potential Habitat (FPH) of *Mussismilia harttii* in a scenario of reduction of greenhouse gas emissions (RCP 8.5) in the year 2100. FPH includes regions with kept, new, and lost suitability compared with the present (CPH). Highlighted figures (a, b, c, d, e) show the concentration of the highest number of suitable areas. a) Rio Grande do Norte and Paraíba States; b) Pernambuco and Alagoas States; c) north of Bahia State; d) south of Bahia State; and e) Espírito Santo State.

In the current scenario (CPH), 60 % of the suitable areas are shallower than 20 m deep, 30 % between 20 - 50 m, and there are no suitable areas for the species north of the São Francisco River beyond 50 m. In the south, 0.87 % of the current suitable area corresponds to bathymetric ranges of 50 - 100 m (Table 3). In the three future scenarios (RCPs), 60 % of the new areas suitable for the species were concentrated between 20 m and 50 m, mostly to the south of the São Francisco River (Table 3).

In summary, in the future scenarios there was a latitudinal restriction of appropriate areas for *M. harttii* (- 6.751 ° to - 19.894 ° latitud), but it increased (67 - 88 %) towards deeper waters.

Discussion

Visualization and Interpretation of Ecological Niche Models

Predicting and mapping potential suitable habitats for threatened and endangered species is critical for monitoring and restoring their natural populations [78]. In this sense, the modeling approach is an effective tool, which can predict the direction of contractions and expansions of species distribution [79], producing probability maps for presence or relative suitability of a species [80].

Table 3. Areas (km²) of suitable habitats by depth ranges

Model	Depth	0 - 20 m	20 - 50 m	50 - 75 m	75 - 100 m				
CPH	North	3155.1	458.8	0	0				
	South	14635.8	8567.9	189.4	16.1				
		Lost areas (km ²)				New areas (km ²)			
	Depth	0 - 20 m	20 - 50 m	50-75 m	75 - 100 m	0 - 20 m	20 - 50 m	50 - 75 m	75 - 100 m
RCP 2.6	North	641.6	174.2	0	0	1519.8	7935.2	1789.7	1123.9
	South	2924.7	3881.1	290.6	75.2	5155	15078.9	3854.8	1992.5
RCP 4.5	North	687.7	150	0	0	1987.7	9168.7	2010.2	1271.7
	South	1923	3679.7	374.1	75.2	5786	18209.2	4855.1	2550.3
RCP 8.5	North	772.6	108.4	0	0	2087.3	9369.7	1983.1	1247.5
	South	2428.2	4132.2	282.6	22.6	5473.7	18523.6	5495.7	2516

Table 3. Values of current potential habitat areas (CPH) and future potential habitat areas for *Mussismilia harttii* in three different projected climatic scenarios for the year 2100 (RCP 2.6, RCP 4.5 and RCP 8.5), north and south of the São Francisco River, arranged in four depth ranges.

Besides elevated CPH validation indexes (AUC and AUCratio were 0.979 and 1.934446, respectively), literature data (not geo-referenced and therefore not used in the model) also record *M. harttii* in areas indicated by the model as suitable for the species, such as the southern portion of the Abrolhos bank at Espírito Santo State [81] and at coastal reefs of Rio Grande do Norte State [82]. A model that fails to omit known points of presence is more flawed than those that predict unknown inhabited areas [83]. These unknown areas do not represent a model prediction error, but provide a precise representation of the spatial extent of habitable conditions for the species [70].

The area of potential species habitat is generally larger than the real distribution [56] and projections beyond the time interval of a training dataset (distribution in future dates) require cautious interpretations to avoid possible misinterpretations [84]. Such caution is because AUC values tend to increase when the selected background area is larger than the observed current habitat of a species [85]. Although the AUC values (close to 1) showed that the models performed very well with the results [77, 78] (better

than any model generated with a set of random predictors [71], it was necessary to use a different approach metric for evaluate the models. In the AUC metric, the weight of commission errors is much lower than that of omission errors, which makes it an inappropriate performance measurement [86].

The AUCratio also showed a good performance of the model, with values above 1 [70] and close to 2. These results allowed us to evaluate the statistical significance of the AUC itself [86]. In this way, it is more appropriate to evaluate the model performances [72]. The thresholds used to generate the binary maps are best suited for applications in Ecological Niche Templates [87] by better predicting independent occurrence data [46].

Environmental variables and *M. harttii*'s habitat

Even though the effects of each environmental variable over the population dynamics are unknown [88], the variables chosen to model the habitat suitability for *M. harttii* are in accordance with default conditions in previous studies on anthozoans [62]. Nitrates are the most common form of dissolved inorganic nitrogen in coastal waters, being the main contributor for the CPH [89]. Long exposure to high nitrate levels may lead to bleaching in some corals, due to zooxanthellae loss, on the other hand, in high temperatures, the nitrate enhancement may sustain the remaining zooxanthellae for a short period until their reestablishment, as a compensatory mechanism [90]. Calcite is one of the most common forms of calcium carbonate [91], and it was the second most important variable for the CPH. Studies indicate that calcification ratios in tropical reef-building corals will be reduced in 20 - 60 %, when CO₂ concentrations reach twice the pre-industrial concentration levels (around 560 ppm) [92].

Future habitat scenarios for *M. harttii* were mostly influenced by salinity and temperature. However, shifting of suitable habitats to deeper areas can be related with several factors. Future climate projections show not only a temperature increase of the ocean. Temperature increase will affect regimes of winds, ocean circulation and, consequently, precipitation and continental runoff, which directly influences the salinity in coastal waters [93, 94]. As result, higher turbidity and lower salinity are expected in such areas. Despite Brazilian corals as a whole are considered resistant to the input of terrigenous sediments [88], *M. harttii* has preference for clear waters, in which it is more abundant than in turbid zones [95]. Typically, corals dwell habitats under

salinities between 32 and 40 [96]. Fall in salinity, even in short term, may lead to reduction of fertility [97], increase of susceptibility to bacterial infections [98], being potentially lethal to corals and their endosymbionts [99, 100].

Temperature, salinity and light have major effects on where reef-building corals grow [100]. Despite the temperature showed the lowest contribution for the CPH, it is undoubtedly determinant for the future persistence of coral species, as 50% of these corals are threatened by climate changes [11, 12]. Our results also show the importance of the temperature in the FPH for *M. harttii*. This species suffer thermal stress in temperatures higher than 31.0°C, leading to long-term damage or death [101]. In fact, a recent study reported massive coral bleaching events in temperatures above 27° in Abrolhos reefs [102], which concentrate most records of *M. harttii* in the present study (fig 1).

Another important factor is the competition with algae (macroalgae and filamentous algae). A recent study on Brazilian benthic communities showed that such organisms dominate reefs down to 15 m deep [103]. Algae are favored by anthropic impacts, such as reduction of herbivorous/grazer fishes by overfishing, and increase of nutrients from land [104, 105]. Thus, in future scenarios, algae will likely continue to be favoured, and its competition with corals tend to reduce coverage of the later in shallow waters. In contrast, deeper areas would be less susceptible to the influence of runoff, temperature and salinity changes. Despite the lack of earlier baselines for Brazilian benthic communities, it is possible to affirm that the current scenario is result of a sum of anthropic impacts, as studies back in the 1960's describe distinctive zonation and coverage in these communities [106].

Current distribution of *M. harttii*

Most of the current suitable distribution area for *M. harttii* (CPH) is southwards of the Rio São Francisco river, where most published records are concentrated. Despite records in the coast of the Espírito Santo State (~ 19 ° S) were absent in our analyses, that area is known as the southernmost distribution limit for the species [95], with the highest percentage of CPH. That region coincides with a center of diversity within the Brazilian Province (20 ° S to 23 ° S), as indicated for benthic organisms, such as algae, invertebrates and fishes [103; 107; 108; 109]. That center is favored by the confluence of currents in the Brazilian coast, creating a transition zone between tropical and

subtropical diversity [103]. Despite a limited number of records of *M. harttii* and a smaller percentage of CPH to the north of the São Francisco river, the species is the main reef-builder northwards the São Francisco river [14].

Most records of *Mussismilia harttii* are from shallow reefs, between 2 and 6 meters [106] and consequently close to the coast. However, scattered records show this species occupying deeper reefs (up to 25 m) [81] and even at mesophotic depths [20]. Similarly, most of the CPH is concentrated in shallow waters (0 - 20 m), but with deeper suitable habitats commonly occurring, especially in the southern portion of species distribution.

***Mussismilia harttii*'s response to climate change by the end of the 21st century**

Future distribution models (RCP 2.6, RCP 4.5 and RCP 8.5) of *M. harttii* showed expansion of suitable areas, in relation to the current habitat, towards deeper sites where there are few records of this species. Concomitantly, there was a reduction of suitable shallow water areas, especially at the southernmost distribution limit, which suffered the greatest losses (Fig 3e, 4e and 5e). A similar effect is expected in the same area (mainly in the Espírito Santo State), as previous ENMs studies also showed losses for the zoanthid *Palythoa caribaeorum* [62].

A recent study on *M. harttii* [82] estimates a decline of its populations in their current geographic range in shallow waters. Our results also indicate a future scenario (RCP 8.5) with a loss of 25 % of the current suitable area (7,746.6 km² lost) in shallow waters (0 - 20 m), concentrated mainly in the southernmost distribution of the species (Espírito Santo State) (Table 2). Conversely, the results show a 55 % increase at deeper areas, 20 - 50 m (Table 3). Thus, in a future scenario, the species would lose suitable habitats in coastal shallow sectors, followed by a gain of deeper habitats, which could serve as refugia in face of climate changes.

Deep sea refugia strategy

The “deep reef refugia hypothesis” (DRRH) considers that coastal anthropic impacts and thermal stress effects are progressively reduced with depth [110, 111, 112]. Therefore, mesophotic coral ecosystems, between 30 and 150 m, have been treated as

important refugia for shallow reefs diversity [113; 114], temporarily supporting coral populations from shallow-reefs under stress conditions [115]. Such areas would provide shelter in which these populations might persist and from which would subsequently expand [116], recovering previously damaged areas [103, 117].

The reduction of shallow suitable areas and increase of deeper habitats suggest the potential of *M. harttii* for using mesophotic reefs as refugia, ensuring its subsistence. However, the DRRH is more adequate for species with wide depth distribution ranges [103] and presupposes larvae exchange between deep and shallow populations [118], which have been demonstrated to be local and species-specific [119]. Despite *M. harttii* is particularly representative in shallow waters (2-6 m), scattered records show this species occupying deeper reefs (up to 80 m) [20, 81, 120] (S12 Appendix). which reinforces the potential of the species to occupy deep mesophotic areas.

Even showing wide depth ranges, connectivity between coral populations is not always continuous along bathymetric gradients [121]. Consequently, it is still unknown if deeper populations of *M. harttii* would serve as genetic stocks for shallow waters, as most of its deep records are sparse and rare [111, 118]. In any case, the expansion of deeper suitable areas may result in the expansion of deeper populations of *M. harttii*, regardless of the maintenance of coastal populations. In case of connectivity, such refugia would contribute for the recolonization of the coastal zone affected .

Studies using of global climate models mostly suggest that few shallow coral species will persist under a sea surface temperature increase of 2 ° C in the next one hundred years [122]. Nevertheless, given the current slowness in mitigation measures, it is expected an increase of 3,1 ° C in the same period (RCP 8.5) [123]. In such scenarios, identify and protect deep sea refugia must become a priority for species conservation [114].

Threats and perspectives for conservation

The main global threats to coral species are related with greenhouse gas emissions (RCP), especially CO₂ [104]. Effects of such impacts have lead to decline of biodiversity in reefs of Brazil and of the world, through increase of sea temperature and ocean acidification [11]. Local impacts boost these effects through higher sedimentation, multiple biological invasions, bleaching, coral diseases and, consequently, loose of diversity on reef environments [11, 124, 125, 126]. Such impacts

are frequently related to disorganised urban growth, pollution, messy tourism practices and overfishing [127, 128, 129]. In the literature *Mussismilia harttii* used to be described as forming extensive bands on coastal reefs, showing colonies usually up to 1 m in diameter [106]. Currently, this is a rare scenario for most of these reefs, which often have a low coral coverage, not corresponding the descriptions of the 1970's.

Environmental changes have triggered reorganisations in reef ecological relationships, zonation and dominance, in processes also called *phase-shifts* [130]. In most reefs, for example, scleractinian dominance have been replaced mainly by macroalgae [105], octocorals [131], sponges [132] and/or zoanthids [133, 134, 135], the latter is the case of the Brazilian reefs [136]. In these reefs, *M. harttii* is also threatened by the dominance of invasive species, such as *Tubastraea* spp. [137], which even more compromises its resilience of shallow reefs.

The accelerated loss of biodiversity and habitats is one of the worst crisis of the present time, as evidenced by the ever increasing species red lists. All current and future scenarios showed herein alert for the relevance of the endemism and the role of *M. harttii* as a reef builder in Brazilian reefs. Currently, the species is classified as “in risk of extinction” [19], and the perspective of reduction of suitable shallow areas highlight the urgency of priority conservation measures. Future environmental politics, therefore, must focus not only in the recover of coastal populations, but also on the conservation of mesophotic coral ecosystems (MCE's). Despite being less affected by climate changes, MCE's are impacted by human activities, such as fisheries, mining and drilling [119, 138] and measures to protect deeper ecosystems should be prioritized in environmental policies for marine conservation, especially in Brazil.

Supporting information

S1 Appendix. Pearson correlation matrix of environmental variables. Pearson correlation matrix of 39 environmental variables, in which the 12 variables with no correlation greater than 0.8 were chosen.

S2 Appendix. Occurrence records used to generate maps of Current Potential Habitat and Future Potential Habitat. Georeference (latitude and longitude), source and author of occurrence records used to generate the CPH and FCP models.

S3 Appendix. Occurrence records used to evaluate models through AUCratio.

Georeference (latitude and longitude) and author of occurrence records used to evaluate the models through AUCratio.

S4 Appendix. Maxent output of Current Potential Habitat.

Maxent output with values of threshold, AUC, percentage of the predicted area and number of occurrences used to generate the Current Potential Habitat model.

S5 Appendix. Output of the ntbox used to evaluate the AUCratio of CPH.

Values of AUCratio for a AUC_{random} (at level of 0.5) and the AUC_{actual} (calibrating 5% of omission and 500 bootstrap interactions).

S6 Appendix. Maxent output of FPH (RCP 2.6).

Maxent output with values of threshold, AUC, percentage of the predicted area and number of occurrences used to generate the FPH model (RCP 2.6).

S7 Appendix. Output of the ntbox used to evaluate the AUCratio of FPH (RCP

2.6). Values of AUCratio for a AUC_{random} (at level of 0.5) and the AUC_{actual} (calibrating 5% of omission and 500 bootstrap interactions).

S8 Appendix. Maxent output of FPH (RCP 4.5).

Maxent output with values of threshold, AUC, percentage of the predicted area and number of occurrences used to generate the FPH model (RCP 4.5).

S9 Appendix. Output of the ntbox used to evaluate the AUCratio of FPH (RCP

4.5). Values of AUCratio for a AUC_{random} (at level of 0.5) and the AUC_{actual} (calibrating 5% of omission and 500 bootstrap interactions).

S10 Appendix. Maxent output of FPH (RCP 8.5).

Maxent output with values of threshold, AUC, percentage of the predicted area and number of occurrences used to generate the FPH model (RCP 8.5).

S11 Appendix. Output of the ntbox used to evaluate the AUCratio of FPH (RCP

8.5). Values of AUCratio for a AUC_{random} (at level of 0.5) and the AUC_{actual} (calibrating 5% of omission and 500 bootstrap interactions).

S12 Appendix. Unpublished work. Cordeiro, RTS; Amaral, FMD. Ocorrência de cnidários construtores de recifes em ambientes de profundidade no Nordeste do Brasil. In: Abstracts of XIV Congreso Latinoamericano de Ciencias del Mar, 2011, Balneário Camboriú - SC, Brazil.

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References

1. Huang C, Morlighem JÉ, Cai J, Liao Q, Pérez CD, Gomes PB, et al. Identification of long non-coding RNAs in two anthozoan species and their possible implications for coral bleaching. *Sci Rep.* 2017;7(1): 5333.
2. Harley CDG, Hughes AR, Hultgren KM, Miner BG, Sorte CJB, Thornber CS, et al. The impacts of climate change in coastal marine systems. *Ecol. Lett.* 2006;9(2): 228-241.
3. Sartor D. Dinâmica temporal e influência de variáveis ambientais no recrutamento de peixes recifais do Banco dos Abrolhos, BA, Brasil. PhD Thesis, Universidade de São Paulo. 2015. Available from: <http://www.teses.usp.br/teses/disponiveis/41/41134/tde-29092015-140146/pt-br.php>.
4. Nogueira MM, Neves E, Johnsson R. Effects of habitat structure on the epifaunal community in *Mussismilia* corals: does coral morphology influence the richness and abundance of associated crustacean fauna? *Helgol Mar Res.* 2015;69(2): 221.

5. Canário R, Badaró MF, Johnsson R, Neves EG. A new species of *Troglocarcinus* (Decapoda: Brachyura: Cryptochiridae) symbiotic with the Brazilian endemic coral *Mussismilia* (Anthozoa: Scleractinia: Mussidae). *Mar Biol Res.* 2015;11(1): 76-85.
6. Santos PS, Soledade GO, Almeida AO. Decapod crustaceans on dead coral from reef areas on the coast of Bahia, Brazil. *Nauplius.* 2012;20(2): 145-69.
7. Soares R. Duas novas espécies de crustáceos associados a *Mussismilia* Ortmann 1890 (Cnidaria, Scleractinia) no litoral da Bahia, Brasil. MSc Thesis, Universidade Federal de Bahia. 2013. Available from: <http://www.repositorio.ufba.br/ri/handle/ri/13063>.
8. do Nascimento CW, Alves AM, dos Santos AA, de Almeida Almeida WR, Brito KL, Oliveira IS, et al. Checklist of phytobenthos from Boipeba Island, Bahia, Brazil, emphasizing the morphological features of *Nitophyllum punctatum* (Rhodophyta, Ceramiales). *Check list.* 2015;11(4): 1704.
9. Mariath R, Riosmena-Rodriguez R, Figueiredo M. *Lithothamnion steneckii* sp. nov. and *Pneophyllum conicum*: new coralline red algae (Corallinales, Rhodophyta) for coral reefs of Brazil. *Algae.* 2012;27(4): 249-258.
10. Nava H, Figueroa-Camacho AG. Rehabilitation of damaged reefs: Outcome of the use of recently broken coral fragments and healed coral fragments of Pocilloporid corals on rocky boulders. *Mar Ecol (Berl).* 2017;38(5): e12456.
11. Wilkinson C. Status of coral reefs of the world: 2008. Townsville: Global Coral Reef Monitoring Network and Reef and Rainforest Research Centre; 2008.
12. Leão ZM, Kikuchi RK, Ferreira BP, Neves EG, Sovierzoski HH, Oliveira MD, et al. Brazilian coral reefs in a period of global change: A synthesis. *Braz J Oceanogr.* 2016;64(SPE2): 97-116.
13. Moura RL, Amado-Filho GM, Moraes FC, Brasileiro PS, Salomon PS, Mahiques MM, et al. An extensive reef system at the Amazon River mouth. *Sci Adv.* 2016;2(4): e1501252.

14. Rogers R, de Oliveira Correal G, De Oliveira TC, De Carvalho LL, Mazurek P, Barbosa JE, et al. Coral health rapid assessment in marginal reef sites. *Mar Biol Res.* 2014;10(6): 612-24.
15. Budd AF, Fukami H, Smith ND, Knowlton N. Taxonomic classification of the reef coral family Mussidae (Cnidaria: Anthozoa: Scleractinia). *Zool J Linn Soc.* 2012;166(3): 465-529.
16. Castro CB, Pires DO. Brazilian coral reefs: what we already know and what is still missing. *Bull Mar Sci.* 2001;69(2): 357-371.
17. Castro CB, Medeiros MS, Loiola, LL. Octocorallia (Cnidaria: Anthozoa) from Brazilian reefs. *J Nat Hist.* 2010; 44(13-14): 763-827.
18. Zilberberg C, Peluso L, Marques JA, Cunha H. Polymorphic microsatellite loci for endemic *Mussismilia* corals (Anthozoa: Scleractinia) of the southwest Atlantic Ocean. *J Hered.* 2014;105(4): 572-5.
19. Pires D, De Paula, Ferreira B, Francini-Filho R, Gaspar A, Mendes L, Negrão F, et al. *Mussismilia harttii* (Verrill, 1868). In: ICMBio (eds). Livro Vermelho da Fauna Brasileira Ameaçada de Extinção. Brasília: Ministério do Meio Ambiente; 2018. pp 660-664.
20. Hetzel B, Castro C. Corais do Sul da Bahia. Rio de Janeiro: Nova Fronteira; 1994.
21. Kikuchi RK, Oliveira MD, Leão ZM, Silva RM, Martins PM. Os recifes de Tinharé-Boipeba-Camamu, Bahia. In Rio Oil & Gas Expo and Conference. Proceedings of Rio Oil and Gas Expo and Conference. Rio de Janeiro: Instituto Brasileiro de Petróleo, Gás e Biocombustíveis; 2008. pp. 1-8.
22. Tyberghein L, Verbruggen H, Pauly K, Troupin C, Mineur F, De Clerck O. Bio-ORACLE: a global environmental dataset for marine species distribution modelling. *Glob Ecol Biogeogr.* 2012;21(2): 272-81.

23. Peterson AT, Soberon J, Pearson RG, Anderson RP, Martínez-Meyer E, Nakamura M, et al. *Ecological Niches and Geographic Distributions*. Princeton: Princeton University Press; 2012.
24. Franklin J. *Mapping species distributions: spatial inference and prediction*. Cambridge: Cambridge University Press; 2010.
25. Pearson RG, Raxworthy CJ, Nakamura M, Townsend Peterson A. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *J Biogeogr*. 2007;34(1): 102-17.
26. Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates CJ. A statistical explanation of MaxEnt for ecologists. *Divers Distrib*. 2011;17(1): 43-57.
27. Phillips SJ, Dudík M. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography*. 2008;31(2): 161-75.
28. Riul P, Targino CH, Júnior LA, Creed JC, Horta PA, Costa GC. Invasive potential of the coral *Tubastraea coccinea* in the southwest Atlantic. *Mar Ecol Prog Ser*. 2013;480: 73-81.
29. Leathwick J, Moilanen A, Francis M, Elith J, Taylor P, Julian K, et al. Novel methods for the design and evaluation of marine protected areas in offshore waters. *Conserv Lett*. 2008;1(2): 91-102.
30. Eakin C, Liu G, Gomez A, De La Cour J, Heron S, Skirving W, et al. Global coral bleaching 2014–2017: status and an appeal for observations. *Reef Encounter*. 2016;31(1): 20-26.
31. Heron SF, Eakin CM, Douvère F, Anderson KL, Day JC, Geiger E, et al. *Impacts of climate change on World Heritage coral reefs: A first global scientific assessment*. Paris: UNESCO World Heritage Centre. 2017.
32. Barrows CW, Rotenberry JT, Allen MF. Assessing sensitivity to climate change and drought variability of a sand dune endemic lizard. *Biol Conserv*. 2010;143(3): 731-736.

- 33.** Warren DL, Seifert SN. Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. *Ecol Appl.* 2011;21(2): 335-342.
- 34.** Becker J, Sandwell D, Smith W, Braud J, Binder B, Depner J, et al. Global bathymetry and elevation data at 30 arc seconds resolution: SRTM30_PLUS. *Marine Geodesy.* 2009;32(4): 355-371.
- 35.** Barve N, Barve V, Jiménez-Valverde A, Lira-Noriega A, Maher S, Peterson A, et al. The crucial role of the accessible area in ecological niche modeling and species distribution modeling. *Ecol Modell.* 2011;222(11): 1810-1819.
- 36.** Soberon J, Peterson AT. Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodiversity Informatics.* 2005; 2: 1-10.
- 37.** Tassarolo G, Ladle R, Rangel T, Hortal J. Temporal degradation of data limits biodiversity research. *Ecol Evol.* 2017;7(17): 6863-6870.
- 38.** Munday PL. Habitat loss, resource specialization, and extinction on coral reefs. *Glob Chang Biol.* 2004;10(10): 1642-1647.
- 39.** Cavalcante FR, Borges SC, Crispim EF, Amaral FD. Checklist e abundância dos Cnidários nos ambientes recifais de Maragogi, Alagoas. *Trop Oceanogr.* 42(2). doi: 10.5914/to.2014.0112.
- 40.** Kuhn T, Cunze S, Kochmann J, Klimpel S. Environmental variables and definitive host distribution: a habitat suitability modelling for endo helminth parasites in the marine realm. *Sci Rep.* 2016;6: 30246.
- 41.** Boria RA, Olson LE, Goodman SM, Anderson RP. Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. *Ecol Modell.* 2014;275:73-77.
- 42.** Brown JL. SDM toolbox: a python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. *Methods Ecol Evol.* 2014;5(7): 694-700.

43. Giannini TC, Siqueira MF, Acosta AL, Barreto FC, Saraiva AM, Santos IA. Desafios atuais da modelagem preditiva de distribuição de espécies. *Rodriguésia*. 2012;63(3): 733-749.
44. Raftery AE, Zimmer A, Frierson DM, Startz R, Liu P. Less than 2 C warming by 2100 unlikely. *Nat Clim Chang*. 2017;7(9): 637.
45. Assis J, Tyberghein L, Bosch S, Verbruggen H, Serrão EA, De Clerck O. Bio-ORACLE v2. 0: Extending marine data layers for bioclimatic modelling. *Glob Ecol Biogeogr*. 2018;27(3): 277-84.
46. Peterson AT, Raghavan RK. The geographic distribution of *Ixodes scapularis* (Acari: Ixodidae) revisited: The importance of assumptions about error balance. *J Med Entomol*. 2017;54(4): 1080-1084.
47. Chapman AD, Muñoz ME, Koch I. Environmental information: placing biodiversity phenomena in an ecological and environmental context. *Biodiversity Informatics*. 2005; 2.
48. Breiner FT, Guisan A, Bergamini A, Nobis MP. Overcoming limitations of modelling rare species by using ensembles of small models. *Methods Ecol Evol*. 2015;6(10): 1210-1218.
49. Ficitola GF, Bonardi A, Múcher CA, Gilissen NL, Padoa-Schioppa E. How many predictors in species distribution models at the landscape scale? Land use versus LiDAR-derived canopy height. *Int J Geogr Inf Sci*. 2014;28(8): 1723-1739.
50. Elith J, Leathwick J. Species distribution models: ecological explanation and prediction across space and time. *Annu Rev Ecol Evol Syst*. 2009;40: 677-697.
51. IPCC. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge: Cambridge University Press. 2013.
52. Van Vuuren D, Edmonds J, Kainuma M, Riahi K, Thomson A, Hibbard K, et al. The representative concentration pathways: an overview. *Clim Change*. 2011;109(1-2): 5.

- 53.** Van Vuuren DP, Den Elzen MG, Lucas PL, Eickhout B, Strengers BJ, Van Ruijven et al. Stabilizing greenhouse gas concentrations at low levels: an assessment of reduction strategies and costs. *Clim Change*. 2007;81(2): 119-159.
- 54.** Wise M, Calvin K, Thomson A, Clarke L, Bond-Lamberty B, Sands R, et al. Implications of limiting CO₂ concentrations for land use and energy. *Science*. 2009;324(5931):1183-1186.
- 55.** Riahi K, Grübler A, Nakicenovic N. Scenarios of long-term socio-economic and environmental development under climate stabilization. *Technol Forecast Soc Change*. 2007;74(7): 887-935.
- 56.** Phillips SJ, Anderson RP, Schapire RE. Maximum entropy modeling of species geographic distributions. *Ecol Modell*. 2006;25(3-4): 231-259.
- 57.** Radosavljevic A, Anderson R. Making better Maxent models of species distributions: complexity, overfitting and evaluation. *J Biogeogr*. 2014;41(4): 629-643.
- 58.** Phillips SJ, Anderson RP, Dudík M, Schapire RE, Blair ME. Opening the black box: an open-source release of Maxent. *Ecography*. 2017;40(7): 887-893.
- 59.** Warren DL. In defense of ‘niche modeling’. *Trends Ecol. Evol*. 2012;27(9): 497-500.
- 60.** Elith J, Graham C, Anderson R, Dudík M, Ferrier S, Guisan A, et al. Novel methods improve prediction of species’ distributions from occurrence data. *Ecography*. 2006;29(2): 129-151.
- 61.** Baldwin R. Use of maximum entropy modeling in wildlife research. *Entropy*. 2009;11(4): 854-866.
- 62.** Durante LM, Cruz IC, Lotufo TM. The effect of climate change on the distribution of a tropical zoanthid (*Palythoa caribaeorum*) and its ecological implications. *PeerJ*. 2018;6: e4777.
- 63.** Peterson AT. Mapping disease transmission risk: enriching models using biogeography and ecology. Johns Hopkins University Press. 2014.

- 64.** Peterson AT. Predicting the geography of species' invasions via ecological niche modeling. *Q Rev Biol.* 2003;78(4): 419-433.
- 65.** Phillips, S. J. 2017. A Brief Tutorial on Maxent. 2017. Available from url: http://biodiversityinformatics.amnh.org/open_source/maxent/. Cited 17 October 2018.
- 66.** Biber-Freudenberger L, Ziemacki J, Tonnang H, Borgemeister C. Future risks of pest species under changing climatic conditions. *PloS One.* 2016;11(4): e0153237.
- 67.** Porfirio L, Harris R, Lefroy E, Hugh S, Gould S, Lee G, et al. Improving the use of species distribution models in conservation planning and management under climate change. *PLoS One.* 2014;9(11): e113749.
- 68.** Adhikari D, Reshi Z, Datta B, Samant S, Chettri A, Upadhaya K, et al. Inventory and characterization of new populations through ecological niche modelling improve threat assessment. *Curr Sci.* 2018;114(3): 519-531.
- 69.** Fawcett T. ROC graphs: Notes and practical considerations for researchers. *Pattern Recognit Lett.* 2004;31(1): 1-38.
- 70.** Peterson A, Papeş M, Soberón J. Rethinking receiver operating characteristic analysis applications in ecological niche modeling. *Ecol Modell.* 2008;213(1): 63-72.
- 71.** Fourcade Y, Besnard A, Secondi J. Paintings predict the distribution of species, or the challenge of selecting environmental predictors and evaluation statistics. *Glob Ecol Biogeogr.* 2018;27(2): 245-56.
- 72.** Lobo J, Jiménez-Valverde A, Real R. AUC: a misleading measure of the performance of predictive distribution models. *Glob Ecol Biogeogr.* 2008;17(2): 145-51.
- 73.** Idohou R, Peterson A, Assogbadjo A, Vihotogbe R, Padonou E, Kakai R. Identification of potential areas for wild palm cultivation in the Republic of Benin through remote sensing and ecological niche modeling. *Genet Resour Crop Evol.* 2017;64(6): 1383-93.

74. Reddy M, Begum H, Sunil N, Pandravada S, Sivaraj N. Assessing climate suitability for sustainable vegetable Roselle (*Hibiscus sabdariffa* var. *sabdariffa* L.) cultivation in India using MaxEnt model. *Agricultural and Biological Sciences Journal*. 2015;1(2):62-70.
75. R Core. R: A language and environment for statistical computing. Viena: R Foundation for Statistical Computing; 2014.
76. Guisan A, Thuiller W. Predicting species distribution: offering more than simple habitat models. *Ecol Lett*. 2005;8(9): 993-1009.
77. Liu C, White M, Newell G. Selecting thresholds for the prediction of species occurrence with presence-only data. *J Biogeogr*. 2013;40(4): 778-789.
78. Kuria MW, Ngumi VW, Njenga PK. MaxEnt Modeling for Predicting a Suitable Habitat for a Threatened and Endangered Medicinal Plant Species *Strychnos henningsii* in Kenya. *International Journal of Innovative Research and Knowledge*. 2017; 2(11): 61-78.
79. Araújo M, Pearson R, Thuiller W, Erhard M. Validation of species–climate impact models under climate change. *Glob Chang Biol*. 2005;11(9): 1504-1513.
80. Kumar S, Neven LG, Yee WL. Evaluating correlative and mechanistic niche models for assessing the risk of pest establishment. *Ecosphere*. 2014;5(7): 1-23.
81. Mazzei EF, Bertoncini AA, Pinheiro HT, Machado LF, Vilar CC, Guabiroba HC, et al. Newly discovered reefs in the southern Abrolhos Bank, Brazil: anthropogenic impacts and urgent conservation needs. *Mar Pollut Bull*. 2017;114(1): 123-133.
82. Lima GV. Avaliação do estado de conservação do coral endêmico *Mussismilia harttii* (Verrill, 1868) (Cnidaria: Anthozoa) no Brasil. M.Sc. Tese, Universidade Federal de Pernambuco. 2017. Available from: <https://repositorio.ufpe.br/handle/123456789/25918>

- 83.** Raxworthy CJ, Martinez-Meyer E, Horning N, Nussbaum R, Schneider G, Ortega-Huerta M, et al. Predicting distributions of known and unknown reptile species in Madagascar. *Nature*. 2003;426(6968): 837.
- 84.** Basher Z, Costello M. The past, present and future distribution of a deep-sea shrimp in the Southern Ocean. *PeerJ*. 2016;4: e1713.
- 85.** Jiménez-Valverde A. Insights into the area under the receiver operating characteristic curve (AUC) as a discrimination measure in species distribution modelling. *Glob Ecol Biogeogr*. 2012;21(4): 498-507.
- 86.** Narváez-Romero C, Reyes-Puig C, Valle D, Brito J. New records and estimation of the potential distribution of the stump-tailed porcupine *Coendou rufescens*. *Therya*. 2018;9(2): 137.
- 87.** Peterson A, Soberón J, Pearson R, Anderson R, Martínez-Meyer E, Nakamura M, et al. *Ecological niches and geographic distributions*. Princeton and Oxford: Princeton University Press. 2011.
- 88.** Robinson L, Elith J, Hobday A, Pearson R, Kendall B, Possingham H, et al. Pushing the limits in marine species distribution modelling: lessons from the land present challenges and opportunities. *Glob Ecol Biogeogr*. 2011;20(6):7 89-802.
- 89.** Marubini F, Davies P. Nitrate increases zooxanthellae population density and reduces skeletogenesis in corals. *Mar Biol*. 1996;127(2): 319-328.
- 90.** Schlöder C, D'Croz L. Responses of massive and branching coral species to the combined effects of water temperature and nitrate enrichment. *J Exp Mar Bio Ecol*. 2004;313(2): 255-268.
- 91.** Adey WH. Coral reefs: algal structured and mediated ecosystems in shallow, turbulent, alkaline waters. *J Phycol*. 1998;34(3): 393-406.
- 92.** Gattuso J, Frankignoulle M, Bourge I, Romaine S, Buddemeier R. Effect of calcium carbonate saturation of seawater on coral calcification. *Glob Planet Change*. 1998;18(1): 37-46.

- 93.** Jokiel P, Hunter C, Taguchi S, Watarai L. Ecological impact of a fresh-water “reef kill” in Kaneohe Bay, Oahu, Hawaii. *Coral Reefs*. 1993;12(3-4): 177-184.
- 94.** Trenberth KE. Changes in precipitation with climate change. *Climate Research*. 2011;47(1-2): 123-138.
- 95.** Leão Z, Kikuchi R, Testa V. Corals and coral reefs of Brazil. In: Jorge Cortez, editor. *Latin American coral reefs*. Amsterdam: Elsevier. 2003. pp. 9-52.
- 96.** Veron, John Edward Norwood, and John Edward Norwood Veron. *Corals of Australia and the Indo-pacific*. Sydney: Angus & Robertson. 1986.
- 97.** Richmond RH. Coral reefs: present problems and future concerns resulting from anthropogenic disturbance. *Am Zool*. 1993;33(6): 524-536.
- 98.** Shore-Maggio A, Aeby G, Callahan S. Influence of salinity and sedimentation on *Vibrio* infection of the Hawaiian coral *Montipora capitata*. *Dis Aquat Organ*. 2018;128(1): 63-71.
- 99.** Mayfield AB, Gates RD. Osmoregulation in anthozoan–dinoflagellate symbiosis. *Comp Biochem Physiol A Mol Integr Physiol*. 2007;147(1): 1-10.
- 100.** Hoegh-Guldberg O. Climate change, coral bleaching and the future of the world's coral reefs. *Mar Freshw Res*. 1999;50(8): 839-866.
- 101.** Winter A, Chaloub R, Duarte G. Photosynthetic responses of corals *Mussismilia harttii* (Verrill, 1867) from turbid waters to changes in temperature and presence/absence of light. *Braz J Oceanogr*. 2016;64(3): 203-216.
- 102.** Lisboa D, Kikuchi R, Leão Z. El Niño, Sea Surface Temperature Anomaly and Coral Bleaching in the South Atlantic: A Chain of Events Modeled With a Bayesian Approach. *J Geophys Res Oceans*. 2018;123(4): 2554-2569.
- 103.** Aued A, Smith F, Quimbayo J, Cândido D, Longo G, Ferreira C, et al. Large-scale patterns of benthic marine communities in the Brazilian Province. *PloS One*. 2018;13(6): e0198452.

- 104.** Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, et al. Coral reefs under rapid climate change and ocean acidification. *Science*. 2007;318(5857): 1737-42.
- 105.** Mumby PJ, Dahlgren CP, Harborne AR, Kappel CV, Micheli F, Brumbaugh DR, et al. Fishing, trophic cascades, and the process of grazing on coral reefs. *Science*. 2006;311(5757): 98-101.
- 106.** Laborel J, Madréporaires et hydrocoralliaires récifaux gives côtes brésiliennes. *Systématique, écologie, répartition verticale et géographique. Résultats Scientifiques des Campagnes de la "Calypso"*. 1970;(9): 171–229.
- 107.** Floeter S, Guimarães R, Rocha L, Ferreira C, Rangel C, Gasparini J. Geographic variation in reef-fish assemblages along the Brazilian coast. *Glob Ecol Biogeogr*. 2001;10(4): 423-431.
- 108.** Miloslavich P, Klein E, Díaz J, Hernandez C, Bigatti G, Campos L, et al. Marine biodiversity in the Atlantic and Pacific coasts of South America: knowledge and gaps. *PloS One*. 2011;6(1): e14631.
- 109.** Barroso C, Lotufo T, Matthews-Cascon H. Biogeography of Brazilian prosobranch gastropods and their Atlantic relationships. *J Biogeogr*. 2016;43(12): 2477-2488.
- 110.** Smith TB, Glynn PW, Maté JL, Toth LT, Gyory J. A depth refugium from catastrophic coral bleaching prevents regional extinction. *Ecology*. 2014;95(6): 1663-73.
- 111.** Rocha L, Pinheiro H, Shepherd B, Papastamatiou Y, Luiz O, Pyle R, et al. Mesophotic coral ecosystems are threatened and ecologically distinct from shallow water reefs. *Science*. 2018;361(6399): 281-284.
- 112.** Bongaerts P, Ridgway T, Sampayo EM, Hoegh-Guldberg O. Assessing the ‘deep reef refugia’ hypothesis: focus on Caribbean reefs. *Coral reefs*. 2010;29(2): 309-27.

- 113.** Riegl B, Piller W. Possible refugia for reefs in times of environmental stress. *Int J Earth Sci.* 2003;92(4): 520-531.
- 114.** Ashcroft M. Identifying refugia from climate change. *J Biogeogr.* 2010;37(8): 1407-1413.
- 115.** Frieler K, Meinshausen M, Mengel M, Braun N, Hare W. A scaling approach to probabilistic assessment of regional climate change. *J Clim.* 2012;25(9): 3117-3144.
- 116.** Magoulick D, Kobza R. The role of refugia for fishes during drought: a review and synthesis. *Freshw Biol.* 2003; 48(7): 1186-1198.
- 118.** Lesser M, Slattery M, Leichter J. Ecology of mesophotic coral reefs. *J Exp Mar Bio Ecol.* 2009;1(375): 1-8.
- 119.** Ramirez-Llodra E, Tyler P, Baker M, Bergstad O, Clark M, Escobar E, et al. Man and the last great wilderness: human impact on the deep sea. *PLoS One.* 2011;6(8): e22588.
- 120.** Castro CB, Pires DO, Medeiros MS, Loiola LL, Arantes RC, Thiago CM et al. Filo Cnidaria. Corais. In: Lavrado HP, Ignacio BL, editors. Biodiversidade bentônica da região central da Zona Econômica Exclusiva Brasileira. Rio de Janeiro: Museu Nacional. 2006;147-192.
- 121.** Costantini F, Aurelle D, Ledoux J, Abbiati M. Population genetic structure of *Corallium rubrum* in the Mediterranean Sea: diversity, phylogeography, and bathymetric patterns. In: Goffredo S, Dubinsky Z, editors. *The Cnidaria, Past, Present and Future.* Berlin: Springer; 2016 pp. 717-728.
- 122.** Cacciapaglia C, Woesik R. Reef-coral refugia in a rapidly changing ocean. *Glob Chang Biol.* 2015;21(6): 2272-2282.
- 123.** Keppel G, Van Niel K, Wardell-Johnson G, Yates C, Byrne M, Mucina L, et al. Refugia: identifying and understanding safe havens for biodiversity under climate change. *Glob Ecol Biogeogr.* 2012;21(4): 393-404.

- 124.** Ferreira BP, Maida M. Monitoramento dos recifes de coral do Brasil. MMA, Secretaria de Biodiversidade e Florestas. 2006.
- 125.** Assis RC, Câmara GL, Vila-Nova DA, Leal AF, Oliveira AC, Soares CL. Percepção sócio-ambiental dos turistas e trabalhadores da praia de Porto de Galinhas (Pernambuco-Brasil) acerca do ecossistema recifal. *Revista de Gestão Costeira Integrada*. 2009;9(3): 71-78.
- 126.** Bruno JF, Selig ER. Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. *PLoS One*. 2007;2(8): e711.
- 127.** West JM, Salm RV. Resistance and resilience to coral bleaching: implications for coral reef conservation and management. *Conserv Biol*. 2003;17(4): 956-967.
- 128.** Buddemeier RW, Kleypas JA, Aronson RB. Potential contributions of climate change to stresses on coral reef ecosystems. *Coral reefs and global climate change*. Pew Center on Global Climate Change, Virginia, USA. 2004
- 129.** Melo RD, Crispim MC, Lima ER. O turismo em ambientes recifais: em busca da transição para a sustentabilidade. *Caderno Virtual de Turismo*. 2005;5(4): 34-42.
- 130.** Done TJ. Phase shifts in coral reef communities and their ecological significance. *Hydrobiologia*. 1992;247(1-3): 121-132.
- 131.** Costantini F, Gori A, Lopez-González P, Bramanti L, Rossi S, Gili J, et al. Limited genetic connectivity between gorgonian morphotypes along a depth gradient. *PloS One*. 2016;11(8): e0160678.
- 132.** Bell JJ, Davy SK, Jones T, Taylor MW, Webster NS. Could some coral reefs become sponge reefs as our climate changes? *Glob Chang Biol*. 2013;19(9): 2613-2624.
- 133.** Cruz IC, Kikuchi RK, Longo LL, Creed JC. Evidence of a phase shift to *Epizoanthus gabrieli* Carlgreen, 1951 (Order Zoanthidea) and loss of coral cover on reefs in the Southwest Atlantic. *Mar Ecol*. 2014;36(3): 318-325.

- 134.** Cruz IC, Meira VH, Kikuchi RK, & Creed JC. The role of competition in the phase shift to dominance of the zoanthid *Palythoa* cf. *variabilis* on coral reefs. *Mar Environ Res.* 2016;115: 28-35.
- 135.** Cruz IC, Waters LG, Kikuchi RK, Leão ZM, Turra A. Marginal coral reefs show high susceptibility to phase shift. *Mar Pollut Bull.* 2018;135: 551-561.
- 136.** Francini-Filho RB, Coni EO, Meirelles PM, Amado-Filho GM, Thompson FL, Pereira-Filho GH, et al. Dynamics of coral reef benthic assemblages of the Abrolhos Bank, eastern Brazil: inferences on natural and anthropogenic drivers. *PloS One.* 2013;8(1): e54260.
- 137.** Creed JC. Two invasive alien azooxanthellate corals, *Tubastraea coccinea* and *Tubastraea tagusensis*, dominate the native zooxanthellate *Mussismilia hispida* in Brazil. *Coral Reefs.* 2006;25(3): 350.
- 138.** Leão ZMAN, Kikuchi RKP, Oliveira MDM. The Coral Reef Province of Brazil. In: Sheppard C, editor. *World Seas: an Environmental Evaluation. Volume I: Europe, the Americas and West Africa.* Amsterdam: Elsevier; 2019. pp. 813-833.

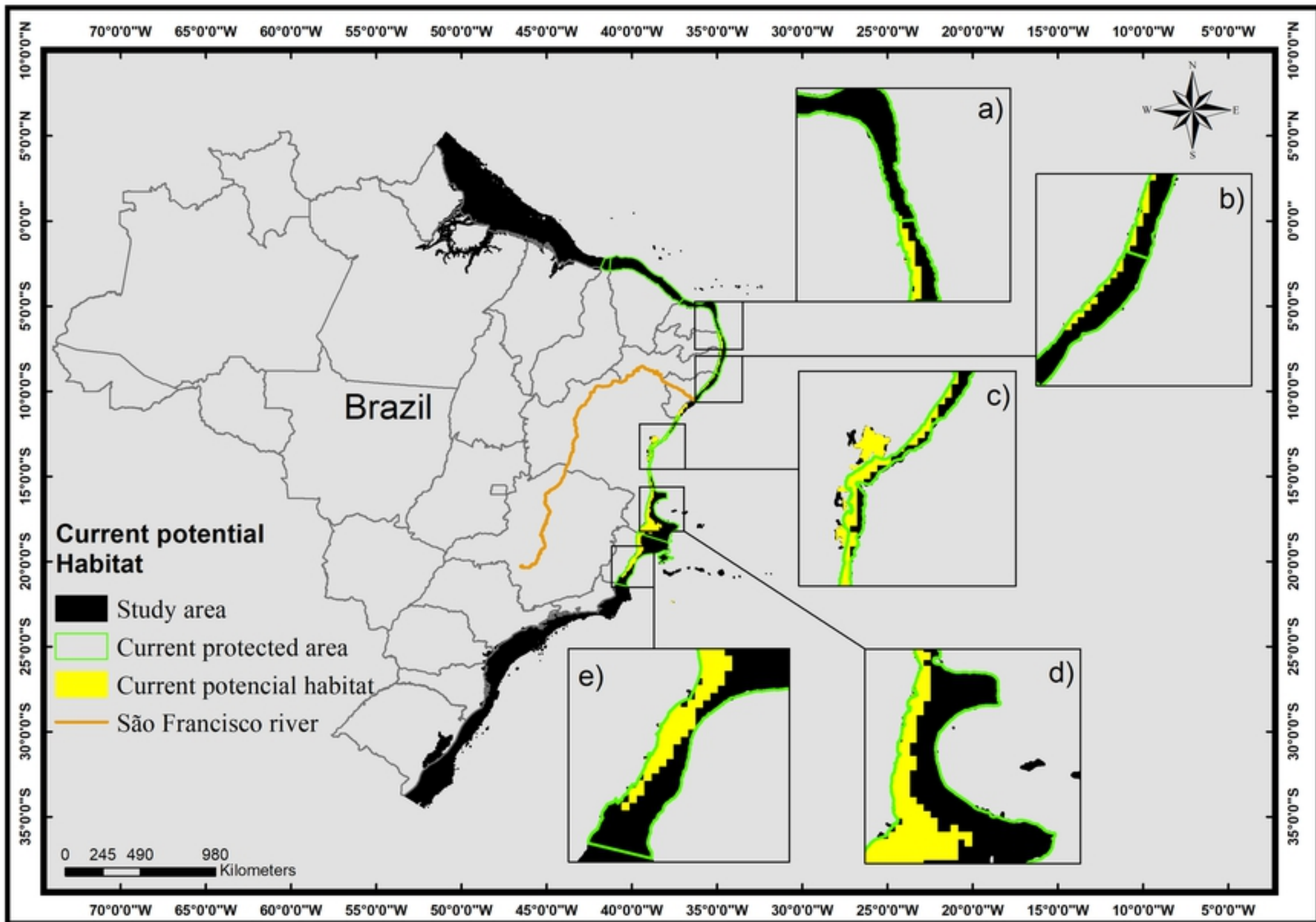


Figure 2

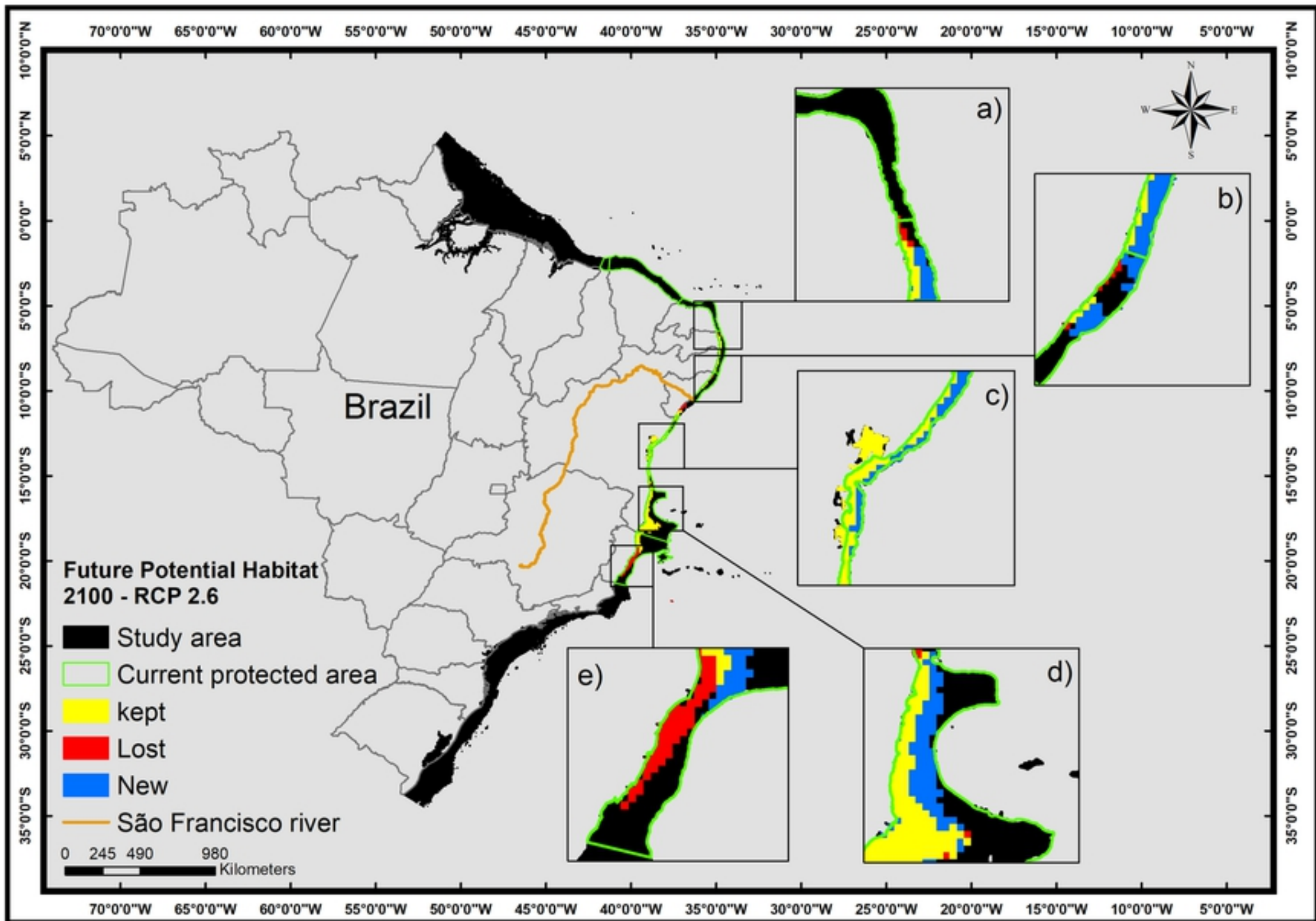


Figure 3

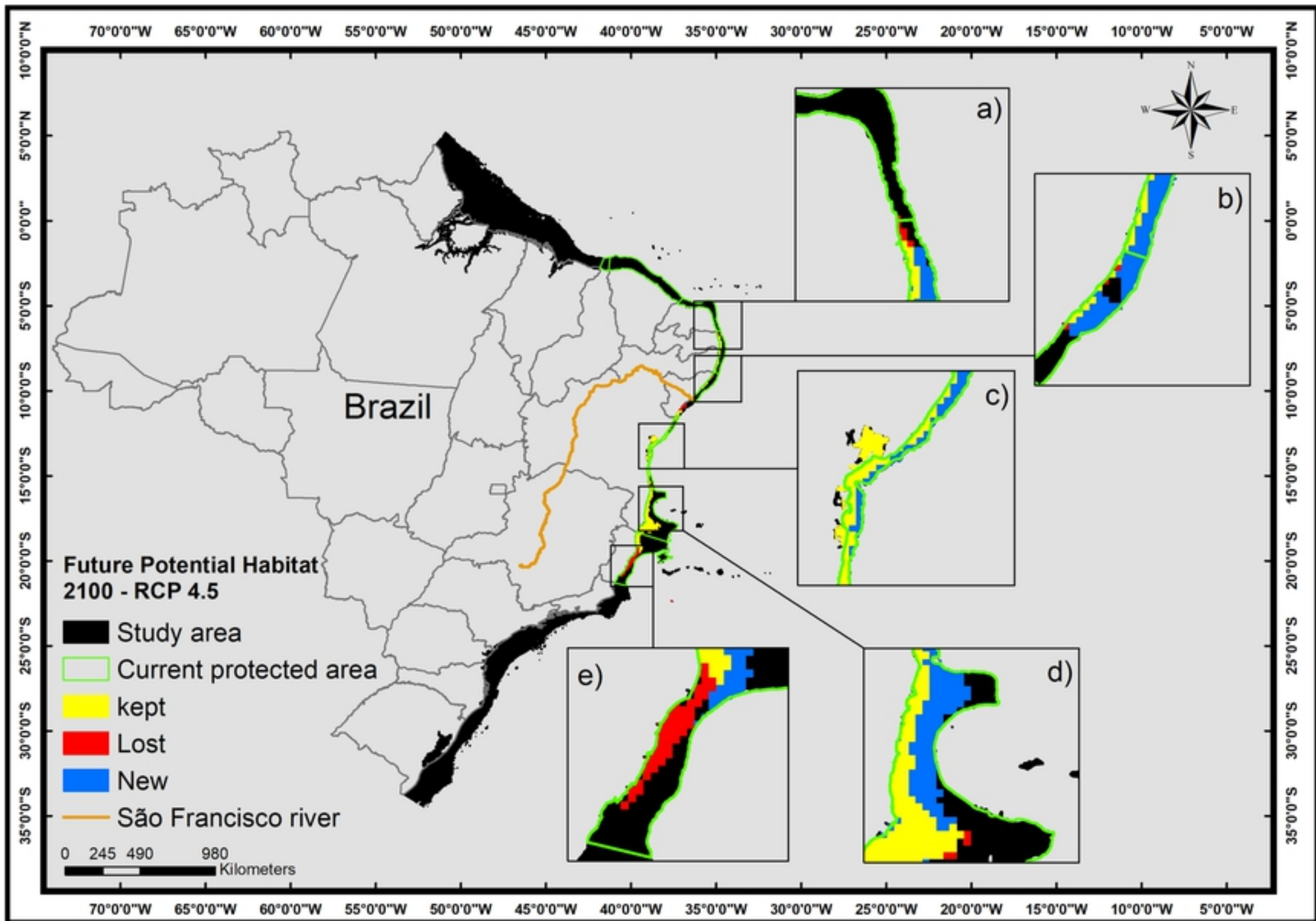


Figure 4

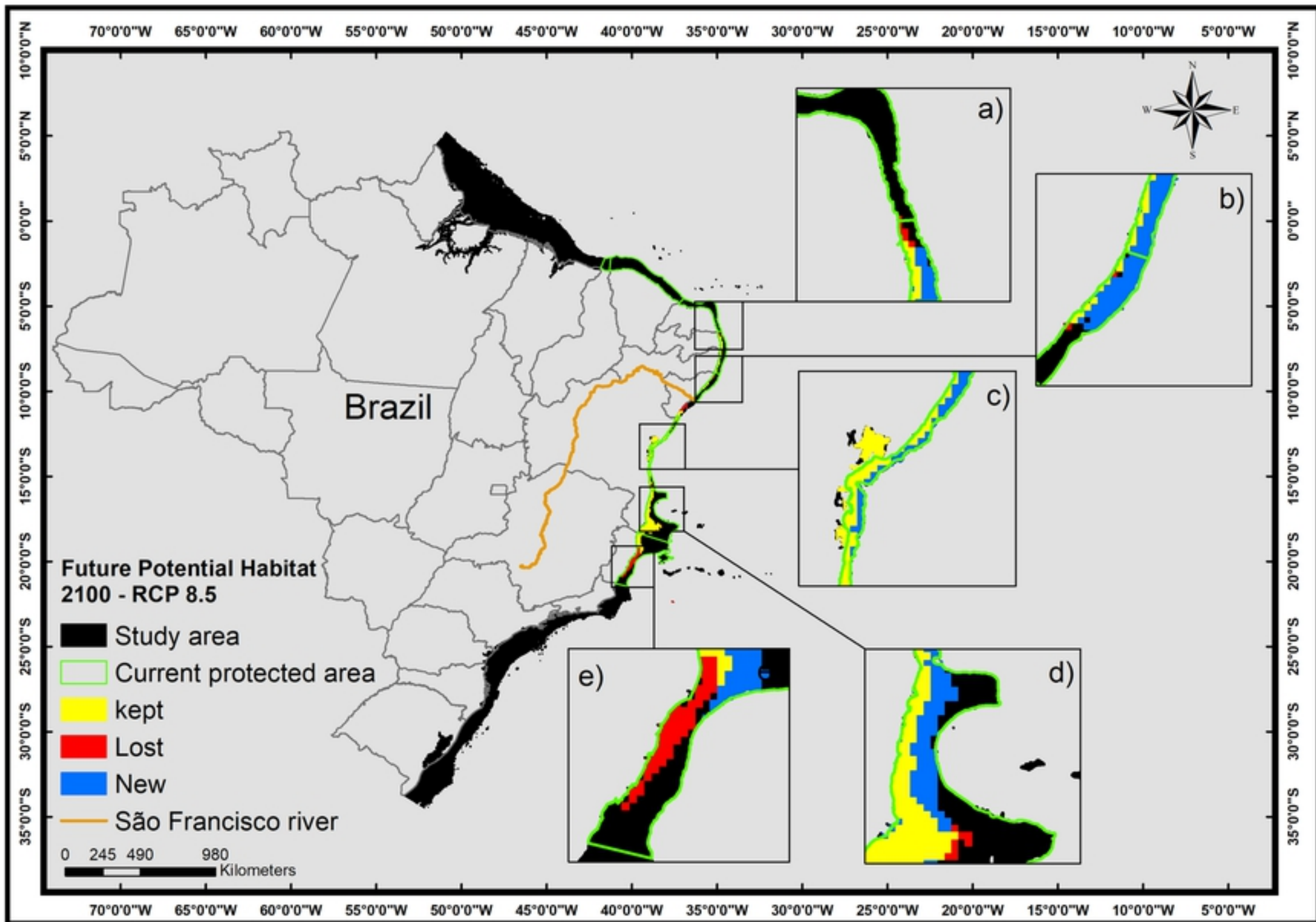


Figure 5

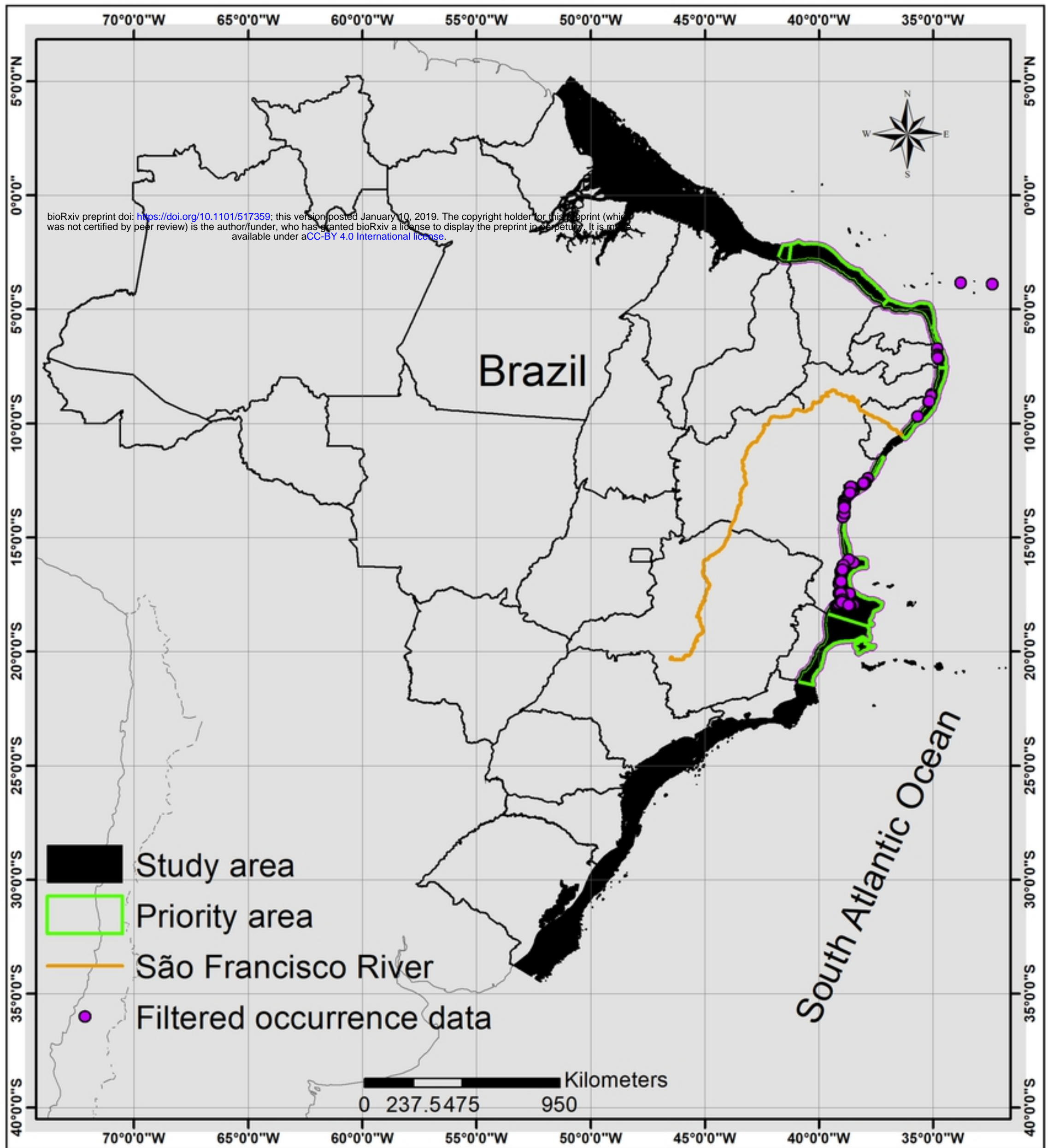


Figure 1