

Pablo Riul

**MODELAGEM DE DISTRIBUIÇÃO DE ESPÉCIES BÊNTHICAS
MARINHAS NA COSTA DO BRASIL: BIOINVASÃO,
CONSERVAÇÃO E EFEITO DAS MUDANÇAS CLIMÁTICAS**

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Orientador: Prof. Dr. Paulo Antunes
Horta

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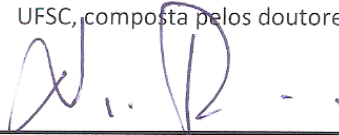
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**“Modelagem de distribuição de espécies bênticas marinhas na costa do Brasil:
Bioinvasão, conservação e efeito das mudanças climáticas”**

Por

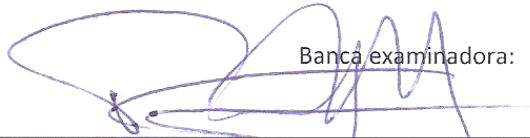
Pablo Riul

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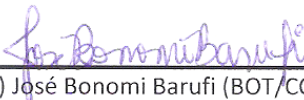
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“Geographical distributional areas are the shadows produced by taxa on the geographical screen. To study them one needs to measure ghosts.”

(Rapoport, 1982)

RESUMO

A distribuição geográfica de muitas espécies é ainda insuficientemente conhecida (“*The Wallacean shortfall*”) o que pode limitar até mesmo os estudos mais básicos de Ecologia e Conservação e o manejo da biodiversidade. Esse problema é particularmente crítico para organismos bênticos, como os abordados nesse estudo, e para regiões megadiversas como o Brasil. Nesse contexto, a modelagem de distribuição de espécies é uma ferramenta versátil que permite responder diversas questões ecológicas. Os modelos de distribuição de espécies utilizam a relação entre dados de ocorrência das espécies e variáveis ambientais georreferenciados para estimar a área geográfica na qual uma espécie pode ocorrer. Neste trabalho foram utilizadas diferentes técnicas de modelagem de distribuição de espécies para responder questões de bioinvasão, Ecologia da Conservação e efeito das mudanças climáticas em bentos da costa do Brasil. No capítulo 1, foram modeladas as distribuições das espécies de coral *Tubastraea coccinea* (invasora) e *Mussismilia hispida* (endêmica) para identificar a área de potencial sobreposição entre as distribuições da espécie invasora e da espécie endêmica. Foi demonstrado que a espécie invasora pode vir a ocorrer em grande parte da costa do Brasil, incluindo a maioria das áreas marinhas protegidas. No capítulo 2, foi testada a hipótese de que o viés geográfico amostral (esforço amostral diferente ao longo da área de estudo) nos dados de ocorrência empregados em modelos de distribuição de espécies modifica o resultado da análise de priorização espacial para a conservação. Quando o viés geográfico não é corrigido, o portfólio de conservação gerado aponta áreas com maior esforço amostral como as mais importantes e áreas pouco amostradas como menos importantes para a conservação. No capítulo 3, foi testada a hipótese de que as mudanças climáticas podem promover mudanças nas distribuições de seis espécies de macroalgas na costa do Brasil com diferentes padrões biogeográficos: cosmopolitas (*Ceramium brasiliense* e *Cryptonemia delicatula*), tropicais (*Dictyopteris jolyana* e *Gelidium coarctatum*) e subtropicais (*Levringea brasiliensis* e *Plocamium brasiliense*). Os resultados indicam uma forte tendência de deslocamento nas distribuições das espécies em direção aos polos, independentemente da afinidade biogeográfica.

Palavras-chave: Modelos de distribuição de espécies. Bentos da costa do Brasil. Macroalgas. Priorização Espacial para Conservação. Corais.

ABSTRACT

The geographical distribution of many species is still poorly known (The Wallacean shortfall) limiting even the most basic studies in Ecology and Conservation and the management of biodiversity. This issue is particularly critic for benthic organisms, such as the object of this study and megadiverse regions, such as Brazil, and. In this contexto, species distribution modeling is a useful tool allowing to answer several ecological questions. Species Distribution Models (SDMs) uses geo-referenced species occurrences linked with abiotic and/or biotic information from these localities to estimate the habitat suitability (i.e. areas of suitable conditions in which the species is likely to occur) in a geographical space. In this study we used distinct modeling techniques to answer questions of bioinvasion, Conservation Ecology and the effects of climate change in benthic species of the Brazillian coast. In chapter 1 we modeled the distribution of the coral species *Tubastraea coccinea* (invasive) and *Mussismilia hispida* (endemic) to identify potential overlap areas in the distribution of both species. We show the invasive species to have the potential to occur in most of Brazillian coast, including most of Marine Protected areas, threatening the endemic reef builder species. In chapter 2 we tested the hypothesis of geographical sampling bias (sampling effort unevenly distributed in space) in occurrence data used in SDMs changes the results of spatial conservation prioritization analysis. When sampling bias is not accounted for, the generated conservation portfolios selects areas with higher sampling effort as the most important whereas the less sampled areas are pointed as less importante for conservation. In chapter 3, we tested the hypothesis that climate change can promote changes in geographical distribution of six marine macroalgae species in Brazillian coast with distinct biogeographical affinities: cosmopolitans (*Ceramium brasiliense* and *Cryptonemia delicatula*), tropical (*Dictyopteris jolyana* and *Gelidium coarctatum*) and subtropical (*Leveringea brasiliensis* and *Plocamium brasiliense*). The results show a strong trend of poleward range shift in the species distributions regardless of their biogeographical affinity.

Keywords: Species distribution models. Brazillian coastal benthic species. macroalgae. Spatial Conservation Prioritization. Corals.

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1 INTRODUÇÃO GERAL

“Many areas of the world remain seriously under-collected for most taxa, with the result that even for higher plants, reliable, systematic species range maps — the necessary basis for robust analyses of diversity patterns — are available only for a fraction of the earth’s surface”

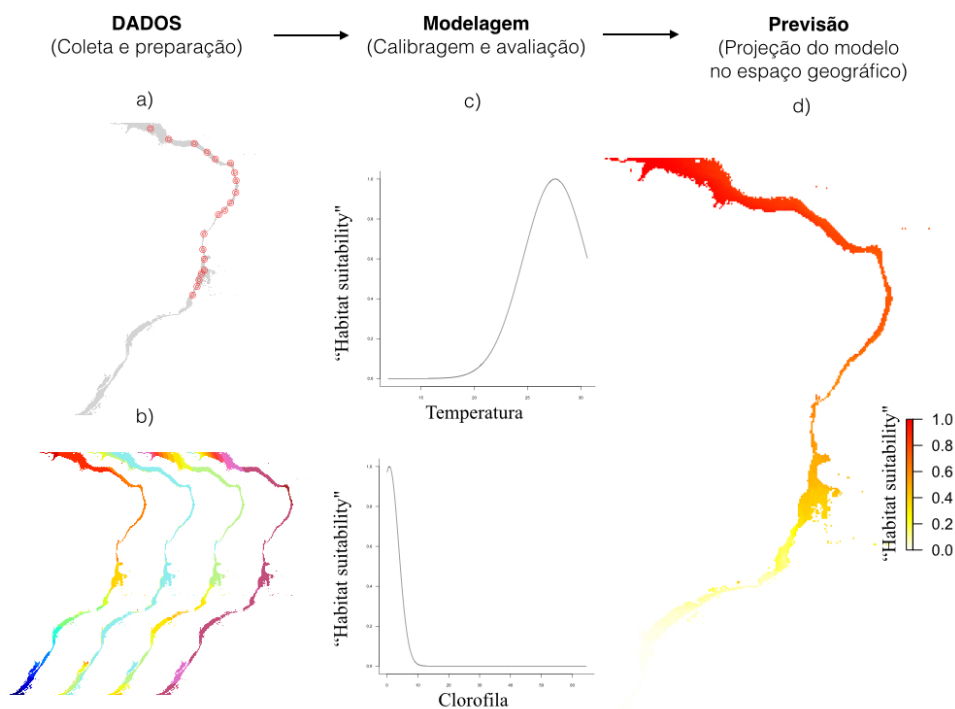
Whittaker et al., 2005

A distribuição geográfica da maioria das espécies é, ainda, insuficientemente conhecida (Whittaker et al., 2005; Tsoar et al. 2007; Hortal et al., 2008), o que pode limitar os estudos mais básicos de Ecologia e Conservação. As deficiências em nosso conhecimento das distribuições das espécies ocorrem desde escalas locais até globais sendo esse problema denominado The Wallacean shortfall (Lomolino, 2004). Uma das principais causas é a falta de um planejamento amostral sistemático em escalas biogeográficas relevantes nos inventários da biodiversidade (Whittaker et al., 2005), em outras palavras, geralmente estão sendo inventariadas regiões geopolíticas (ou parte delas) em vez de domínios biogeográficos. Embora a biodiversidade de alguns táxons em determinadas regiões seja relativamente bem conhecida, em outras regiões e para certos grupos taxonômicos, as lacunas são mais pronunciadas (Hortal et al., 2008). Esse problema é particularmente crítico para organismos bentônicos, como os abordados nesse estudo, e regiões megadiversas, como o Brasil.

O interesse nos fatores que determinam as distribuições das espécies é recorrente na Biogeografia (Darwin, 1859; Wallace, 1876; MacArthur, 1972; Holt e Keitt 2005; Sexton et al., 2009) com a finalidade de compreender/prever efeitos das alterações antropogênicas no ambiente natural, no clima e nos bens e serviços prestados pelos ecossistemas. Esses fatores podem ser divididos em: abióticos (como temperatura ou salinidade), bióticos (competição ou predação), e também fatores relacionados ao movimento (dispersão), e a interação entre esses fatores determina as distribuições das espécies (ver Soberón, 2007).

Os modelos de distribuição de espécies (Species distribution models), cuja utilização aumentou consideravelmente na última década (Robinson et al., 2011) consistem em uma útil ferramenta para reconstruir ou prever distribuições geográficas de espécies. O método usa a relação entre dados georreferenciados de ocorrência da espécie estudada (Figura 1a) e variáveis georreferenciadas relevantes para a sua distribuição (Figura 1b) para criar um modelo de nicho ecológico (Figura 1c) que pode ser projetado no espaço geográfico (Figura 1d), gerando uma previsão da distribuição da espécie (Elith et al., 2006; Elith e Leathwick 2009; Peterson et al., 2011).

Figura 1 - Representação resumida do processo de modelagem de distribuição de espécies. a) Dados de ocorrência georreferenciadas da espécie, b) Variáveis ecológicas relevantes para a distribuição da espécie georreferenciadas, c) Curvas resposta de um modelo de nicho ecológico e d) previsão da distribuição da espécie no espaço geográfico. A escala representa o habitat suitability, uma métrica de quão propício é o ambiente para a ocorrência da espécie.



Os modelos de distribuição de espécies vêm sendo aplicados a um diverso conjunto de questões ecológicas e biogeográficas. Por exemplo, examinando as congruências e/ou incongruências entre distribuições atuais e potenciais, é possível separar os papéis de fatores ecológicos e históricos determinantes das distribuições de espécies (Swenson 2006; Costa et al., 2008). Os modelos também podem ser usados em estudos de conservatismo de nicho (Tingley et al., 2014), ou identificar áreas com riqueza elevada de espécies (Garcia, 2006) e áreas para amostrar espécies raras (Guisan et al., 2006). Os modelos de distribuição de espécies são úteis para avaliar o potencial invasivo de espécies exóticas em novos ambientes (Peterson e Vieglais, 2001; Lozier et al., 2011; Vaclavik e Meentemeyer, 2012). Além disso, os modelos também têm sido usados para gerar mapas de distribuição que são empregados em análise de priorização espacial para a conservação (Faleiro et al., 2013; Fajardo et al., 2014; Lessmann et al., 2014; Sobral et al., 2014) e para prever os efeitos das mudanças climáticas nas distribuições das espécies (Araújo e Rahbek, 2006; Hijmans e Graham 2006; Martinez et al., 2012).

Embora os modelos de distribuição de espécies venham sendo empregados com sucesso em ambientes terrestres na última década (ver Elith e Leathwick, 2009 para uma revisão), eles foram pouco aplicados a organismos de ambientes marinhos (Robinson et al., 2011). Possivelmente, as dificuldades em obter dados ambientais dos oceanos do mundo, em uma escala de precisão relevante, podem ter impedido a popularização desses modelos em organismos de ambientes marinhos. Entretanto, recentemente, um conjunto de variáveis ambientais marinhas com cobertura global, o Bio-Oracle (Tyberghein et al. 2012), foi disponibilizado, o que vem possibilitando vários estudos de modelagem de distribuição de espécies marinhas (Coro et al., 2015; Martin et al., 2014; Jueterbock et al., 2013; Tyberghein et al. 2012).

Além das limitações impostas pelas variáveis ambientais, outro ponto importante é o viés geográfico amostral (quando o esforço amostral está distribuído de maneira heterogênea) nos dados de ocorrência. Basicamente o viés geográfico pode gerar um viés ambiental nos modelos, ou seja, quando as ocorrências estão concentradas numa dada região geográfica, o modelo gerado é enviesado afetando as previsões (Phillips et al., 2009; Kramer-Schadt et al., 2013). O viés é um problema frequente na grande maioria dos bancos de dados que reúnem informações de herbários, museus e outras coleções (Boakes et al., 2010; Beck et al., 2011; Jetz et al., 2012). Comumente, o viés é causado por maior acessibilidade a certas áreas, por exemplo, a proximidade de estradas e/ou maior densidade populacional (Barbosa et al., 2010, Kent e Carmel, 2011), maior esforço amostral dentro de unidades de conservação (Reddy e Dávalos, 2003), ou qualquer motivo que leve a menor ou maior esforço em uma determinada parte da área de ocorrência da espécie.

O viés pode provocar sobreajuste (*overfitting*) nos modelos (Anderson e Gonzalez, 2011) gerando previsões adequadas para o conjunto enviesado de ocorrências em vez de previsões para a distribuição da espécie em si. Existem vários métodos para lidar com o viés nos modelos (Phillips et al., 2009; Anderson e Gonzalez, 2011; Kramer-Schadt et al., 2013; Syfert et al., 2013; Fourcade et al., 2014), entre os mais comuns destacam-se a seleção dos pontos do background de acordo com a intensidade da amostragem (Target Group Background Phillips et al. 2009), a filtragem individual das ocorrências para reduzir sua intensidade em áreas com maior esforço amostral (Kramer-Schadt et al., 2013) e o ajuste fino (*fine-tuning*) da regularização do modelo (Anderson e Gonzalez, 2011). Independentemente do método, quando detectado o viés sempre deve ser corrigido para que os modelos sejam capazes de gerar previsões adequadas.

1.1 OBJETIVOS

1.1.1 Objetivo Geral

O objetivo deste trabalho foi investigar casos de estudo de bioinvasão, Biogeografia da Conservação e do efeito potencial das mudanças climáticas em organismos bentônicos na costa do Brasil utilizando modelagem de distribuição de espécies.

1.1.2 Objetivos Específicos

Modelar as distribuições das espécies de coral *Mussismilia hispida* (endêmica) e *Tubastraea coccinea* (invasora) para identificar a área de potencial sobreposição entre as suas distribuições (Artigo I);

Testar a hipótese de que o viés geográfico amostral nos dados de ocorrência empregados em modelos de distribuição de espécies pode modificar a análise de priorização espacial para a conservação (Artigo II);

Testar a hipótese de que as mudanças climáticas podem promover mudanças nas distribuições de espécies de macroalgas na costa do Brasil com diferentes padrões biogeográficos: cosmopolitas (*Ceramium brasiliense* e *Cryptonemia delicatula*), subtropicais (*Levringea brasiliensis* e *Plocamium brasiliense*) e tropicais (*Dictyopteris jolyana* e *Gelidium coarctatum*) (Artigo III).

2 ARTIGO I

RIUL, P.; Targino, C. H.; Júnior, L. A. C.; Creed, J. C.; Horta, P. A.; Costa, G. C. 2013. **Invasive potential of the coral *Tubastraea coccinea* in the southwest Atlantic.** Marine Ecology Progress Series (Halstenbek), v. 480, p. 73-81

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Invasive potential of the coral *Tubastraea coccinea* in the southwest Atlantic

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ABSTRACT

The orange cup coral *Tubastraea coccinea* was the first scleractinean to invade the western Atlantic. The species occurs throughout the Gulf of Mexico and the Caribbean Sea and has now established itself in the southwest Atlantic along the Brazilian coast. *T. coccinea* modifies native benthic communities, competes with an endemic coral species and demonstrates widespread invasive potential. We used species distribution modeling (SDM) to predict climatically suitable habitats for *T. coccinea* along the coastline of the southwestern Atlantic and identify the extent of the putative effects of this species on the native coral *Mussismilia hispida* by estimating areas of potential overlap between these species. The resulting SDMs predicted a large area of climatically suitable habitat available for invasion by *T. coccinea* and also predicted widespread occurrence of the endemic *M. hispida* along the Brazilian coast. The prediction of the *T. coccinea* distribution model suggests that suitable environmental conditions for the species occur throughout most of the littoral zone, including most of Brazil's marine protected areas. The overlap of the SDMs of *M. hispida* and *T. coccinea* revealed a large area with high habitat suitability for both species. Considering the invasive potential of *T. coccinea* and its ecological consequences, we concluded that this alien species could change the benthic communities of most of the shallow Brazilian coast and, as the invasive and native coral species have been shown to be antagonistic, *T. coccinea* represents a serious threat to *M. hispida* throughout most of its potential geographical distribution.

KEY WORDS: Bio-Oracle · Coral reefs · Invasion Ecology · Southwestern Atlantic · Species distribution modeling

INTRODUCTION

As a consequence of increased human mobility and global warming processes, the redistribution of world biodiversity and consequent species introductions and biological invasions have become more frequent (Macreadie et al. 2011). Biological invasion is considered to be one of the most important mechanisms of biodiversity loss (Sax et al. 2007), due to the negative effects of species interactions, changes in community structure (Shiganova 1998, Levine et al. 2004, Vilà et al. 2011) and ecosystem functioning (Vitousek et al. 1997, Stachowicz et al. 2002). These changes can have severe economical effects (Pimentel et al. 2001).

Being able to accurately predict the potential spread of an invasive species is valuable, as management initiatives (such as population registering, monitoring and controlling) can be focused where best suited to mitigate the negative effects of biological invasions. Interestingly, not all species, when transported beyond their natural range, are able to establish viable populations, spread and become invasive. Species invasion is a complex biological process and many hypotheses have been formulated to explain which factors drive the invasion process. One of the most cited hypothesis (Keane & Crawley 2002, Callaway & Ridenour 2004, Mitchell et al. 2006) states that when arriving in a new region a species experiences a release from its previous biological interactions and no longer has to deal with competitors, predators and pathogens present in its native region. Therefore, in this relatively enemy free space, the invader is able to outperform native species. Ultimately, in order for the invasion process to be successful, the invader must gain access to a new region and be able to cope with a new set of abiotic and biotic conditions.

The overarching factors that determine geographic distributions of species are: how organisms relate to their environment (i.e. niche requirements); interspecific interactions such as competition, predation, parasitism (Chave et al. 2002) and historical factors such as lack of dispersal opportunities (Brown et al. 1996). The intersection between these factors will determine species distributions (see Biotic, Abiotic and Migration BAM diagram in Soberón 2007). Environmental conditions (e.g. species abiotic niche requirements) are considered to be the main factor limiting species distributions at large geographical scales (Pearson & Dawson 2003, Soberón 2007, Soberón & Nakamura 2009). In the case of biological invasion, some consider the first and most important filters to be the abiotic barriers. Invaders are thought to have a greater chance of establishing a viable population if they are introduced to an area with a climate that closely matches their original range (Mack 1996, Duncan et al. 1999). Often, this climate-matching hypothesis is used as an underlying assumption in studies aimed at trying to predict the potential spread of invasive species using techniques such as species distribution modeling

(SDM) (e.g. Peterson & Vieglais 2001). Despite some scattered evidence that niche shifts may occur during the invasion process, a recent metaanalysis showed that climatic niche requirements of invasive species are conserved between their native and invaded ranges (Petitpierre et al. 2012).

SDM has emerged as a powerful tool for reconstructing or predicting species distributions and its use has grown impressively over the last decade (Robinson et al. 2011). SDM has also played a major role in assessing invasion potential and proliferation of exotic species in new environments (Peterson & Vieglais 2001, Lozier & Mills 2011, Vaclavik & Meentemeyer 2012). Although SDMs have been successfully employed in the terrestrial realm over the last decade (Elith & Leathwick 2009), they have clearly been underused in marine environments (Robinson et al. 2011). The difficulty of obtaining environmental data sets for the world's oceans at a relevant scale of precision has prevented widespread use of SDM in marine biogeographical and macroecological studies. However, Bio-Oracle (Tyberghein et al. 2012), a recently developed dataset of environmental variables for the world's oceans, has become available and will help us to shed light on various aspects of species distributions in marine environments.

The orange cup coral *Tubastraea coccinea* Lesson 1829, originally described from Bora Bora, today has a circumtropical distribution and was the first documented scleractinean coral to invade the western Atlantic (Cairns 2000). The species was first reported in the western Atlantic in 1943 in Puerto Rico and currently is successfully established in the Bahamas, throughout the Caribbean to Venezuela, into the northern Gulf of Mexico and into the Florida Keys (Cairns 1994, Cairns 2000, Fenner 2001, Fenner & Banks 2004, Sammarco et al. 2012). In the late 1980s, *T. coccinea* was first reported in the southwest Atlantic along the Brazilian coastline and occurs on rocky shores, oil platforms, ship hulls and underneath boulders along Bahia, Rio de Janeiro and São Paulo states, as well as on an oil platform further south off Santa Catarina state (Castro & Pires 2001, Ferreira 2003, Lopes 2009, Mantelatto et al. 2011, Sampaio et al. 2012). These reports have raised concerns over the effects of *T. coccinea* on the benthic environments where the species is establishing. Recently, the species has been reported to cause necrosis and deformation of *Mussismilia hispida* (Verrill 1901), a native reef-forming coral species endemic to Brazil, when co-occurring at a distance of <5 cm, with the potential to dominate and even exclude native species (Creed 2006). Experimental and descriptive studies have shown that *T. coccinea* and its (also invasive) congener *T. tagusensis* Wells, 1982 change the structure of benthic communities of invaded tropical rocky shores over time to a point where they have become, effectively, completely different communities (Lages et al. 2010, 2011). *M. hispida* colonies were shown to develop deformations in areas where they co-occur (Creed 2006) and different organisms colonized dead areas on the native coral including *T. coccinea* itself (Lages et al. 2010). Furthermore, recent in situ bioassays demonstrated that predation rates by generalist fishes were reduced by extracts of *Tubastraea* spp. (Lages et al. 2010), suggesting chemical defenses. In

addition, the settlement patterns of various macrobenthic species were altered on experimental substrates with chemical extracts of the invasive coral (Lages et al. 2010). In their study, the authors observed a reduction in colonization by the crustose coralline algae (Lages et al. 2010). *T. coccinea* and its invasive congener *T. tagusensis* modify the structure of benthic tropical rocky-shore communities (Lages et al. 2011), as there is a positive relationship between *Tubastraea* density and change in community structure. It has been estimated that a complete community dissimilarity (100 %) occurs when the invader cover reaches 45 % (Lages et al. 2011).

Considering the effects caused by the range expansion of the invasive coral species worldwide and the deleterious influence of this species on an endemic reef-builder as well as on overall benthic community, herein we employed SDM to: (1) generate predictive maps of climatically suitable habitat for the native *Mussismilia hispida* and the invasive *Tubastraea coccinea* in the southwestern Atlantic; and (2) overlap the distribution of *T. coccinea* and *M. hispida* in the southwest Atlantic to assess the extent of the putative effects of the alien species.

MATERIALS AND METHODS

To generate the SDMs, we collected occurrence data for the studied species from several sources. We performed searches for '*Mussismilia hispida*' and '*Tubastraea coccinea*' using the scientific indexes Web of Knowledge, ScienceDirect, PubMed and Scielo. We also accessed the geographic distribution databases Ocean Biogeographic Information System (OBIS) (Vanden Berghe 2011), The Global Biodiversity Information Facility (GBIF), and the Brazilian Thesis and Dissertation Database (Banco de Teses da Capes).

First, the data were examined in order to remove duplicate and incorrect entries (e.g. terrestrial records). As sampling bias in occurrence points is known to influence the results of SDMs (Phillips et al. 2009) and our data were not collected in a systematic fashion, more intensive sampling effort in some areas may have resulted in sampling bias. For this reason, we used the software OccurrenceThinner (Verbruggen 2012) to remove possible sampling bias in our datasets. OccurrenceThinner uses the species occurrence records and a kernel density grid file representing the region of study to filter occurrence records based on the kernel density at the coordinates of the occurrence records, omitting more occurrence records from densely sampled regions. Finally, the resulting datasets for *Tubastraea coccinea* and *Mussismilia hispida* contained 149 and 77 unique localities respectively. To improve predictions of the distribution of *T. coccinea* in the invaded area, the models were produced incorporating the information of environmental tolerances of the species in both native and invaded areas (see Jiménez-Valverde et al. 2011 for a review).

To build the SDMs, we used environmental variables from the Bio-Oracle dataset (Tyberghein et al. 2012). Ecological theory posits that many factors may determine species distributions. Bio-Oracle was assembled in order

to maximize different potential factors that may influence marine species distributions, including physical, chemical and biological variables. The dataset is composed of 23 environmental layers of geophysical, biotic and climate rasters for world oceans in a 5 arcmin spatial resolution. A multivariate analysis of the dataset revealed that different variables have different dimensions of potential factors affecting species distributions. More details on the variables and dataset can be seen in Tyberghein et al. (2012). To avoid modeling issues relating to over-parameterization and multicollinearity of environmental layers, we adopted a variable selection procedure as described in Rissler & Apodaca 2007. First, we built a correlation matrix among all variables. We then identified highly correlated variables ($r > 0.9$) and excluded one of them from the model based on their biological relevance. We built another correlation matrix and repeated the procedure until all variables kept in the model had correlations < 0.9 . The final set of predictors with their biological relevance for species distribution is presented in Table 1. Data manipulation was performed in raster package (Hijmans & Etten 2012) and correlation analysis on R vs. 2.15 (R Core Team 2012).

There are several algorithms to create SDMs with different advantages and caveats (Elith et al. 2006). To overcome these modeling challenges, one solution is to create an ensemble of predictions from multiple SDMs approaches (Araújo & New 2007). Herein, we created an ensemble model based on the predictions produced by 10 different algorithms: Artificial Neural Networks (ANN), Classification and Regression Tree (CTA), Flexible Discriminant Analysis (FDA), Generalized Additive Models (GAM), Generalized Boosted Regression Modeling (GBM), Generalized Linear Models (GLM), Multivariate Adaptive Regression Splines (MARS), Maximum Entropy (MAXENT), Random Forest (RF) and Surface Range Envelope (SRE). SDMs were built using 10 runs (partitioned subsets of the full dataset) and 1000 randomly selected pseudoabsences with equal weighting for presences and absences. These parameters are recommended for increasing model accuracy (Barbet-Massin et al. 2012). Additionally, presence and pseudo-absence were randomly separated into subsets with 70 and 30% of records used to calibrate and evaluate the accuracy of the models, respectively, according to the area under the receiver–operating characteristic (ROC) curve (AUC), Cohen’s Kappa (KAPPA) and True skill statistic (TSS). The importance of the predictors to each model (Table S1) and their evaluation metrics (Table S2) and fitted functions (Figs. S1 to S18) are provided as supplementary material (www.int-res.com/articles/suppl/m480p073_supp.pdf). Ensembles were created using a conservative classification where only highest quality models according to the TSS evaluation metric threshold (i.e. $TSS > 0.8$) were retained. This procedure generated predictions with the consensual mean probability (of the retained models) of climatically suitable habitat for both species. Finally, to estimate the putative area where the species may co-occur, we used the total consensus (i.e. the mean of all projections) and TSS (as evaluation metric and associated threshold) to transform the logistic probabilities into presence and absence

(binary transformation). All modeling was performed using the R package Biomod2 (Thuiller et al. 2009, 2012).

RESULTS

The resulting ensemble models based on 10 algorithms performed well with evaluation scores ≥ 0.95 , except for Kappa, for both *Tubastraea coccinea* (AUC = 0.993; KAPPA = 0.858; TSS = 0.95) and *Mussismilia hispida* (AUC = 0.996; KAPPA = 0.881; TSS = 0.967). Predictor contribution varied across models and species (see Table S1). Overall, the variables: minimal chlorophyll a (chl a) (chlomin), maximal diffuse attenuation (damax), min. diffuse attenuation (damin), mean sea surface temperature (sstmean), calcite and maximal cloud cover (cloudmax) contributed to the higher number of models for both species. Maximal photosynthetically available radiation (parmax), pH, salinity, silicate, max. chl a (chlomax) and nitrate were less important. For *T. coccinea*, damin, chlomin and sstmean contributed more, and damax, calcite and sstmean contributed more for *M. hispida*. For both species, higher probabilities of occurrence were found in the coastal zone, decreasing progressively towards the ocean, except in the Abrolhos Bank where they remained high. The predicted habitat suitability maps for both species and the putative cooccurrence area are presented in Figs. 1 & 2. The *T. coccinea* model successfully predicted the occurrence of the species along the Brazilian coast where it has been considered an invasive species since the early 1980s (Fig. 1). This prediction suggests that the species will find suitable habitat for range expansion continuously from the northern to southern limits of the invaded littoral zone, in addition to putative occurrence in some oceanic islands and the Abrolhos Bank (34° 42' W; 18° S). Lower probabilities were found in the extreme north (from ~1°15'S to 3°N). The model for *M. hispida* predicted the occurrence of the species continuously along the southwest Atlantic coastline from northeast to southeast Brazil, including the Abrolhos Bank (Fig. 2a). Lower probabilities were found above northern (near latitude 5° S) and below the southern (25° S) known limits of the species distribution. The overlap of *M. hispida* and *T. coccinea* revealed a large area with high climatically suitable habitat for both species (Fig. 2b).

DISCUSSION

SDM produced high performance ensemble models according to the evaluation metrics applied. These results indicate high accuracy in the predictive maps produced, increasing the reliability of the models. The main predictors were light-related variables and temperature. These results were well supported by physiological traits of both species, as clearer and warmer waters are more propitious for reef corals species worldwide (Hallock & Schlager 1986, Brown 1997). The predicted distribution of *Tubastraea coccinea* indicates a large area of climatically suitable habitat available for invasion. Regarding *Mussismilia hispida*, the model predicted its occurrence along most of the

Brazilian littoral zone.

Tubastraea coccinea has a circumtropical distribution occurring in eastern, central and western Pacific, Indian Ocean and eastern and western Atlantic (Cairns 1994, Cairns 2000). In spite of its occurrence worldwide, the type specimen was described from Bora Bora, Society Islands, in the South Pacific, and its broad distribution today may have occurred through accidental introductions (Cairns 1994). An alternative hypothesis assumes that the origin of the species is the Cape Verde Islands or Gulf of Guinea in the eastern Atlantic (Cairns 2000). Regardless, *T. coccinea* is considered an alien species in the western Atlantic based on: (1) relatively recent early records of the species, since *T. coccinea* is conspicuous and would hardly go unnoticed; and (2) the lack of paleontological records, since no Caribbean fossils of *Tubastraea* have been found (Cairns 1999).

Tubastraea coccinea was first recorded in the western Atlantic in the early 1940s from Curaçao and the northern coast of Jamaica (Vaughan & Wells 1943). The first record from the Netherlands Antilles was made by Boschma (1953) in the late 1940s; some of these specimens were reportedly attached to ship bottoms (Cairns 2000). Roos (1971) reported an increase in the abundance of *T. coccinea* in Curaçao and along the northern coast of Jamaica, corroborating, according to Cairns (2000), the hypothesis that the species was expanding its range through the Caribbean Sea and increasing in local abundance. Cairns (2000) proposed a scenario to explain the invasion history of *T. coccinea* through the western Atlantic. The species was introduced into the Caribbean at Curaçao or Puerto Rico by ships from the Indo-Pacific. From Curaçao, it rapidly spread to Aruba and Bonaire and then to the Gulf of Cariaco, Sucre, Venezuela and Panama. The species rapidly established in Jamaica after introduction and from Puerto Rico it spread east reaching Saba and west to Silver Bank. It then reached eastern Cuba from Jamaica or Puerto Rico. In the early 2000s, the species was not yet found in Cuba, Bahamas, Florida, the Gulf of Mexico and western Caribbean (Cairns 2000). In 2001, *T. coccinea* was reported in the Gulf of Mexico, at various sites, inhabiting artificial substrates such as oil platforms, ships and airplane wrecks (Fenner 2001, Sammarco et al. 2004) before invading natural hard grounds and reefs (Fenner & Banks 2004).

In Brazil, the genus *Tubastraea* was reported in the late 1980s, when colonies were recorded on offshore oil platforms stationed in the Campos basin, northern Rio de Janeiro State (Castro & Pires 2001); currently, *Tubastraea coccinea* occurs on many rocky shores in the southern Rio de Janeiro state (de Paula & Creed 2005, Creed et al. 2008, Silva et al. 2011). *T. coccinea* was also detected at Arraial do Cabo, eastern Rio de Janeiro, in the late 1990s under rocky boulders and after 1 yr the colonies had tripled in number and size. Ferreira (2003) also reported *T. coccinea* as dominant in the littoral fringe and subtidal zones of rocky shores at Ilha Grande, 300 km south of Arraial do Cabo. De Paula & Creed (2005) reported the genus *Tubastraea* covering a distance of 25 km on the rocky shores at Ilha Grande. More recently, in 2008, the species had expanded 130 km southwest (Mantelatto et al. 2011) to an oil platform in

Santa Catarina state, southern Brazil (Lopes 2009), in addition to newly added records along the northeastern coast of Bahia state (Sampaio et al. 2012).

We demonstrated that *Tubastraea coccinea* will find suitable habitat for range expansion along most of the littoral zone and some oceanic islands, including most of the national marine protected areas. The broad extent of putative occurrence raises serious concerns when considering the already known deleterious effects of this species on native benthic assemblages. This species and its invasive congener are likely able to avoid native fish predators and cause changes in the patterns of settlement of native colonizing organisms (Lages et al. 2010), and dramatically modify the community structure in benthic environments (Lages et al. 2011).

The SDM generated a good prediction of climatically suitable habitat for *Mussismilia hispida*, including an extremely large area, the Abrolhos Bank reef complex, where the continental platform widens to form the main coral reef area in the southern Atlantic. Some degree of under-prediction (e.g. low probabilities of occurrence) was detected in the oceanic islands. The coral genus *Mussismila* is endemic to Brazil and *M. hispida* along with its congeners *M. brazilensis* and *M. hartii* are considered important and abundant reef building species on the Abrolhos Bank (Castro & Pires 2001). *M. hispida* is a shallow water hermatypic coral species occurring from Rio Grande do Norte to São Paulo States, in addition to Parcel do Manoel Luiz, Fernando de Noronha Archipelago and the Rocas Atoll (Laborel 1967, Castro & Pires 2001).

For marine systems only a small number of invasions and their effects have been described so far (Ruiz et al. 1997). Consequently, information on interactions between native and alien species in marine environments is scarce. There is a considerable amount of information on the effects of the green seaweed *Caulerpa taxifolia* (M. Vahl) C. Agardh in the Mediterranean Sea, where negative effects are seen from single populations of native species (Pergent et al. 2008) to whole assemblages and habitat structure (Santini-Bellan et al. 1996). In Brazil, experiments with the alien octocoral *Stereonephthya aff. curvata* (Kükenthal 1905) demonstrated that the species had an allelopathic effect capable of causing necrosis in tissues of the endemic gorgonian *Phyllogorgia dilatata* Esper, 1806 and is also able to avoid fish consumers (Lages et al. 2006).

The overlap of the SDMs of the alien and native species demonstrated a large area of suitable habitat for both *Tubastraea coccinea* and *Mussismilia hispida*. This indicates a preeminent threat to the endemic species through the continued co-occurrence of the 2 species and the known deleterious effect of *T. coccinea* on *M. hispida* (Creed 2006). Considering the interactions of these 2 species, *Tubastraea* may outcompete and even exclude *M. hispida*, as contact between colonies of these genera result in necrosis in *Mussismilia* but not in *Tubastraea* (Creed 2006), so the risk of affecting the populations of *M. hispida* is substantial. Lages et al. (2011) demonstrated the occurrence of dramatic changes on community structure due to the invasion of *Tubastraea* spp. in communities where *M. hispida* was one of the most abundant taxa.

Species distribution modeling is a useful tool for a plethora of studies, including those interested in evaluating the potential effects of biological invasions. When it is possible to couple the results of modeling with information based on experimental and observational studies, such as the studies presented and reported here, SDM is a useful tool for predicting change through native-alien species interactions in a realistic environmental framework. In general terms, SDM has been rarely applied in studies of marine environments due to the difficulties in obtaining data on environmental variables at appropriate scales and spatial resolution for most world regions. We believe that the recently available environmental dataset Bio-Oracle is an important contribution to the marine macroecologist's toolbox. Our results support the concerns raised by Creed (2006) and suggest that further studies of the relationship between *Mussismilia hispida* and *Tubastraea coccinea*, including manipulative experiments of growth, interactions with other species and reproduction of *Tubastraea* in invaded areas, should be conducted to confirm the potential effect of this invader in marine coastal environments.

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Table 1 - Selected environmental predictors with biological justification for their inclusion.

Predictor	Justification for predictor
Mean Calcite Concentration (mol/m ³) - Calcite	Calcite (and aragonite) are needed for coral skeleton accretion (Gattuso et al. 1998)
Minimum Chlorophyll A mg/m ³ - Chlomin	Reef corals are adapted to nutrient deficient, clear water conditions (Hallock and Schlager 1986)
Maximum Chlorophyll A mg/m ³ - Chlmax	Idem
Maximum Cloud cover (%) - Cloudmax	Light is required by zooxanthellate corals and reefs in general (Yentsch et al. 2002)
Minimum Diffuse Attenuation m ⁻¹ - Damin	Idem
Maximum Diffuse Attenuation m ⁻¹ - Damax	idem
Mean Nitrate Concentration µmol/l - Nitrate	Reef corals are adapted to nutrient deficient, clear water conditions (Hallock and Schlager 1986)
Maximum Photosynthetically Available Radiation (Einstein /m ² /day) - Parmax	Light requirements of zooxanthellate corals (Yentsch et al. 2002)
Mean pH - pH	pH is related to coral calcification (Anthony et al. 2008)
Mean Salinity PSS - Salinity	Corals are sensible to wide ranges in salinity (Muthiga and Szmant 1987)
Mean silicate Concentration µmol/l - Silicate	Where coral reefs grow on terrigenous sediments, carbonate and silicate (quartz) sands can be found in close proximity (Rasheed et al. 2003)
Mean Sea Surface Temperature (°C) - SSTMean	Coral distribution is determined by sea surface temperatures (Brown, 1997)

Figure 1 – Distribution of climatically suitable environments for *Tubastraea coccinea* in Southwest Atlantic. Circles represent the unique localities used to train the model.

Figure 2 – Distribution of climatically suitable environments for *Mussismilia hispida* (a) and regions with suitable environments for both species (b) in Southwest Atlantic. Circles represent the unique localities used to train the model of *M. hispida*.



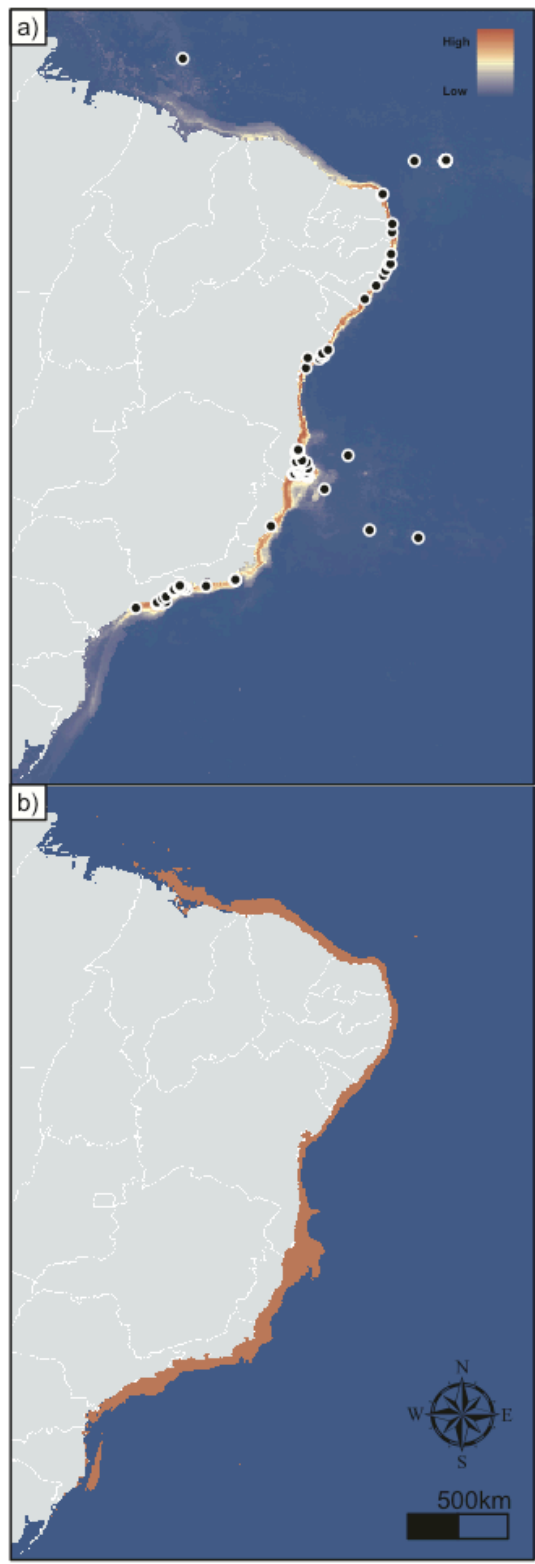


Table S1 – Mean and sd (\pm) AUC, KAPPA and TSS of 10 replicated runs for each model. Note that AUC can not be calculated to SRE once it produces only presence/absence of the species.

Model	Species	Evaluation		
		AUC	KAPPA	TSS
ANN	<i>T. coccinea</i>	0.882 \pm 0.066	0.577 \pm 0.148	0.710 \pm 0.134
	<i>M. hispida</i>	0.932 \pm 0.022	0.750 \pm 0.066	0.797 \pm 0.062
CTA	<i>T. coccinea</i>	0.889 \pm 0.032	0.662 \pm 0.072	0.763 \pm 0.054
	<i>M. hispida</i>	0.881 \pm 0.065	0.639 \pm 0.106	0.779 \pm 0.100
FDA	<i>T. coccinea</i>	0.936 \pm 0.014	0.645 \pm 0.040	0.750 \pm 0.045
	<i>M. hispida</i>	0.906 \pm 0.034	0.781 \pm 0.089	0.801 \pm 0.074
GAM	<i>T. coccinea</i>	0.938 \pm 0.017	0.707 \pm 0.040	0.773 \pm 0.042
	<i>M. hispida</i>	0.914 \pm 0.046	0.731 \pm 0.086	0.758 \pm 0.091
GBM	<i>T. coccinea</i>	0.958 \pm 0.015	0.749 \pm 0.053	0.825 \pm 0.048
	<i>M. hispida</i>	0.936 \pm 0.047	0.752 \pm 0.095	0.839 \pm 0.075
GLM	<i>T. coccinea</i>	0.876 \pm 0.045	0.572 \pm 0.111	0.699 \pm 0.075
	<i>M. hispida</i>	0.845 \pm 0.053	0.498 \pm 0.175	0.688 \pm 0.102
MARS	<i>T. coccinea</i>	0.943 \pm 0.015	0.716 \pm 0.042	0.791 \pm 0.034
	<i>M. hispida</i>	0.895 \pm 0.061	0.762 \pm 0.091	0.787 \pm 0.074
MAXENT	<i>T. coccinea</i>	0.957 \pm 0.016	0.740 \pm 0.046	0.801 \pm 0.040
	<i>M. hispida</i>	0.941 \pm 0.036	0.735 \pm 0.078	0.816 \pm 0.080
RF	<i>T. coccinea</i>	0.959 \pm 0.012	0.787 \pm 0.041	0.824 \pm 0.036
	<i>M. hispida</i>	0.949 \pm 0.034	0.783 \pm 0.083	0.836 \pm 0.078
SRE	<i>T. coccinea</i>	-	0.405 \pm 0.086	0.452 \pm 0.100
	<i>M. hispida</i>	-	0.520 \pm 0.087	0.516 \pm 0.132

	<i>M.</i> <i>hispidida</i>	0.012	0.183	0.087	0.465	0.344	0	0.37	1	0.072	0.25	6	0.359	0.3	0.652
	<i>T.</i> <i>coccinea</i>	0.078	0	0.16	0.283	0	0.66	0.06	7	0.138	0	0	0.047	0	0.08
MARS	<i>M.</i> <i>hispidida</i>	0	0.183	0.489	0	1	0.23	0	0	0	0	0	0.17	0.168	0.037
	<i>T.</i> <i>coccinea</i>	0.247	0.089	0.313	0.126	0.011	0.01	0.11	2	0.007	0	0	0.009	0.003	0.226
MAXE	<i>M.</i> <i>hispidida</i>	0.452	0.101	0.25	0.011	0.123	0.00	0.12	6	0.022	0.16	7	0.15	0.031	0.161
NT	<i>T.</i> <i>coccinea</i>	0.095	0.018	0.116	0.112	0.016	0.04	0.07	1	0.005	0.01	1	0.01	0.027	0.113
RF	<i>M.</i> <i>hispidida</i>	0.048	0.027	0.059	0.015	0.01	0.01	0.02	3	0.013	0.03	4	0.059	0.014	0.042
	<i>T.</i> <i>coccinea</i>	0.085	0.046	0.053	0.049	0.047	0.04	0.06	3	0.024	0.04	7	0.032	0.016	0.137
SRE	<i>M.</i> <i>hispidida</i>	0.073	0.009	0.055	0.073	0.021	0.01	0.09	5	0.049	0.04	7	0.03	0.009	0.182

Figures S1-S18 – Fitted functions to each SDM algorithm by predictor for *Tubastraea coccinea* and *Mussismilia hispida*.

Figure S1 – ANN fitted functions by predictor for *Tubastraea coccinea*.

Figure S2 – CTA fitted functions by predictor for *Tubastraea coccinea*.

Figure S3 – FDA fitted functions by predictor for *Tubastraea coccinea*.

Figure S4 – GAM fitted functions by predictor for *Tubastraea coccinea*.

Figure S5 – GBM fitted functions by predictor for *Tubastraea coccinea*.

Figure S6 – GLM fitted functions by predictor for *Tubastraea coccinea*.

Figure S7 – MARS fitted functions by predictor for *Tubastraea coccinea*.

Figure S8 – MaxEnt fitted functions by predictor for *Tubastraea coccinea*.

Figure S9 – RF fitted functions by predictor for *Tubastraea coccinea*.

Figure S10 – ANN fitted functions by predictor for *Mussismilia hispida*.

Figure S11 – CTA fitted functions by predictor for *Mussismilia hispida*.

Figure S12 – FDA fitted functions by predictor for *Mussismilia hispida*.

Figure S13 – GAM fitted functions by predictor for *Mussismilia hispida*.

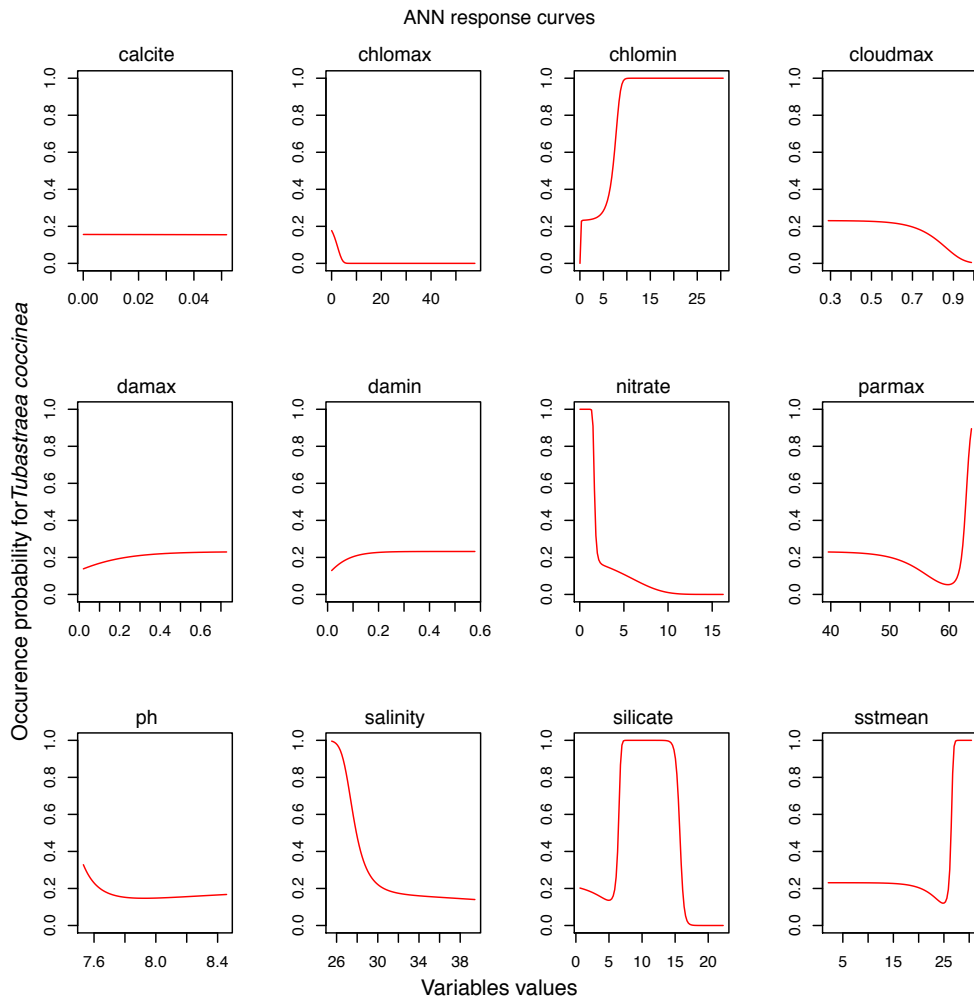
Figure S14 – GBM fitted functions by predictor for *Mussismilia hispida*.

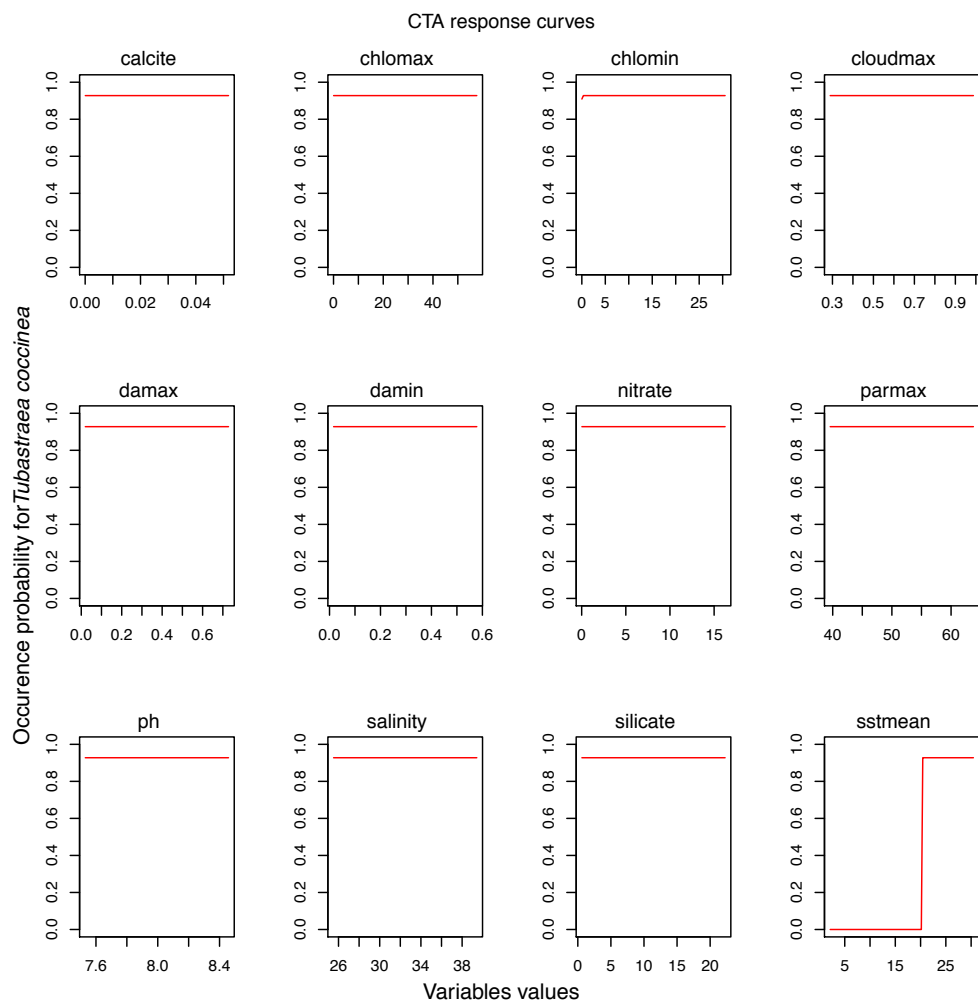
Figure S15 – GLM fitted functions by predictor for *Mussismilia hispida*.

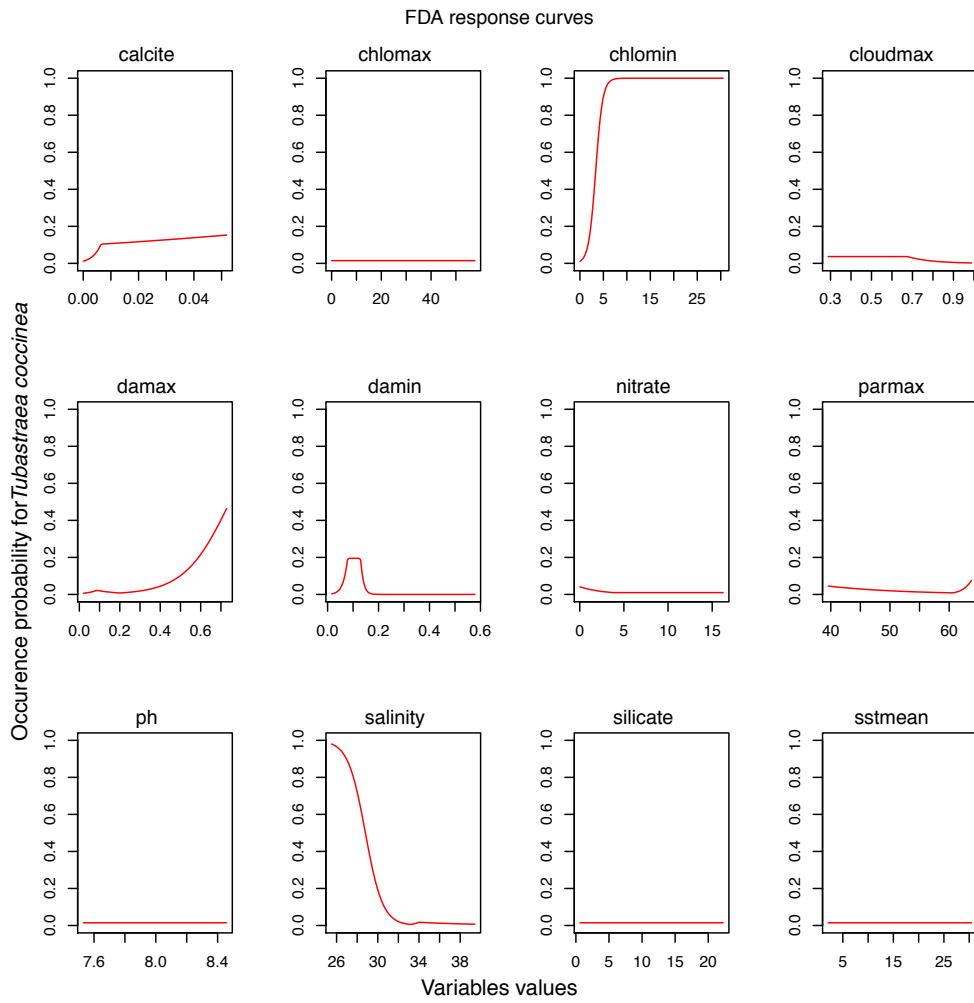
Figure S16 – MARS fitted functions by predictor for *Mussismilia hispida*.

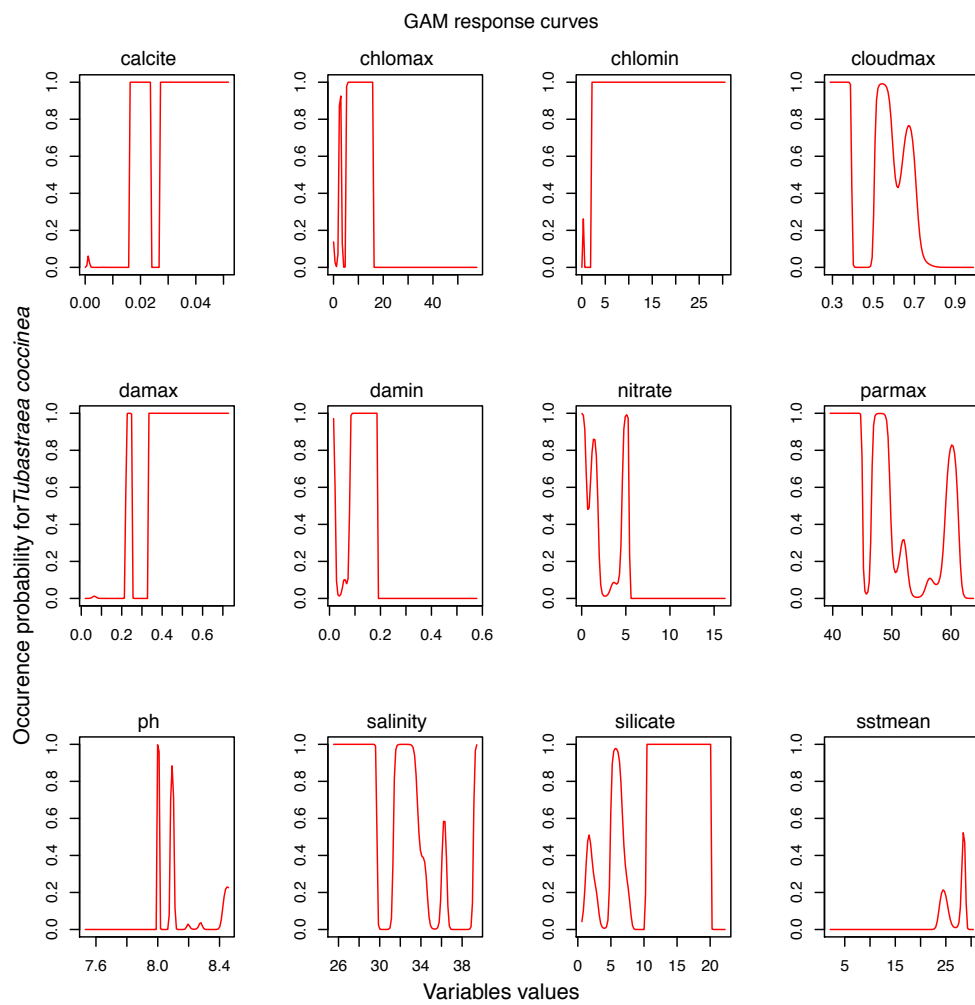
Figure S17 – MaxEnt fitted functions by predictor for *Mussismilia hispida*.

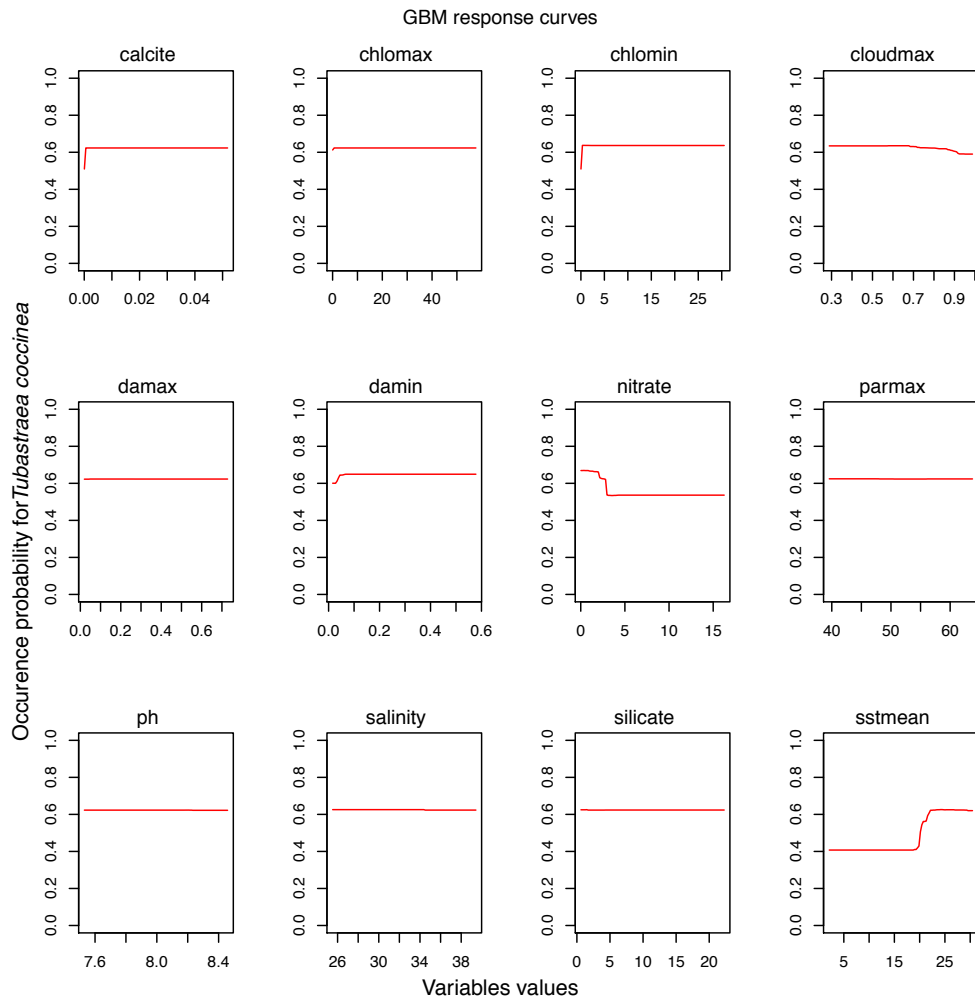
Figure S18 – RF fitted functions by predictor for *Mussismilia hispida*.

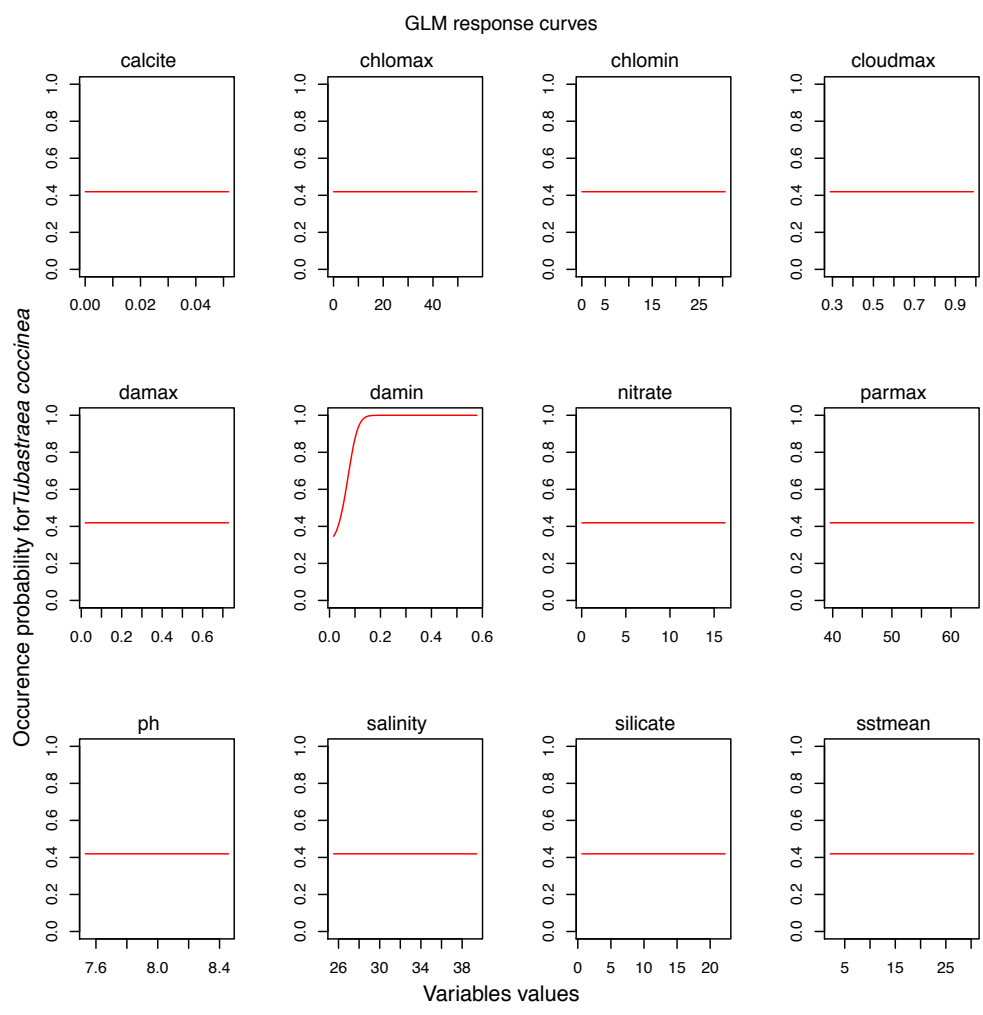


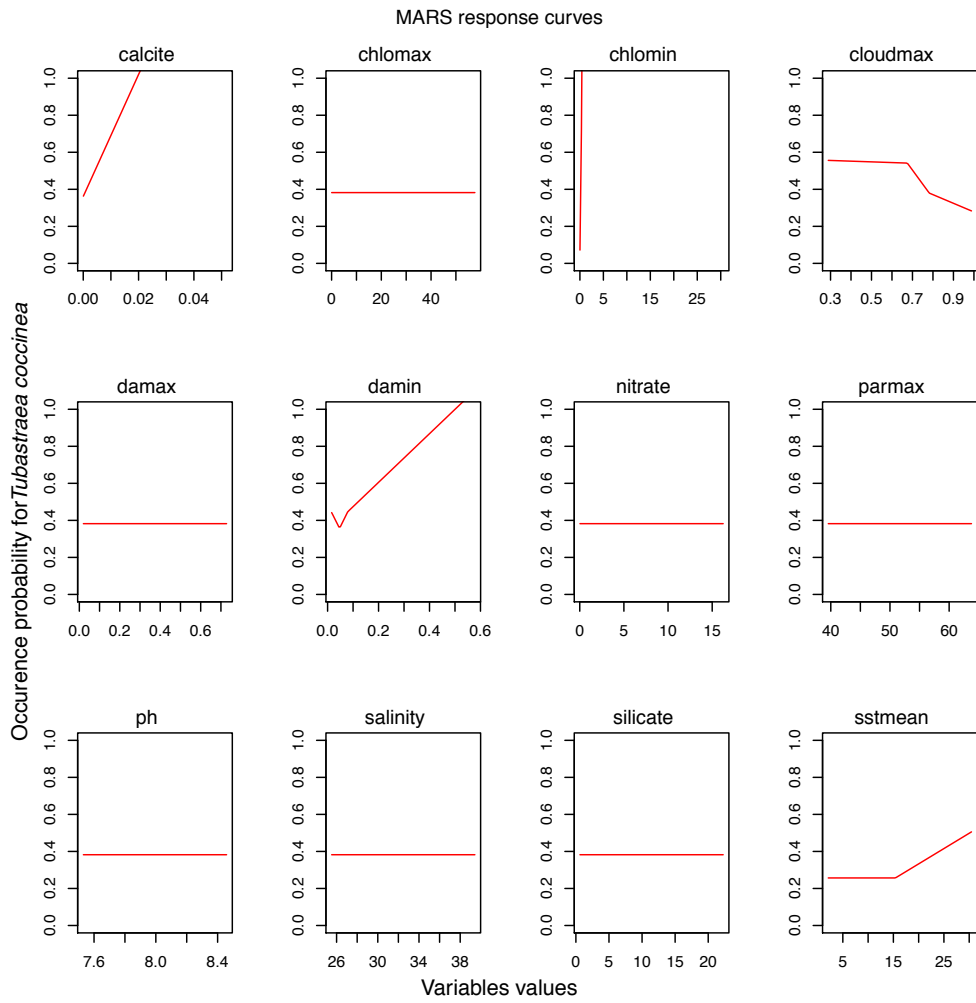


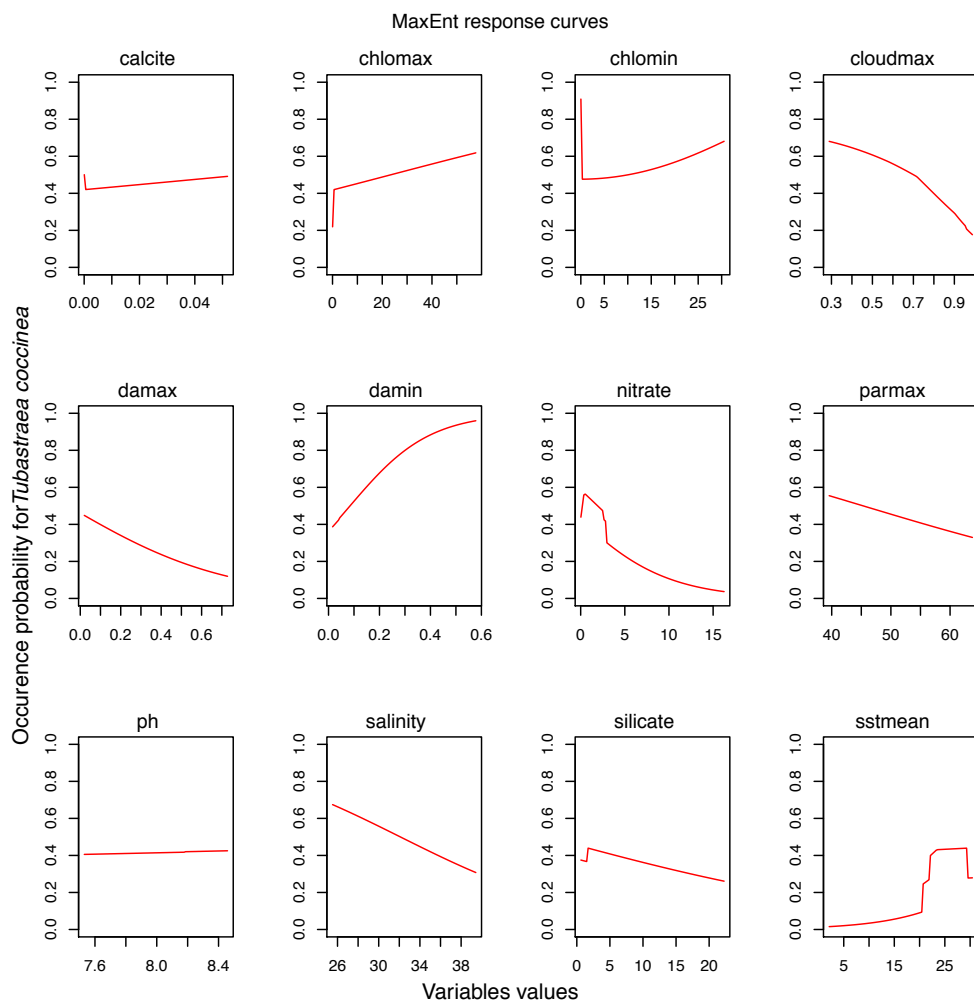


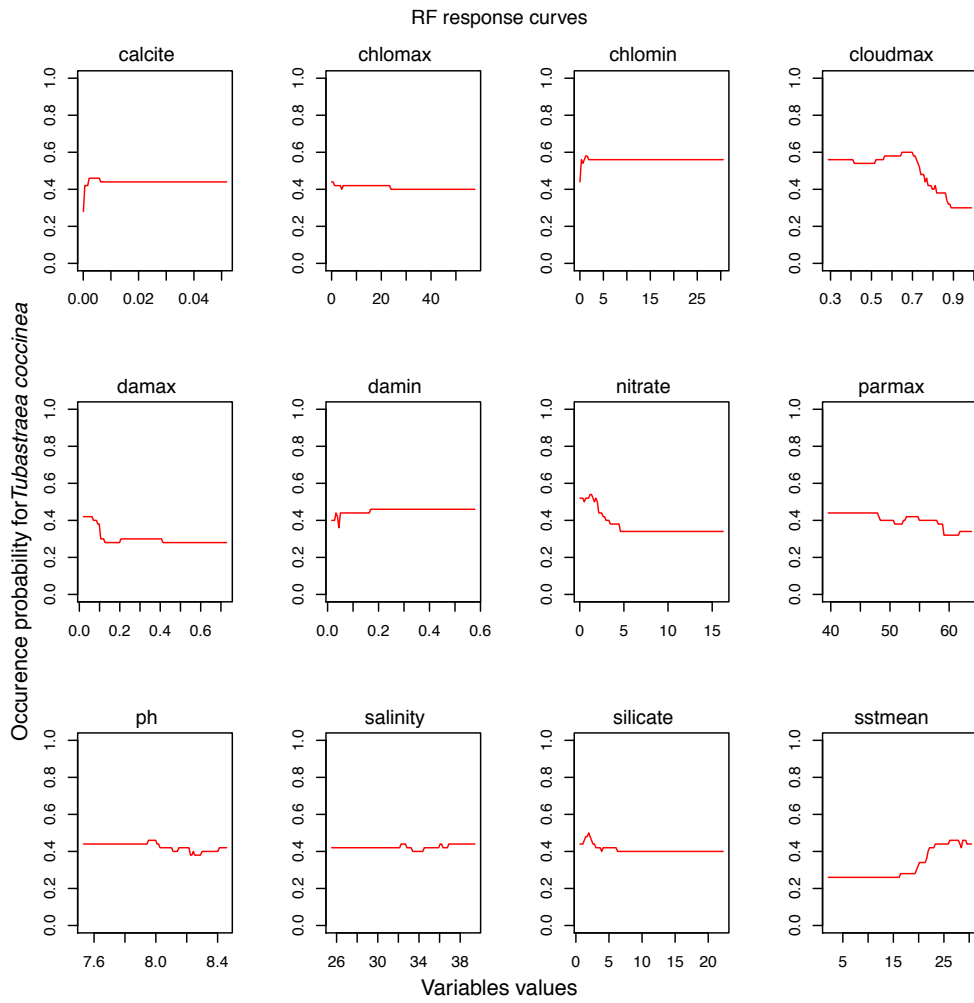


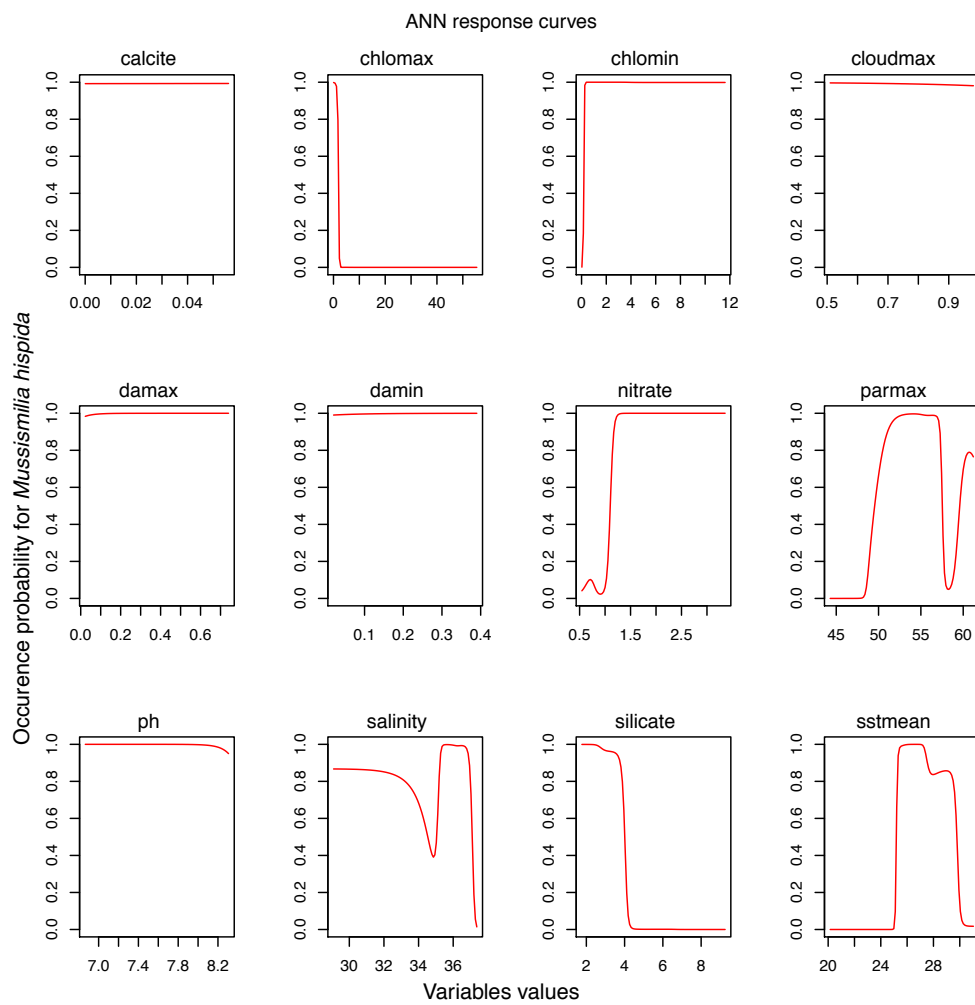


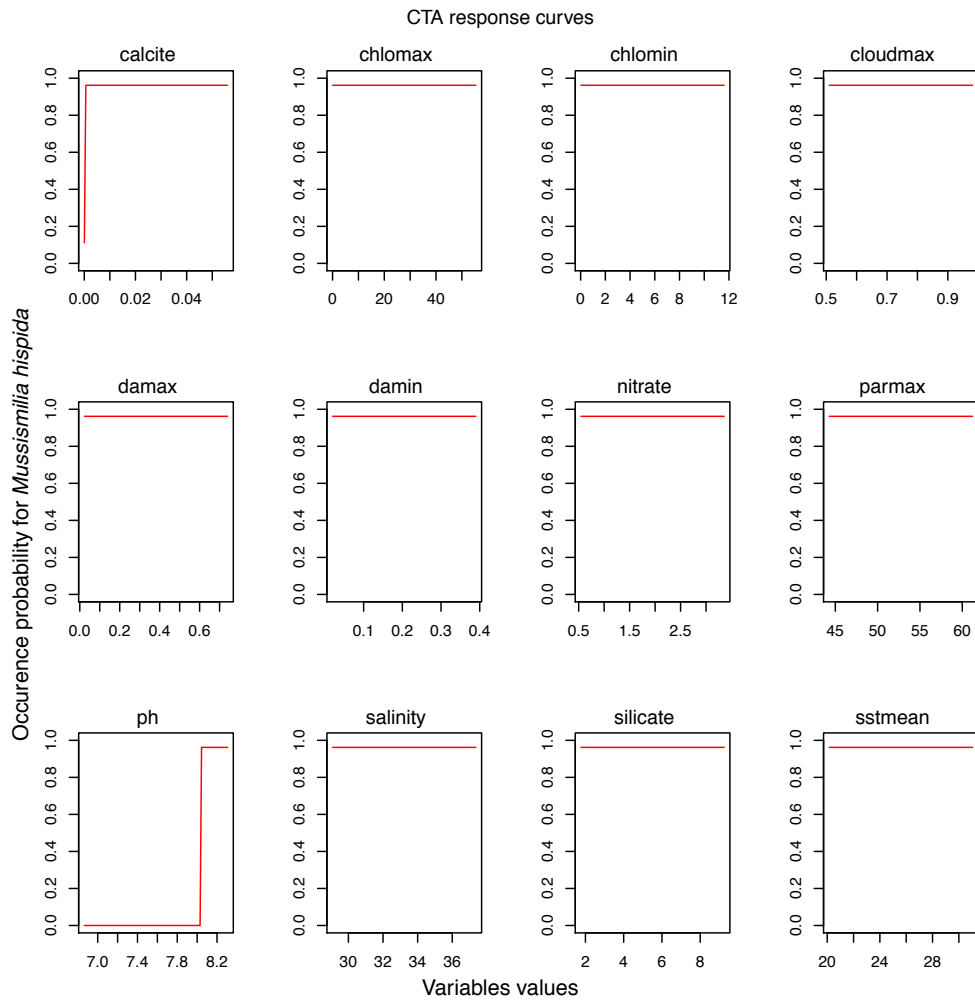


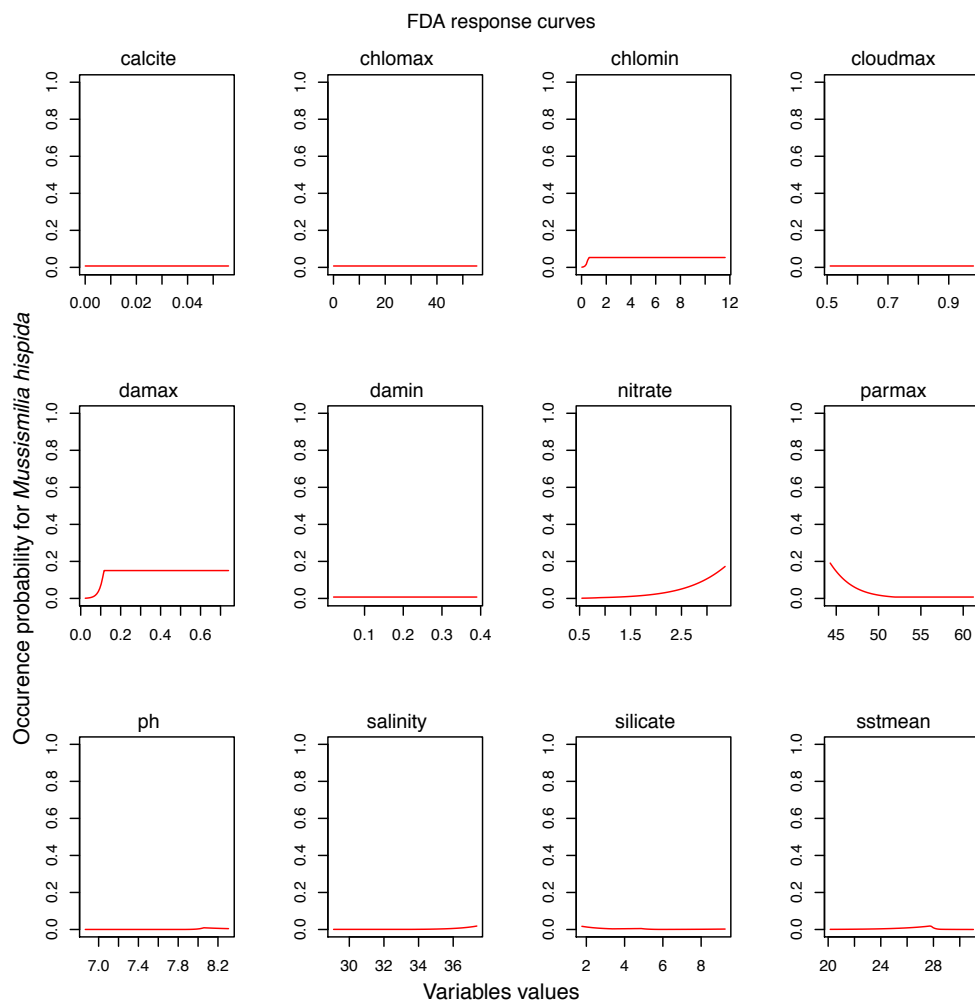


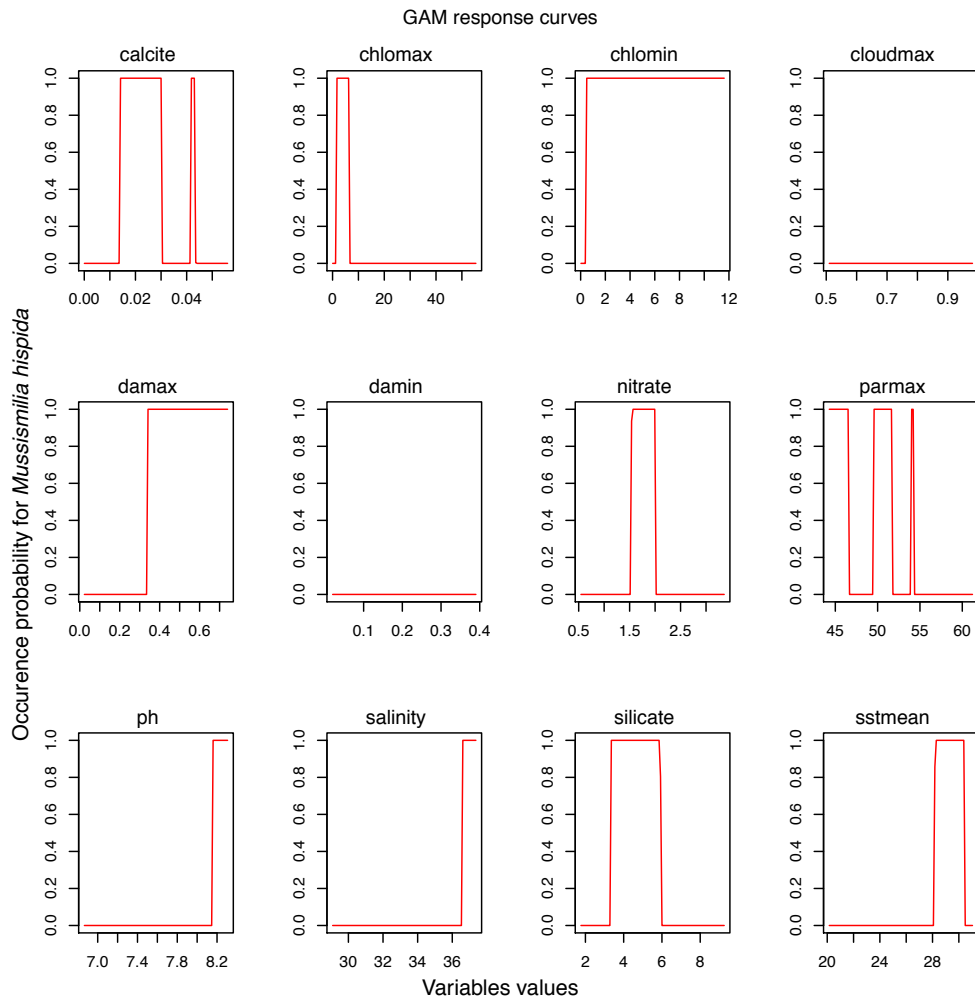


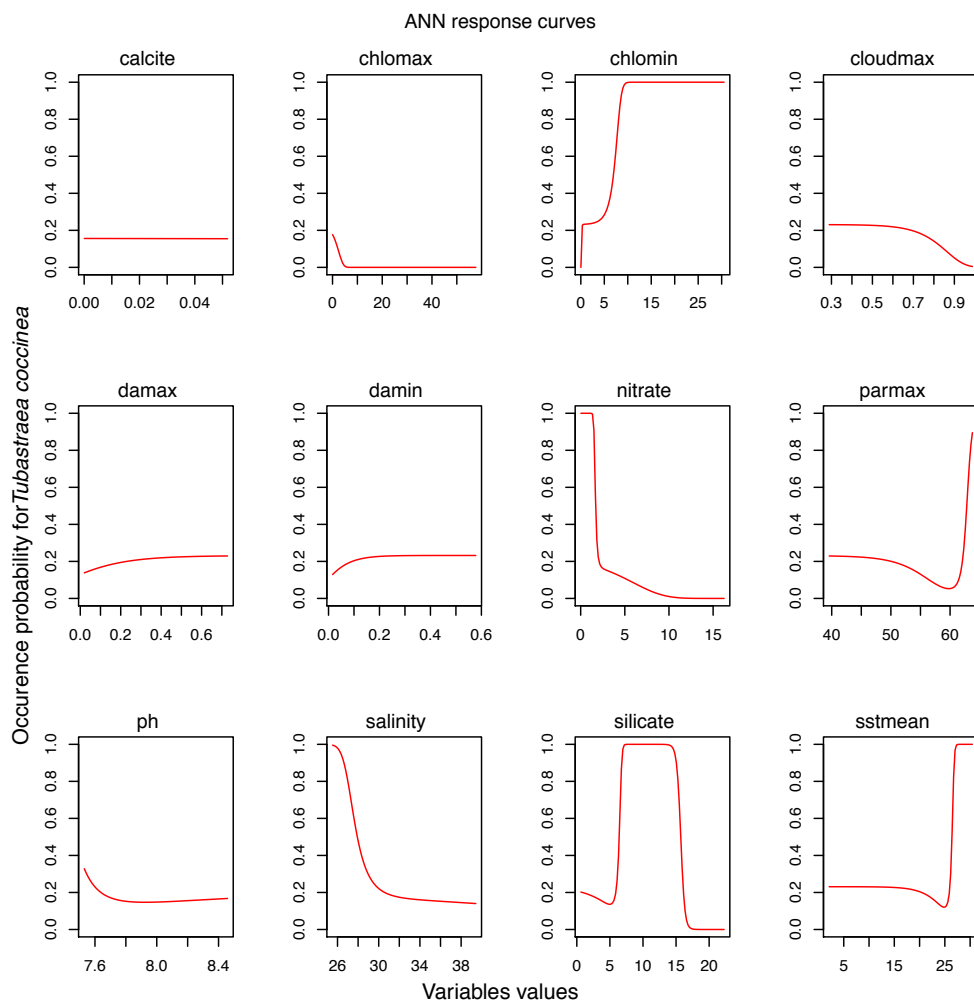


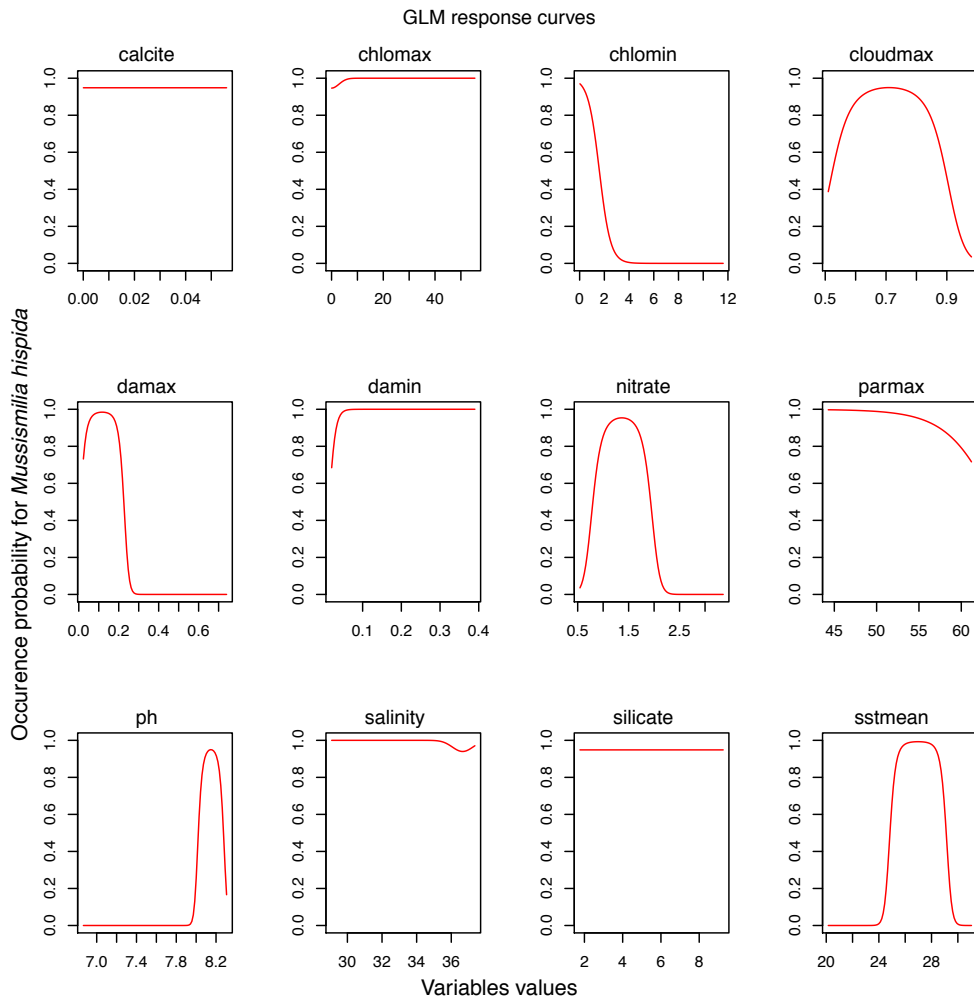


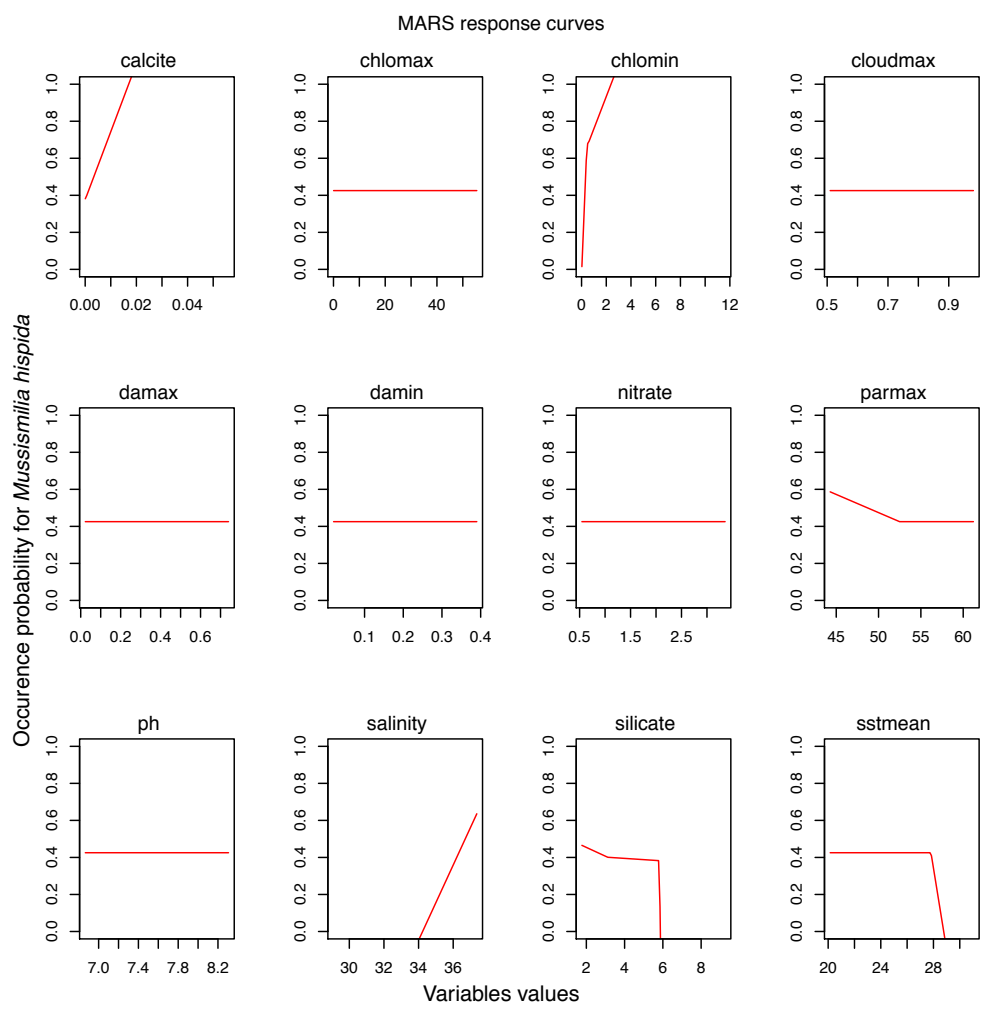


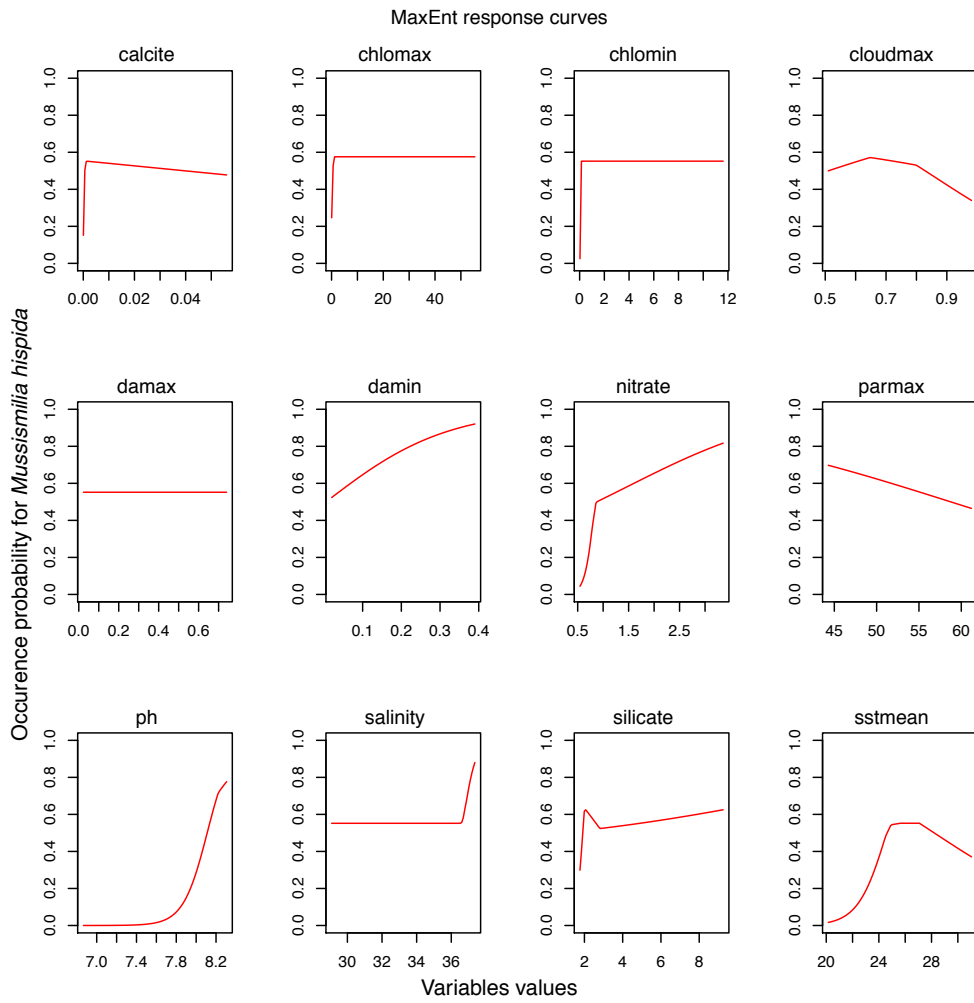


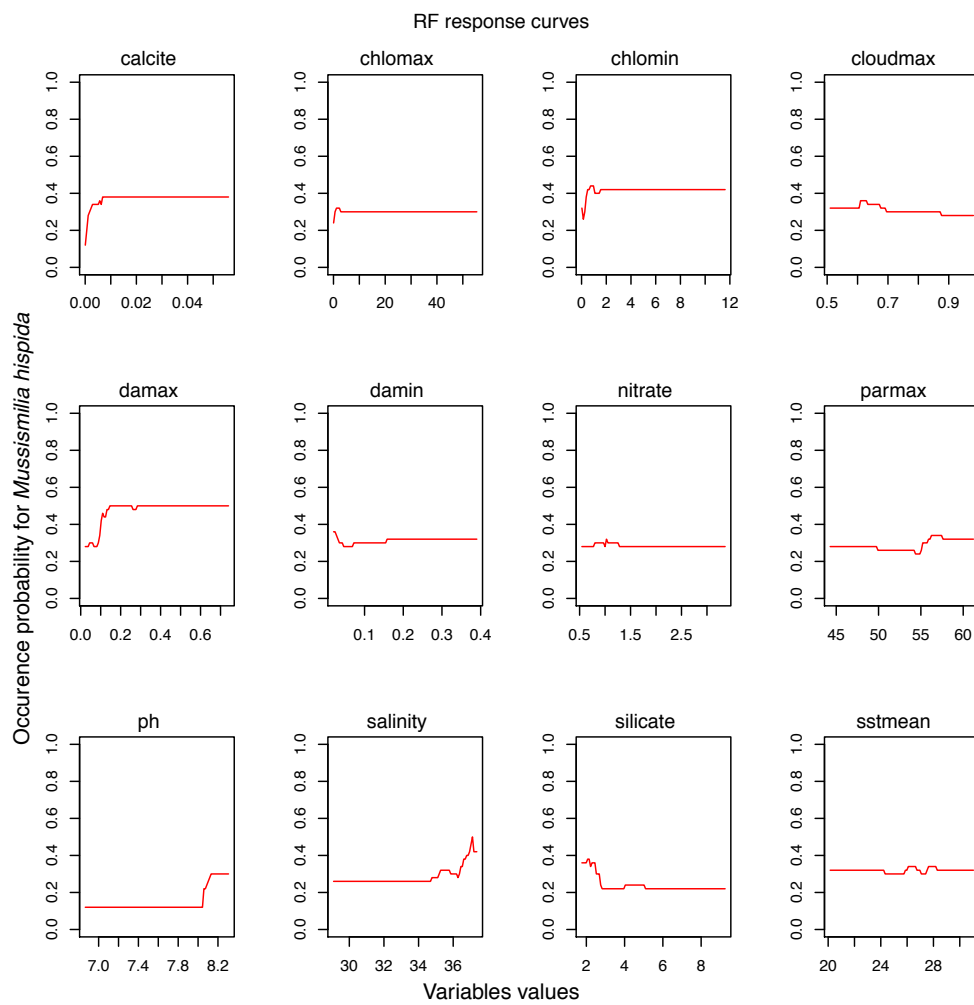












3 ARTIGO II

RIUL, P.; Carranza, A.; Di Minin, E.; Costa, G. C.; Horta, P. A.; Pagliosa, P. R. 2015. **Geographical sampling bias changes spatial conservation prioritization**

Artigo formatado para a revista Conservation Biology

GEOGRAPHICAL SAMPLING BIAS CHANGES SPATIAL CONSERVATION PRIORITIZATION

Running head: Bias in conservation prioritization

Keywords: NONATO base, polychaetes, Spatial conservation planning, Species Distribution Modeling, Zonation software.

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Abstract

Species distribution modeling is increasingly used to estimate geographical distributions of species for spatial conservation prioritization. However, most biodiversity data is geographically biased (when sampling effort is unevenly distributed). Herein we tested for the first time if and how geographical sampling bias affects the outcomes of

spatial conservation prioritization. We used two strategies to estimate the distributions of 40 soft-bottom polychaete species in the coast of the southwestern Atlantic: i) random selection of background (sampling bias is not incorporated), and ii) selection of background according to sampling intensity (sampling bias is incorporated). Our results show spatial conservation prioritization is affected by sampling bias, assigning higher conservation priority to cells according to higher sampling intensity. However, when sampling bias is accounted, the portfolio was less affected by sampling intensity, increasing the prioritization of areas for which little information was available. Finally, the performance curves revealed an overestimation in the proportion of distributions remaining with a decrease in landscape lost when geographical sampling bias was not incorporated. Also, the average and minimum representations were higher when sampling bias was accounted. We conclude that sampling bias can strongly affect spatial conservation prioritization, potentially leading to misallocation of conservation resource to areas with high sampling intensity. We recommend sampling bias should always be considered in spatial conservation prioritization whenever data from well-designed field surveys are unavailable.

Introduction

Spatial conservation prioritization (SCP) is a field of conservation biology that aims to select priority areas for conservation when limited resources should be allocated effectively (Moilanen et al. 2009; Di Minin et al. 2014). An important stage of SCP deals with compiling the most appropriate data on the spatial distributions of biodiversity features (e.g. species) (Rondinini et al. 2006), critical to answer questions in conservation biogeography (Whittaker et al. 2005). Based on the distribution of biodiversity (i.e. species, environments, ecosystem services) and/or conservation cost features (i.e. alternative land uses), SCP provides multi-disciplinary informed support for either conservation or alternative land use actions (Di Minin et al. 2013).

One critical limitation of SCP is data quality. Uncertainties in feature distributions (i.e. inaccuracy in our knowledge of species distributions) are prone to occur (Hortal et al. 2008, Moilanen 2012). For this reason, data quality imperatively constrains the prioritization process. When data are not available, data acquisition and preparation becomes the most time-consuming stage in SCP (Lehtomäki & Moilanen 2013). Alternatively, SCP often relies on the use of surrogates (such as habitat types or ecosystem services) for representing many

aspects of biodiversity (e.g. Di Minin & Moilanen, 2014). Major sources of uncertainties are commission (assuming the species is present in a place it is absent) and omission (assuming the species is absent in a place it is present) errors (Rondinini et al. 2006). Because of commission and omission errors, uncertainties may flaw SCP by misallocating conservation efforts in areas that are not efficient to promote long-term persistence of biodiversity (Moilanen et al. 2006). In practical terms, commission error may lead to the prioritization of areas unable to protect features' distribution, while omission error may underestimate the conservation value of potentially important areas.

Currently, lack of comprehensive information regarding species distributions is widespread (Tsoar et al. 2007; Hortal et al. 2008) and thus species distribution modeling (SDM) is one convenient way to estimate species distribution for SCP (Lei et al. 2003; Wilson et al. 2005; Moilanen et al. 2008) and for assessing conservation status of species (Domínguez-Domínguez et al. 2006). SDM uses the relationship between species presence-absence or presence-only data and environmental variables to estimate the geographical area in which species are likely to occur (Elith et al. 2006, Elith & Leathwick 2009a). However, geographical sampling bias (when sampling effort is unevenly distributed across space) is known to be widespread in web-based biodiversity databases (Boakes et al. 2010; Beck et al. 2011; Jetz et al. 2012) and represent a primary cause of uncertainty when estimating species distributions by SDM. Geographical sampling bias is caused by higher site accessibility, for example because of proximity to roads, and/or human population size (Barbosa et al. 2010, Kent & Carmel, 2011), higher sampling effort in particular sites, for example inside protected areas (Reddy & Dávalos, 2003), or any reason leading to more or less sample effort devoted to an area across the landscape.

One important assumption of SDM is that occurrence data represent a random sample from the environmental space being modeled (Phillips et al. 2006). However, when data on biodiversity are geographically biased, better-sampled areas are most likely to show a higher number of occurrence records. For this reason, geographical bias may lead to sampling bias in environmental space (Phillips et al. 2009) and affect SDM predictions (Kramer-Schadt et al. 2013, Syfert et al. 2013). Sampling bias can contribute to model overfit (Anderson & Gonzalez, 2011) and thus generate predictions of suitable habitats for the known occurrences instead of estimating the suitable habitats for the species.

Our incomplete knowledge of species distributions continues to challenge conservation actions (Hortal et al. 2008). Uncertainty in building SDM can change priority allocation in SCP (Moilanen et al. 2009). Despite the growing awareness on sampling bias effects on SDM (Hortal et al. 2008; Lobo 2008; Phillips et al. 2009; Costa et al. 2010; Bystriakova et al. 2012; Kramer-Schadt et al. 2013; Syfert et al. 2013) it is rarely considered and in many cases neglected in SCP (Yackulic et al. 2013, Fourcade et al. 2014). We expect that when sampling bias is not addressed in SDM, the SCP will allocate conservation priorities according to sampling bias (higher priorities to cells with more occurrence). Alternatively, as SCP rank priorities over the entire landscape based in balanced complementarity, the analysis will search for sites where features are currently under or not represented, so the effect of sampling bias may be evened out spatially. Here we test the hypothesis that geographical sampling bias in occurrence data used by SDM can affect SCP. To test this hypothesis we used SDM to predict the geographical distribution of 40 species of polychaetes in part of the shallow coast of southwestern Atlantic, by using a biased occurrence dataset from a virtual database. We tested whether geographical sampling bias can mislead SCP leading to the prioritization of cells with highest sampling efforts. We further applied a correction for sampling bias and showed how it changed the selection of conservation priorities and the performance of SCP.

Methods

Occurrence data

To test the effects of sampling bias in SCP we used data from marine polychaetes, key benthic group in the marine realm considering both the number of species and number of individuals. Polychaetes play a key role in benthic ecosystems as bioindicators (Borja et al. 2010), bioturbators (Dorgan et al. 2006) and ecosystem engineers (Jones, 1984) transforming organic matter, remobilizing inorganic particles, and aerating sub-surface sediment layer. Further, several species are used as indicators of environmental quality (Borja et al. 2010). We used occurrence data of polychaetes species between 0 and -35 latitude degrees, along the coasts of Brazil and Uruguay. Note that we are not suggesting that polychaetes are a surrogate for SCP targeting whole marine biodiversity, but only using this data on species distribution to illustrate how geographical sampling bias in occurrences can affect SCP.

Data were extracted from the NONATObase (Pagliosa et al. 2014), a virtual database of polychaete species containing information of occurrences from estuaries, coastal lagoons, continental shelf and continental slope in South Western Atlantic. The NONATObase is maintained by the NONATO network (an association of Brazilian, Uruguayan, and Argentinian experts in polychaetes). Taxonomic validation of regional species names and the establishment of criteria to qualify the reliability of species identification are constantly updated by a taxonomy committee formed by members of the NONATO network. We selected 40 coastal soft-sediment species occurring up to 50 m depth and with at least 25 unique localities (Elith and Leathwick, 2009b) at a resolution of 5 arc minutes across our landscape. Most occurrences were distributed in two main regions (separated by a zone with few records) in southwest and south of the Brazilian coast between 23°S and 28°S latitudes (Fig. 1). Other occurrences are scattered along the coastline except by few areas concentrating more records than the overall pattern such as northeastern Brazil from 7°S to 9°S latitudes and the coast of Uruguay near 34°S latitude. Our data is clearly biased towards the urbanized areas of the coast and location of research institutions with a tradition in Polychaeta taxonomy.

Modeling species distributions

Variables used for SDM were selected to represent the main dimensions known to influence marine coastal benthic species distribution at this spatial scale (Carranza et al. 2009; Miloslavich et al. 2011). To build the models, we used environmental layers from Bio-Oracle (Tyberghein et al. 2012), including physical, chemical and biological layers at a resolution of 5 arcmin (~ 9.2 km). As our goal was to model the distribution of the species at the coastal zone only, the environmental layers were cropped for a maximum depth of 50 m. To avoid modeling over-parameterization and multicollinearity between variables we tested for correlation among all variables, detected highly correlated layers ($r > 0.7$) and excluded one of them from the model based on their biological relevance. Note as overfitting is prone to occur in MaxEnt we used a conservative correlation coefficient for excluding variables. The final set of environmental layers used for modeling and their biological justification consisted of three variables (Table 1).

We used the MaxEnt software for SDM using maximum entropy (Phillips et al. 2006). We chose MaxEnt because it is one of the most popular tools for species distribution modeling (Merow et al. 2013),

allowing for easy comparison and implementation. In addition, MaxEnt has been shown to present a good predictive performance for presence-only modeling in a diverse set of scenarios (Elith et al. 2006). Based on our numbers of occurrences, and to reduce overfitting, MaxEnt models were built using linear, quadratic and hinge features according to Phillips & Dudík (2008). Also, as we were modeling several species, environmental layers were cropped to match the extension of all our sampling points, and default regularization was used (Merow et al. 2013). These procedures were intended to reduce the overestimation of species potential habitat, simultaneously taking into account the likely under-representation of rare and/or operationally hard-to-detect species. Unique localities were randomly partitioned into 100 subsets of 70 and 30% that were used to calibrate and evaluate, respectively, the accuracy of the models. Two distinct measures were used to assess model performance; the area under the receiver operating characteristic curve (AUC - Fielding & Bell, 1997) and the true skill statistics (TSS - Allouche et al. 2006). Despite the existence of criticisms on the use of AUC based on presence-only data for model evaluation (Lobo et al. 2008), here we compared two models of the same species in the same area (Peterson et al. 2011).

There are several methods to deal with geographical biases in SDM (Phillips et al. 2009; Anderson & Gonzalez, 2011; Kramer-Schadt et al. 2013; Syfert et al. 2013; Fourcade et al. 2014). However, our aim here is not to evaluate the performance of the wide array of available SDM methods and different ways to account for geographic bias. Rather, we illustrate the accumulative effects of individual models based on geographically biased occurrence data in SCP. To test the effects of geographical sampling bias, we used two SDM strategies to estimate the geographical distributions for 40 species of soft-bottom polychaetes: i) random selection of background points where sampling bias is not incorporated (Random Background, hereafter RBG), and ii) weighted selection of background points according to sampling intensity where sampling bias is incorporated (Target Group Background (Phillips et al. 2009, as adapted in Fitzpatrick et al. 2013) - hereafter TGB). TGB method uses information on sampling intensity, based on the occurrences of similar species, for selecting MaxEnt background points (higher sampling intensity higher probability of selection). To account for sampling intensity we created a raster with the total number of individuals of polychaetes collected in each cell and used a kernel density probability function to estimate the sampling intensity for all cells in our landscape. This method was based on the target group

background method proposed by Phillips et al. (2009). The key difference is that the kernel density function is used to estimate a sampling intensity for all cells in the landscape, instead of limiting the number of background points by constraining them to the cells with records in our study area ($n=322$). By default, MaxEnt uses 10,000 points to generate the background, however, our study area have far less cells ($n=4663$). To avoid selection of all cells, which would make the two backgrounds the same, we generated the background selecting 1,000 points for each strategy. A visual illustration of random and weighted background selection according to sampling intensity for one species is provided (Appendix S1). Filtering individual species occurrences is an alternative solution to account for sampling bias in SDM (Kramer-Schadt et al. 2003), especially when the number of occurrences is not a limitation. Another alternative is species-specific fine-tuning of model regularization (Anderson & Gonzalez, 2011). We used the TGB approach instead of occurrence filtering because our number of occurrences was low for some species (see Appendix S2). Filtering would reduce even further the number occurrences available to build the models. Also, while modeling many species simultaneously, species-specific fine-tuning would be very time-consuming. SCP assessments are often based on multi-taxa information sometimes containing hundreds of species; therefore, we believe TGB is more appropriate. To assess the effects of background manipulation on the model evaluation scores (AUC and TSS) we compared RBG vs. TGB for each species using Mann-Whitney tests.

Spatial conservation prioritization

We used the SCP software Zonation (Di Minin et al. 2014) to create portfolios using RBG and TGB models. One key feature of Zonation is that it produces a complementarity-based and balanced ranking of conservation priority over the entire landscape, rather than satisfying specific targets with minimum cost (Moilanen et al. 2005). Specifically, it produces the priority ranking via iterative loss minimization, always removing the landscape element that leads to smallest loss of conservation value, accounting for total and remaining distribution of features, weights given to features, feature-specific connectivity, etc. In Zonation, we used the additive-benefit function cell-removal rule that computes a maximum-utility type solution (Arponen et al. 2005, Di Minin et al. 2013, Di Minin & Moilanen 2012), where value is additive across species, and where feature-specific

representation is converted to value via concave power functions, which most commonly are parameterized according to the canonical species–area curve (Moilanen, 2007). Here, the exponent of the power function was set to $z = 0.25$ for all features. In addition, we set the same weight ($w=1$) for each species. We also accounted for aggregation in the final conservation solution by using the boundary length penalty (Lehtomäki & Moilanen, 2013). We also included uncertainty analysis in SCP, by using the standard deviation for each species distribution model developed in MaxEnt (Moilanen et al. 2006). In doing so, we identified the most robust solutions given a level of uncertainty in species distributions.

Zonation analyses produce a spatial conservation portfolio mapping the priorities of each cell across the landscape and also a set of performance curves describing the extent to which each feature remain at each fraction of the landscape (Di Minin et al. 2014). Each curve quantifies the proportion of the original occurrences retained for each biodiversity feature, at each top fraction of the seascape chosen for conservation (Lehtomäki & Moilanen, 2013). Performance curves start from 1.0 because the full landscape includes the full distribution of the species. When no areas are chosen (at the other end) the protection level for the feature is zero. Further, in order to depict the effect of sampling bias under different prioritization scenarios, Zonation generated portfolios based on RBG and TGB were compared. In addition, to illustrate the bias effect on SCP, here we also show the top 10% coastal and marine area according to the target defined from Aichi Biodiversity Targets to 2020 (Convention on Biological Diversity, 2010). Our purpose here is to demonstrate the effects of geographical sampling bias in the SCP, and although we used real data, we assumed that constraints of a real-world conservation planning process (e.g. economic costs, other social and political constraints) were not affecting the prioritization. Zonation can take these factors into account (see Di Minin et al. 2013).

Results

The two distinct evaluation scores used indicate that our models performed well in both modeling scenarios. For RBG models AUC ranged from 0.86 to 0.96 and TSS from 0.56 to 0.81. For TGB models, AUC ranged from 0.77 to 0.94 and TSS from 0.41 to 0.73 (only three species had TSS lower than 0.45). Mann-Whitney U tests indicated a decrease in model performance in both AUC and TSS after accounting

for the sampling bias for most species, with some exceptions where no differences were observed. Model evaluation with the number of unique localities used and mean and standard deviation of AUC and TSS and U test comparisons between models with different background selection for each species is summarized (Appendix S2).

The spatial priority areas for the conservation portfolios generated using RBG and TGB revealed a strong influence of geographical sampling bias (Fig. 2). In the RBG portfolio, the priority areas were concentrated in regions with higher sampling intensity (Fig. 2a). Otherwise, accounting for sampling bias smoothed this clustering effect and produced a more spatially dispersed solution (Fig. 2b). Additionally, in the portfolio based on TGB, the influence of higher sampling intensity was reduced and priority areas were also located in areas with fewer occurrence records (Fig. 2b). For a map depicting the differences between the TGB and RBG portfolios see Appendix S3.

The higher influence of sampling intensity in priority selection can be clearly observed in a map depicting top 10% top priority cells (Fig. 3). In RBG the top 10% cells are constrained to the area with higher sampling intensity (Fig. 3a), whereas in TGB the selection of priority changes and includes areas northwards (Fig. 3b)

Zonation performance curves were also affected by sampling bias (Fig. 4). We observed that the relationship between the proportion of distributions remaining and landscape lost was not linear (Fig. 4a) when the correction was not applied, tending to linearity in unbiased models (Fig. 4b). Also, the average and minimum representations in TGB were higher than in RBG.

Discussion

MaxEnt produced good performance models according to the evaluation metrics and thresholds applied. Here, the correction of sampling bias led to a reduction in AUC and TSS for most of the species. While some studies report increases in the quality of SDM predictions when correcting models for sampling bias (Phillips et al. 2009; Kramer-Schadt et al. 2013), others have also observed reductions (Fitzpatrick et al. 2013; Fourcade et al. 2014). One possible explanation is model performance is known to decrease when background points are taken from a restricted region (VanDerWal et al. 2009), as we corrected the sampling bias by constraining most of background points to higher sampled regions. Although the effect of sampling bias in SDM is reported in the literature, this issue is commonly neglected or poorly

addressed (Yackulic et al. 2013; Fourcade et al. 2014) and to our knowledge this is the first empirical evaluation on the effects of not accounting for sampling bias in conservation portfolios based on SDM.

Here we demonstrate non-corrected individual models force prioritization to areas more densely sampled. In fact, sampling effort is a crucial variable when assessing biodiversity at large spatial scales and ignoring this may lead to flawed predictions of species distributions as environmental bias in the datasets is very influential (Kramer-Schadt et al. 2013). Moreover, when using biased occurrences, one may be generating distribution models for the particular set of samples in which the species occurs, instead of the actual species distribution (Phillips et al. 2009). This is a concerning issue as most of available biodiversity data are already known to be suffering from sampling bias (Yesson et al. 2007; Hortal et al. 2008; Syfert et al. 2013). Therefore, one could argue the use of biased data for setting priorities based on complementarity should be avoided. However, threats to biodiversity such as the extinction debt (Kuussaari et al. 2009), economic development (Turner et al. 2007; Di Minin et al. 2013) and time for implementation (Grantham et al. 2009; Marshall et al. 2014) demand the use of available biased data in certain circumstances (i.e when only biased data is available, resources for additional sampling unavailable and rapid conservation prioritization is required). However, presence-only data should be used with caution and only when it is the only available data (Hermoso et al. 2014). Thus, under these circumstances, one solution to improve the overall prioritization process arises by incorporating correction for sampling bias prior to modeling species distributions. In our case, the correction resulted in portfolios less influenced by sampling bias. Based in our knowledge of the studied system we assume this result is more reasonable, although our originally biased data prevent us of knowing which of our conservation portfolios is more realistic. However, comparing our portfolios with an independent assessment of SCP of Brazilian coast (Villa Nova, 2014), we observed TGB portfolio as being more similar. The independent assessment encompasses our full area of study and was based in biodiversity (including several species of macroalgae, corals and reef fishes and existing marine protected areas) and cost features (fishing pressure and oil and gas exploration).

Sampling bias can potentially lead to the misallocation of conservation resources and decreased return on investment (Reddy and Dávalos 2003; Rondinini et al. 2006; Grand et al. 2007; Kramer-Schadt et al. 2013). Here, RBG models resulted in higher conservation values

for better-sampled cells. To interpret this result we must take into account two issues. First, there is no way to assure that these sites have the highest conservation value for biodiversity features. As mentioned above, they have indeed the highest conservation value for the better-sampled cells, but not necessarily to species distributions. And second, better-sampled areas are often located in more accessible zones, which often present the higher conservation costs and conflict with alternative land uses to conservation (Naidoo et al. 2006; Di Minin et al. 2013). Thus they are very unlikely to be socially and economically suitable for the implementation of conservation action. Also, even if costs are affordable, the cost-benefit of relocating investments in conservation of other areas should be addressed (Underwood et al. 2008). On the other hand, the portfolios based on TGB models reduced the clustering of high priority areas in better-sampled locations, by relocating part of conservation value to the less-sampled sites and scattering priorities across the space. We believe this might result in a more efficient allocation of conservation resources since scattering priorities may be more desirable because biodiversity features and economic costs are not evenly distributed in space (Naidoo et al. 2006; Di Minin et al. 2013). Also, one cannot reduce the priority or even exclude areas from portfolios based on the lack of knowledge rather than a true low conservation value. Moreover, protecting less sampled sites is important because (assuming they are located in less accessible areas) they are more likely to be less impacted than other areas.

Finally, the comparison of performance curves demonstrated that without incorporating sampling bias the relationship between feature distributions and proportion of seascape lost is wrongly estimated. These curves depict the proportion of the original occurrences remaining for biodiversity features when fractions of the landscape are successively retained for conservation (Lehtomäki & Moilanen 2013). The curves for TGB portfolios revealed a more linear relationship between the remaining distribution of biodiversity features and proportion of seascape lost. Thus, when sampling bias is not taken into account, the true rate of proportion of distributions remaining with increase of landscape lost is underestimated. This is important because features' distributions are not retained as the curves suggest when correction is not applied. Also, when accounting for sampling bias the representation levels are higher, so the return of conservation investment is increased.

Establishing priority areas for conservation challenges governments, scientists and decision makers worldwide. Several

ecological, economic, political, and social aspects must be in agreement to efficiently select areas for delimitating conservation units, particularly in broader regional scales. To account for this truly multi-disciplinary task, SCP offers a useful framework to include the required information into a spatial context regarding most of the different conditions required to match successful conservation strategies. However, when using incorrect/biased information on the distribution of species for setting conservation targets based on complementarity our priorities for resource allocation change and hence we may be investing in areas that do not necessarily provide the highest return.

As SCP may be strongly affected by sampling bias we recommend sampling bias should be always taken into account prior to spatial prioritization either whenever data from well-designed field surveys are unavailable or when presence only information gathered for biased datasets is the only source to estimate species distributions for conservation portfolios. We also strongly enforce the need of matching appropriate spatial scales (e.g. national or regional levels) to reach more uniform and less biased sampling surveys for conservation planning and the need to devote more attention to less sampled regions and/or taxa. Finally we also stress the need of further work in order to assess the effects of different ways to account for sampling bias in different SDM and SCP algorithms.

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Supporting Information

The illustration of background selection (Appendix S1), a summary of model evaluations and comparisons (Appendix S2) and differences between conservation portfolios in Fig. 2 (Appendix S3) are available online.

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Table 1. Selected environmental variables used in SDM and their biological justification. mean Chlorophyll A mg/m^3 (Chlomean), Mean Nitrate Concentration $\mu\text{mol/l}$ (Nitrate), Mean pH (pH) and Minimum Sea Surface Temperature ($^{\circ}\text{C}$) - SSTMin

Variable	Justification for predictor
Chlomean	Biomass stock of chlorophyll in water will sink in the soft-bottom, as phytodetritus bulk and may directly affect the diet, reproduction, presence, abundance and biomass of benthic deposit-feeders (Valiela 1995).
Nitrate	The nutrients stimulate bacterial and phytoplankton production, which in turn stimulates zooplankton production, and so on up the food chain. Nitrate concentration may be a limiting factor for the primary production in the marine photic zones (Valiela 1995).
pH	Variation in ocean pH affect distribution of polychaetes in large spatial scales (Benedetti-Cecchi, et al. 2010).
SSTMin	Seawater surface temperature is one of the most influential factors on the distribution of marine species (Dana, 1853).

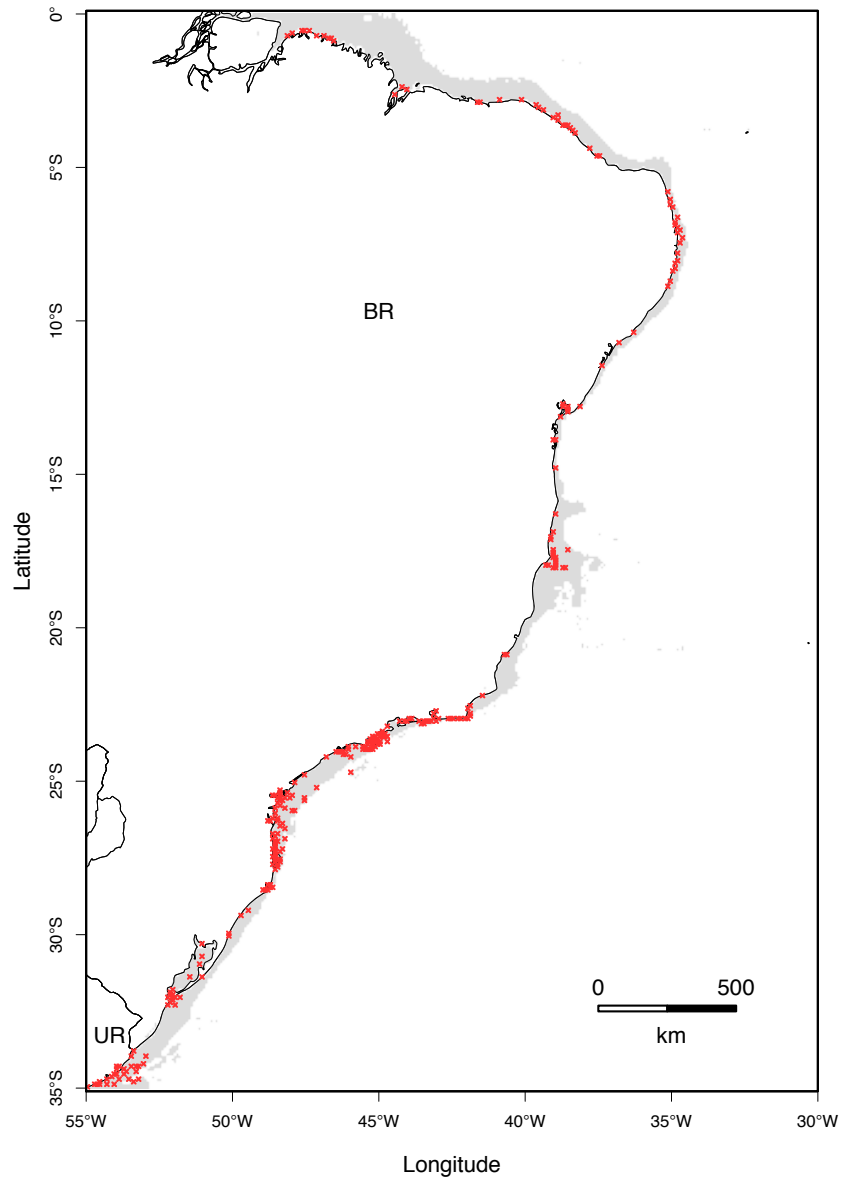
Figure Legends

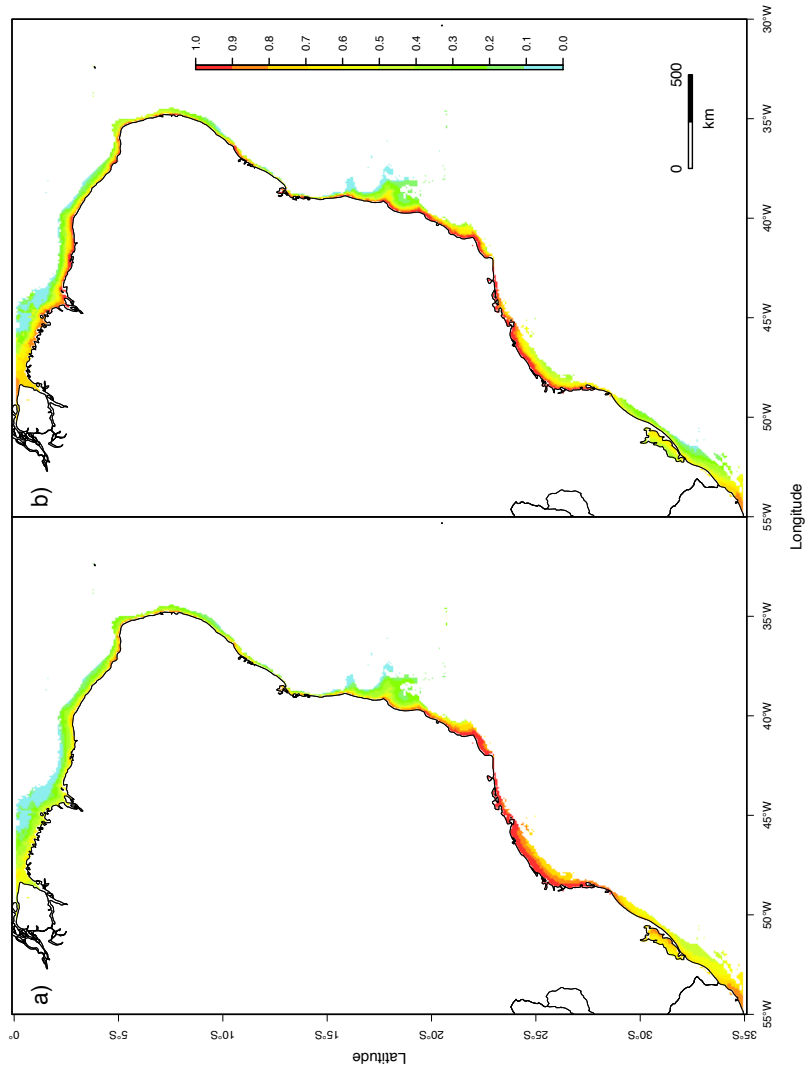
Fig. 1 - Map of southwestern Atlantic depicting the distribution of occurrence records indicating geographical sampling bias in the shallow coasts of Brazil (BR) and Uruguay (UR). Red symbols represent samples.

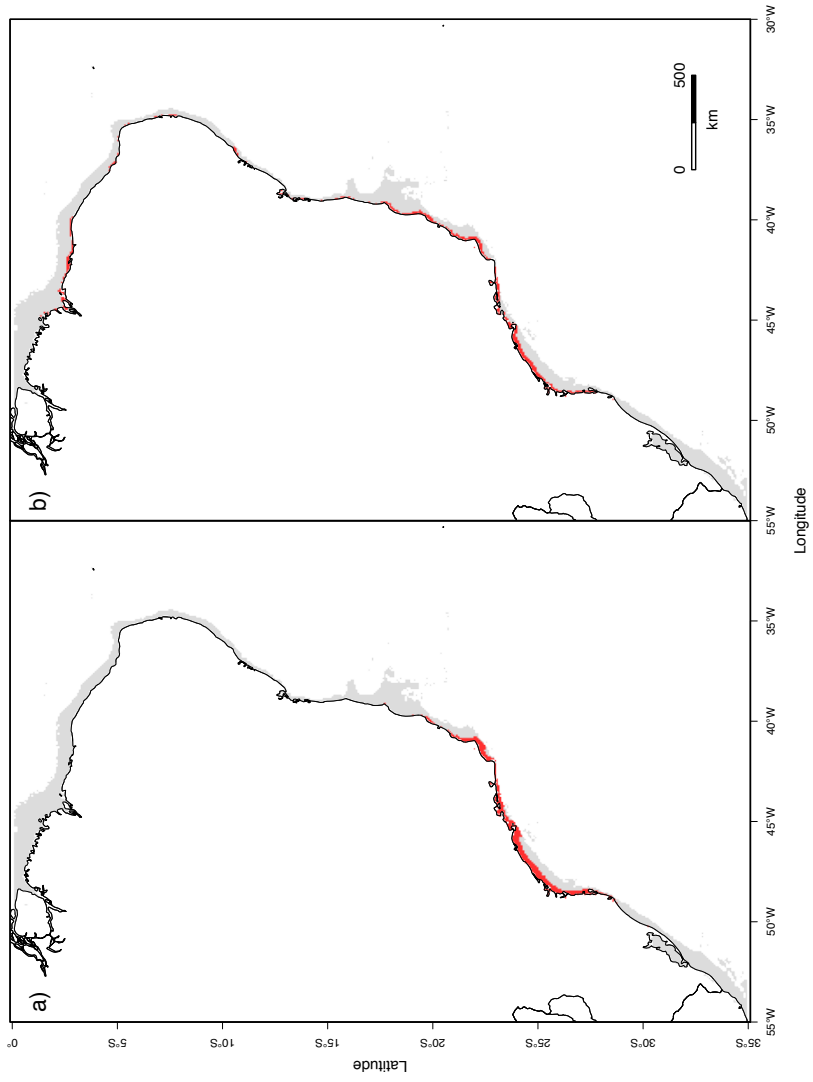
Fig. 2 - Spatial distribution of priority sites for conservation of 40 species of polychaetes along the shallow coast of southwestern Atlantic showing portfolios generated using (a) Random background (RBG) and (b) Target group background (TGB) MaxEnt models.

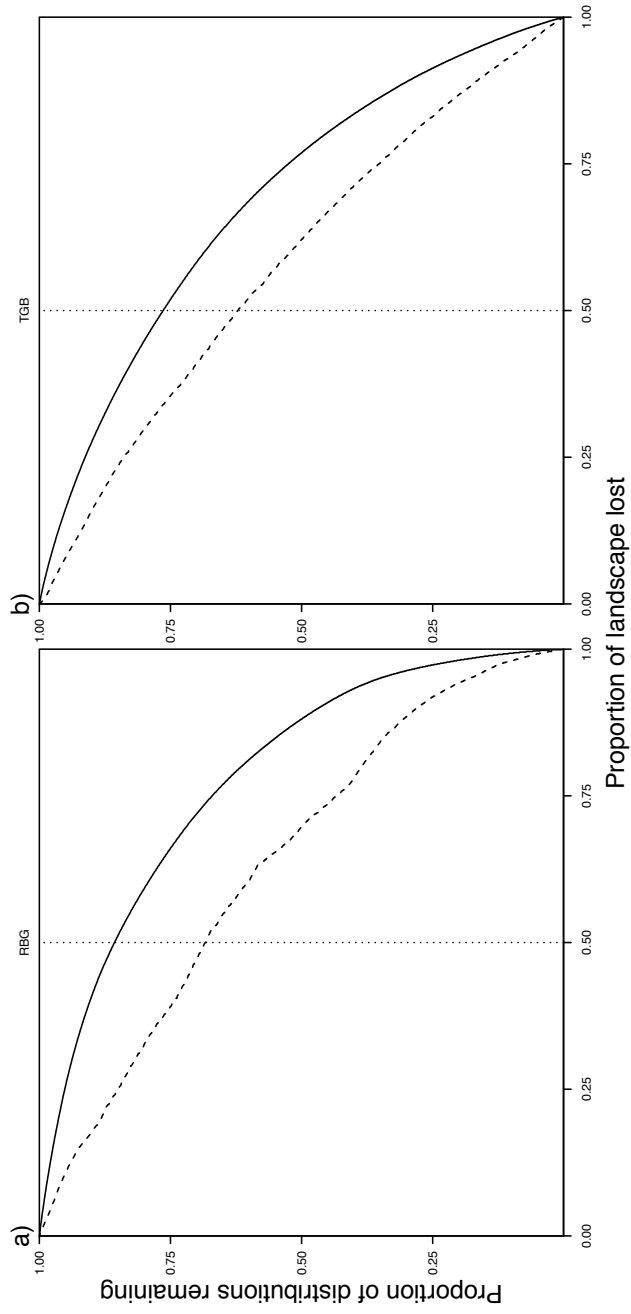
Fig. 3 - Spatial distribution of top 10% priority sites for conservation of 40 species of polychaetes along the shallow coast of southwestern Atlantic showing portfolios generated using Random background (RBG) and (a), Target group background (TGB) MaxEnt models (b).

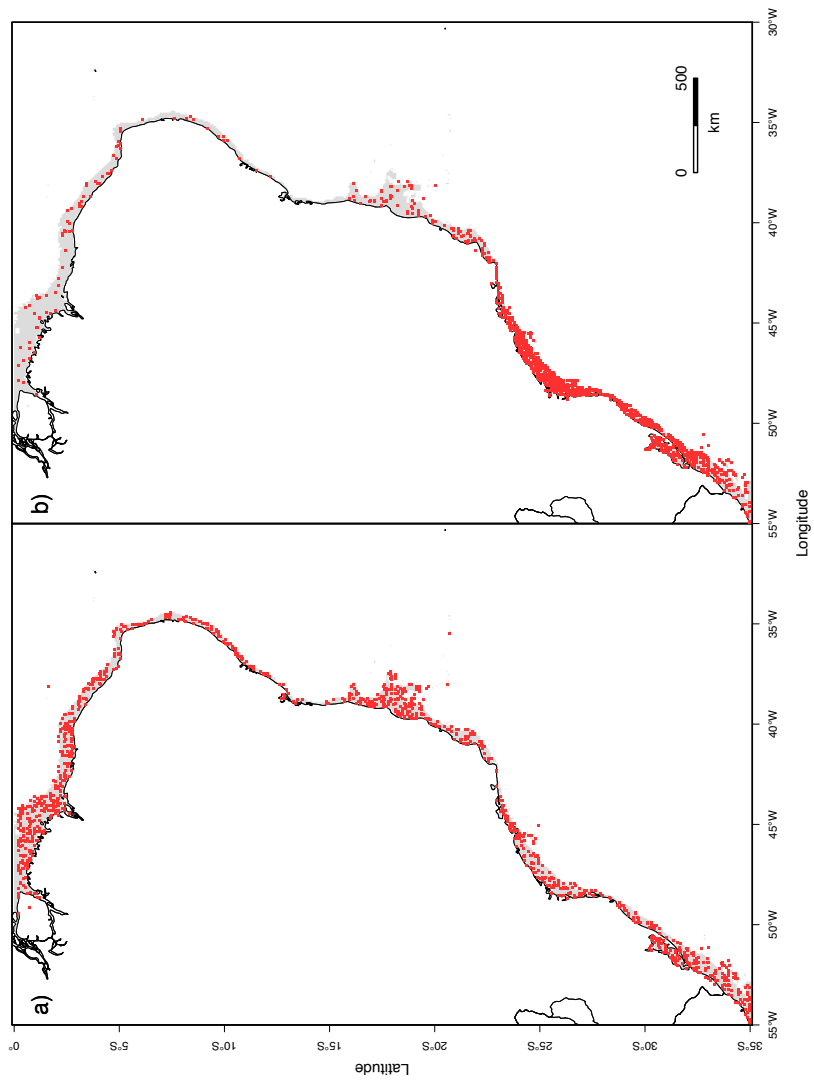
Fig. 4 - Proportion of distributions remaining and proportion of seascape lost for conservation portfolios generated for 40 species of polychaetes along the shallow coast of southwestern Atlantic using (a) Random background (RBG) and (b) Target group background (TGB) MaxEnt models. Solid line is the average lost for all species; dotted line is the feature (species) with the lowest distribution remaining, vertical line indicates 50% of the landscape retained for conservation.











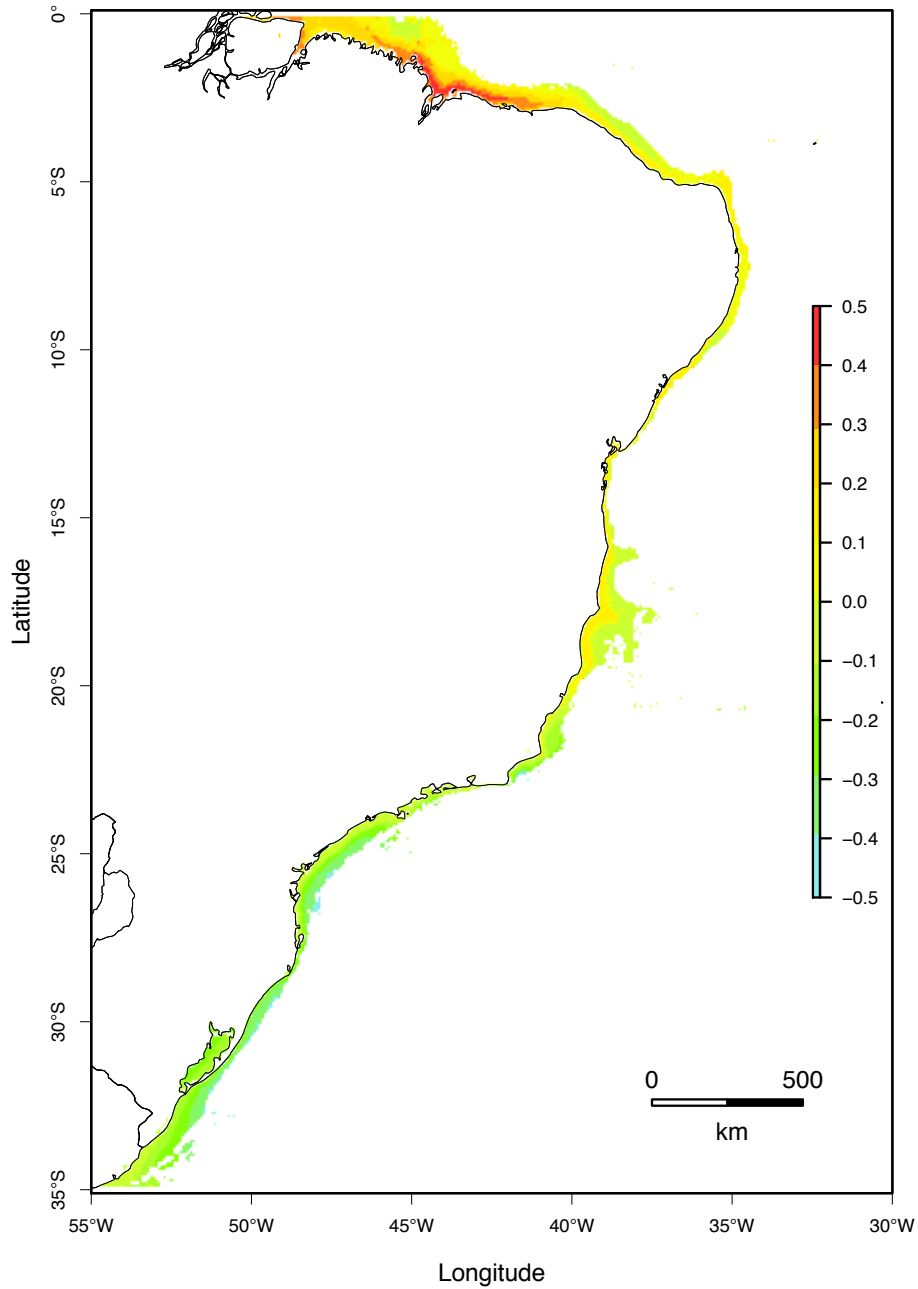
Appendix S2 – Training and testing unique localities, mean (\pm SD) Area under the receiver operating characteristic curve (test AUC) and True skill statistics (TSS) for modeled species and Mann-Whitney Test statistic (W), and p value comparing Random background (RBG) and Target group background (TGB) models.

Species	Training/Testi ng samples	AUC			TSS				
		RBG	TGB	W	P	RBG	TGB	W	P
<i>Alitta succinea</i>	38/12	0.89 (± 0.04)	0.84 (± 0.06)	7582	0.0 (± 0.11)	0.65 (± 0.11)	0.51 (± 0.11)	8275	0.0 (± 0.11)
	22/7	0.92 (± 0.05)	0.84 (± 0.08)	8730	0.0 (± 0.16)	0.71 (± 0.16)	0.56 (± 0.19)	7338	0.0 (± 0.19)
<i>Axiobella brasiliensis</i>	21/7	0.92 (± 0.05)	0.85 (± 0.08)	7934	0.0 (± 0.14)	0.71 (± 0.14)	0.56 (± 0.16)	7651	0.0 (± 0.16)
	24/8	0.9 (± 0.04)	0.88 (± 0.06)	6276	0.0 (± 0.14)	0.66 (± 0.14)	0.6 (± 0.14)	6127	0.0 (± 0.14)
<i>Diopatra cuprea</i>	21/7	0.89 (± 0.06)	0.81 (± 0.09)	7935.	0.0 (± 0.16)	0.61 (± 0.16)	0.41 (± 0.18)	8103.	0.0 (± 0.18)
<i>Diopatra tridentata</i>	33/11	0.88 (± 0.05)	0.79 (± 0.07)	8676	0.0 (± 0.14)	0.59 (± 0.14)	0.43 (± 0.15)	8012.	0.0 (± 0.15)
	33/11	0.86 (± 0.06)	0.77 (± 0.07)	8621.	0.0 (± 0.14)	0.59 (± 0.14)	0.42 (± 0.13)	8118.	0.0 (± 0.13)
<i>Glycinde multidentis</i>	24/8	0.94 (± 0.04)	0.86 (± 0.07)	8435	0.0 (± 0.15)	0.73 (± 0.15)	0.59 (± 0.13)	7622.	0.0 (± 0.13)
	21/7	0.95 (± 0.02)	0.88 (± 0.05)	9394.	0.0 (± 0.18)	0.73 (± 0.18)	0.58 (± 0.17)	7436	0.0 (± 0.17)
<i>Goniada maculata</i>				5	0			5	0

<i>Goniades carolinae</i>	19/6	0.93 (±0.06)	0.86 (±0.07)	7942	0.0	0.73 (±0.15)	0.57 (±0.17)	7612.	0.0
<i>Gymnonereis crosslandi</i>	27/8	0.89 (±0.04)	0.87 (±0.05)	6168	0.0	0.61 (±0.15)	0.58 (±0.11)	5822	0.0
<i>Hempodia californiensis</i>	44/14	0.91 (±0.03)	0.85 (±0.06)	8564.	0.0	0.69 (±0.11)	0.57 (±0.12)	7733.	0.0
<i>Hermundura fauveli</i>	23/7	0.95 (±0.03)	0.93 (±0.04)	6559.	0.0	0.73 (±0.17)	0.71 (±0.13)	5630.	0.1
<i>Hermundura tricuspis</i>	36/11	0.88 (±0.05)	0.8 (±0.08)	8044.	0.0	0.62 (±0.12)	0.47 (±0.15)	7852	0.0
<i>Heteromastus similis</i>	33/11	0.93 (±0.03)	0.88 (±0.04)	8045.	0.0	0.71 (±0.14)	0.63 (±0.12)	6746.	0.0
<i>Isolda pulchella</i>	30/9	0.93 (±0.03)	0.9 (±0.05)	6631	0.0	0.7 (±0.12)	0.66 (±0.13)	5894	0.0
<i>Kinbergomphus difficilis</i>	31/10	0.96 (±0.02)	0.92 (±0.04)	8267.	0.0	0.79 (±0.12)	0.66 (±0.13)	7605.	0.0
<i>Laeonereis acuta</i>	56/18	0.86 (±0.04)	0.85 (±0.04)	6028	0.0	0.6 (±0.11)	0.56 (±0.1)	6386	0.0
<i>Lumbrineris tetraura</i>	22/7	0.87 (±0.08)	0.83 (±0.09)	6504	0.0	0.62 (±0.15)	0.55 (±0.17)	6156	0.0
<i>Magelona papillicornis</i>	33/10	0.93 (±0.03)	0.89 (±0.05)	7596	0.0	0.73 (±0.13)	0.64 (±0.14)	6854.	0.0
<i>Magelona posterolongata</i>	22/7	0.94 (±0.06)	0.9 (±0.05)	7270.	0.0	0.76 (±0.15)	0.66 (±0.16)	6782.	0.0
<i>Magelona variolamellata</i>	36/11	0.91 (±0.03)	0.85 (±0.05)	8268	0.0	0.67 (±0.11)	0.54 (±0.12)	7926.	0.0
<i>Mediomastus</i>	26/8	0.93	0.88	7554	0.0	0.75	0.61	7469.	0.0

<i>Sigambra grubii</i>	72/24	0.86 (± 0.03)	0.8 (± 0.04)	8537. 5	0.0 0	0.59 (± 0.09)	0.49 (± 0.08)	8115. 5	0.0 0
<i>Spiophanes duplex</i>	21/7	0.9 (± 0.06)	0.82 (± 0.07)	8400. 5	0.0 0	0.67 (± 0.16)	0.49 (± 0.15)	8078. 5	0.0 0

Appendix S3 – Detailed differences (subtraction) between Target group background (TGB) and Random background (RBG) conservation portfolios. Positive values are higher priority in TGB portfolio compared to RBG whereas negative values are higher priority cells in RBG compared to TGB.



3 ARTIGO III

Pablo Riul, Brezo Martínéz, Rafael Souza Almeida, Leidson Allan, Paulo Antunes Horta. 2015. **Predicted shifts in southwestern atlantic coastal macroalgae under climate change**

Artigo formatado para a revista Marine Ecology Progress Series

PREDICTED SHIFTS IN SOUTHWESTERN ATLANTIC COASTAL MACROALGAE UNDER CLIMATE CHANGE

Running head: Predicted shifts in macroalgae under climate change

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Abstract

Because of climate change marine species might shift their distributions following environmental suitable conditions. Here, we test the hypotheses that climate change will shift habitat suitability polewards for tropical, tropical warm-temperate and warm-temperate macroalgae. We predicted trends of changes under future climatic scenarios to forecast how macroalgae might respond to climate change in Tropical and warm-temperate coastal reefs in the coast of Southwestern Atlantic from 0 to 35° S. We fitted species distribution models (SDM) to six endemic species of macroalgae in Southwestern Atlantic. We projected these models into future IPCC scenarios and tackled trends of changes in habitat suitability for each species. Minimum sea surface temperature was the principal predictor of macroalgae distribution being selected for all species, regardless of geographical distribution, whereas cloud cover was secondary selected for only one species. Projection of the SDMs under climate change scenarios suggests poleward changes in habitat suitability for all species. Under higher CO₂ emissions, projected changes for all but one species suggests habitat suitability will be limited to part of warm-temperate coast of southwestern Atlantic. The projected changes in habitat suitability provide support for the hypothesis of poleward shifts in distribution of marine species. Considering the

ecological roles of macroalgae we argue even minor local scale changes in distributional patterns of few key species could lead to major structural changes in coastal benthic assemblages threatening the resilience of these ecosystems.

Keywords: Biogeography, habitat loss, seaweed, species distribution model, temperature

Introduction

Assessing the potential impacts and the implications of climate change in biodiversity has become a primary goal in Ecology. Ecological theory predicts climate change will affect the geographical distributions of species (Parmesan 2006, Bellard et al. 2012) and is expected to cause major impacts in biodiversity and ecosystem functioning worldwide (Halpern et al. 2007). In agreement with the predicted scenarios of increase in temperature, climate change is expected to shift species distributions polewards (Parmesan & Yohe, 2003). Species Distribution Models (SDM) uses geo-referenced species occurrences linked with abiotic and/or biotic information from these localities to estimate the “suitable area” in which the species is likely to occur in a geographical space (Elith et al. 2006, Elith & Leathwick 2009). SDM has been successful used to tackle diverse biogeographic questions, such as factors shaping species distributions (Swenson, 2006), identifying areas with high species richness (Garcia, 2006) and for sampling for rare species (Guisan et al. 2006), assessing the invasive potential and proliferation of exotic species in new environments (Peterson & Vieglais 2001, Lozier et al. 2011) and is particularly useful to predicting effects of climate change on species distributions (Araújo & Rahbek 2006, Hijmans & Graham 2006). Yet, although SDM has been widespread in the terrestrial environments in the last decade (Elith & Leathwick 2009), there are markedly few studies for marine organisms (Robinson et al. 2011)

In marine ecosystems, macroalgae are key components of benthic assemblages across world oceans providing food and structuring habitats for in diverse environments. Among the overarching factors affecting macroalgae physiology, temperature plays a major role in shaping the geographic distribution of macroalgae in broad spatial scales (Luning, 1990). Temperature drives macroalgae distribution by limiting their survival and also by regulating growth, photosynthesis and reproduction (Luning, 1990, Eggert, 2012). Macroalgae species are primarily

constrained in a particular interval of minimum and maximum survival temperatures (Eggert, 2012). Within this survival range, from the critical minimum threshold, macroalgae growth and photosynthetic rates increase with temperature, peaking in an intermediate value and then decreasing until the critical lethal maximum temperature (Eggert, 2012).

Recently, changes in distribution of macroalgae species associated with variation in sea surface temperature have increasingly been reported. In northern Atlantic, some populations are extending their range polewards (Hiscock et al. 2004), in the coast of Portugal, Lima et al. (2007) compared the present distribution of 39 species of macroalgae with past distributional data from 1950-60's and found important displacements for more than half of the species. Diéz et al. (2012) reported the disappearing one species and structural changes in macroalgae assemblages from 18 localities when comparing data from 1991 and 2008. In the northern Pacific, Tanaka et al. (2012) observed temperature changes promotes contraction in distributions of temperate and expansion in tropical macroalgae species. In southern Hemisphere, in Australia, Johnson et al. (2011) reported the disappearing of the giant kelp *Macrocystis pyrifera* from many sites in eastern Tasmania related to the intensification of the warmer and nutrient poor East Australian Current. Wernberg et al. (2011a) described poleward range shifts for three species and Wernberg et al. (2011b) documented southward shifts consistent with ocean warming for several macroalgae in both Indian and Pacific oceans in the coasts of Australia.

Coastal reefs occur discontinuously across the southwestern Atlantic, where coral/coralline and rocky reefs are two main environments (Floeter et al. 2006) providing habitats for near 700 species of marine macroalgae (Figueiredo et al. 2008) in tropical and warm-temperate waters. Along the coast of southwestern Atlantic minimum sea surface temperature follows a strong latitudinal gradient with the warmer tropical waters in north decreasing gradually to coldest warm-temperate conditions down south. And in the last three decades, average increases in sea water temperature from 0.1 to 0.4 °C per decade are occurring, in addition with changes in frequency of extreme hot and cold days (Lima & Whetthey, 2012). However, despite of observed changes in temperature, lack of historical data prevents the comparison of past and present macroalgae distributions. Herein we use SDM to assess the responses of six endemic species of macroalgae with different thermal affinities under contrasting future predictions of climate change in southwestern Atlantic. We tested the hypotheses that climate change will shift habitat suitability polewards for coastal macroalgae and

predicted trends of changes to forecast how macroalgae might respond to climate change.

Methods

Study area

The study area is located in the southwestern Atlantic Ocean including part of the coasts of Brazil and Uruguay from 0 to 35° S (Figure 1). Within this area, we choose two large biogeographical regions (realms) following the classification Marine Ecoregions of the World (MEOW - Spalding et al. 2007). The MEOW provides a spatially nested biogeographic classification where the largest units are realms, which are subdivided into provinces, which are subdivided into smallest units named ecoregions. Following Spalding et al. (2007) marine realms are defined as very large biogeographically relevant units sharing a common evolutionary history, presenting strong endemism (including endemic genus and families) whereas water temperature is an important abiotic driver of biodiversity. Biogeographic provinces are large regions that present distinct biotas with some common evolutionary features, whereas endemism occurs mostly at species level and are units limited by distinct abiotic characteristics (such as geomorphological, hydrographic and geochemical features). Ecoregions are small units relatively homogeneous in species composition, but markedly distinguished from adjacent systems, determined by few distinct ecosystems and oceanographic/topographic characteristics. The Tropical Atlantic realm contains two biogeographic provinces, the North Brazilian Shelf and the Tropical Southwestern Atlantic, encompassing three marine ecoregions: Amazonia, Northeastern Brazil and Eastern Brazil (Figure 1). The Temperate South America realm comprises one province, the Warm Temperate Southwestern Atlantic, subdivided into three ecoregions: Southeastern Brazil, Rio Grande and Uruguay-Buenos Aires Shelf (Figure 1).

Occurrence data

Surveys using ‘macroalgae*’ or ‘seaweed*’ and ‘Brazil’ were carried out in the Web of Knowledge (<http://www.webofknowledge.com>), Scopus (<http://www.scopus.com>) and Scielo (<http://www.scielo.org>). Theses were also surveyed in the CAPES databank of Brazilian theses (<http://capesdw.capes.gov.br/>),

accessing information of all graduate programs in biodiversity (oceanography, botany, zoology and ecology). Additionally,

16 sites across the intertidal zone of the Brazilian coast were systematically sampled at nearly each 2.5 degrees of latitude from 2.8 S to 28.6 S. All the information obtained was compiled in a table containing the species, longitude, latitude, province, county, site name, an identification code and source. In some cases no geographical coordinates were provided so these occurrences were not used to avoid commission errors. Data was checked for taxonomic (e.g. synonymia) and geographical inconsistencies (e.g. inverted latitude and longitude, coordinates not matching the site name or coordinates in the countryside far away from the coast). Because the resolution of the environmental layers (near 9.2 km) does not perfectly match the geometric shape of the Brazilian coast, some records were located in cells outside the ocean. To correct this artifact while accounting for accuracy of the records, the coordinates located in a radius of 9.2 km of any valid environmental cell were changed to the nearest cell. As specific information (e.g. which datum was used) on how coordinates were acquired was not given in most cases, records outside this filter were also discarded to avoid inaccuracies. Using these procedures we retrieved and obtained more than 20.000 occurrence records for macroalgae along the Brazilian coast.

To avoid taxonomic biases (i.e. species misidentification) we selected six conspicuous endemic species, accordingly to their geographical distributions. These species were used as surrogates to predict the putative responses of macroalgae to climate change in southwestern Atlantic. *Dictyopteris jolyana* and *Gelidium coarctatum* were classified as tropical species (occurring mostly in Tropical Atlantic realm with few exceptions in transitional zones), *Ceramium brasiliense* and *Cryptonemia delicatula* as tropical-warm-temperate species (occurring in both Tropical Atlantic and Temperate South America realms) and *Levringea brasiliensis* and *Plocamium brasiliense* as warm-temperate species (occurring mostly in Temperate South America realm with few exceptions in transitional zones). For these species, we additionally gathered supplementary data from *specieslink* (CRIA, 2014), an virtual repository network integrating biodiversity data for more than 370 herbarium, museums and other collections of Brazil (<http://smlink.cria.org.br/project?criaLANG=en>). These records also were inspected and whenever necessary corrected accordingly to the procedures described above.

Environmental predictors

We used environmental layers from Bio-Oracle (Tyberghein et al. 2012) at resolution of 5 arcmin (~ 9.2 km) to model species distributions. This dataset is composed of 23 environmental layers of geophysical, biotic and climate rasters for world oceans. As we modeled distribution of species in the coastal zone, the environmental layers were cropped to match only coastal cells. Available variables in Bio-oracle are Calcite concentration (Mean), Chlorophyll A concentration (Mean, Maximum, Minimum and Range), Cloud Cover fraction (Mean, Minimum and Maximum), Diffuse Attenuation (Mean, Minimum and Maximum), Dissolved Oxygen (mean), Nitrate concentration (Mean), pH (mean), Phosphate concentration (mean), Photosynthetically Available Radiation (Maximum and Mean), Salinity (Mean), Sea Surface Temperature (Maximum, Mean, Minimum and Range) and Silicate concentration (Mean). Variables were selected *a priori* according to the main physiological requirements of marine macroalgae (Austin 2002). Most relevant predictors selected for macroalgae were light, nutrients and temperature measures (Lüning 1990, Lobban & Harrison 1997, Eggert et al. 2012, Martinez et al. 2012). Additionally, to control for multi-collinearity, we reduced the set of light, nutrients and temperature variables available in Bio-oracle by detecting highly correlated layers ($r > 0.85$) and excluding one of them accordingly to their ecological relevance. After these selection procedures the environmental layers selected were Maximum Cloud Cover (Cloudmax – Figure 2 a), Mean Nitrate Concentration (Nitrate – Figure 2 b), and Minimum sea surface temperature (SSTmin – Figure 2 c). Minimum sea surface temperature and Maximum sea surface temperature are highly correlated ($r=0.9$), so because in summer and spring the occurrences of upwelling promote discontinuous pulses of cold water in some areas of the coast (Palma & Matano, 2008) we selected the Minimum sea surface temperature for avoiding the inclusion of this noise in our analysis. Maximum Cloud Cover (%) was obtained from the Terra-MODIS-derived cloud fraction data available in a monthly base over 6 years (2005–2010). Mean nitrate concentration ($\mu\text{mol/l}$) was interpolated from *in situ* surface measurements from 1928 to 2008 available in World Ocean Database 2009 (WOD09). Minimum sea surface temperature ($^{\circ}\text{C}$) is the temporal minimum sea surface temperature from monthly climatologies (2002-2009) acquired using the Aqua-MODIS sensor. More details regarding the environmental data are available in Tyberghein et al. (2012).

Species distribution models

We used the software MaxEnt for modeling the distributions of the studied species (Phillips et al. 2006). MaxEnt is one popular tool for species distribution modeling (Merow et al. 2013) and present a good predictive performance for presence-only data (Elith et al. 2006). Models were built using linear and quadratic features only according to Phillips & Dudík (2008). To reduce the potential effects of geographical sampling bias in our models, duplicated records were excluded in each cell. We also generated models using weighted selection of background points according to sampling intensity using the Target Group Background method (Phillips et al. 2009, as adapted in Fitzpatrick et al. 2013). This approach uses information on sampling intensity, based on the occurrences of similar species, for selecting MaxEnt background points (higher sampling intensity higher probability of selection). To account for sampling intensity we created a raster with the total number of records of macroalgae in each cell and used a kernel density probability function to estimate the sampling intensity for all cells in our landscape. By default, MaxEnt uses 10,000 points to generate the background, however, our study area have far less cells ($n=939$). To avoid selection of all cells and/or selecting the same cell more than one time, here we generated the background selecting 6-fold the number of presence points for each species. To improve our predictions we choose to use the most parsimonious models accordingly to the biology of the modelled species (Austin, 2002). Initially we fitted MaxEnt models for each species using their full occurrence data and all available pre selected predictors. Additionally, for each species we also fitted linear and linear and quadratic general linear models (GLM). We then excluded variables that were not selected as important in at least two of the three models (MaxEnt, linear GLM and linear and quadratic GLM) in order to select the predictors to fit the final model (i.e. the most parsimonious) for each species.

Model accuracy was evaluated based in one threshold-independent, the area under the receiver operating characteristic curve (AUC - Fielding & Bell, 1997) and one threshold-dependent measure, the true skill statistics (TSS - Allouche et al. 2006) calculated using the 10-percentile training presence threshold. The AUC values vary from 0.5 to 1 indicating a model no better than random and a model presenting a perfect discrimination respectively (Fielding & Bell, 1997). TSS values vary from -1 to 1, values below 0 represents predictions no

better than random and 1 represents perfect predictions (Allouche et al. 2006). Model validation was performed based in 50 replicated runs of partitioned occurrence data using 80% for training and 20% for testing.

Projection in future scenarios

For assessing if the variations in seawater temperature could potentially change climatic habitat suitability for macroalgae, for each species we projected the final model into future predictions of seawater temperatures under two Intergovernmental Panel on Climate Change (IPCC) scenarios accordingly to the UKMO-HadCM3 model of the World Climate Research Programme Coupled Model Intercomparison Project (WCRP CMIP3). Sea surface temperatures were obtained from monthly mean temperature derivatives (minimum) over a 10-year period (2087–2096). The first scenario, B1, is the more optimistic representing stabilization of atmospheric CO₂ concentration at 550 ppm until 2100. The second projection, A2, is more pessimistic and represents an atmospheric CO₂ concentration higher than 800 ppm until 2100. More details regarding these temperature scenarios are available in Jueteback et al. (2013).

Results

Regardless of the geographical distribution of the modeled species, the minimum sea surface temperature (SSTmin) was the major predictor, presenting the highest gain contribution and being selected for all species (Table 1). In addition to temperature, the maximum cloud cover (Cloudmax) was also selected for one species (Table 1). Maximum cloud cover was selected only in the model of the tropical brown species *Dictyopteris jolyana*, for this species, most records occurred in intermediate cloud cover conditions. SSTmin was selected in species distribution models for all our species. For the tropical species *Dictyopteris jolyana* and *Gelidium coarctatum* we observed a trend of more records occurring with increasing temperature, mostly between 22 and 27 °C (Figure 3, a-b). For the tropical-warm-temperate species *Ceramium brasiliense* and *Cryptonemia delicatula* minimum sea water temperature varied from 14 to 28 °C (Figure 3, c-d). For the warm-temperate species *Levringea brasiliensis* and *Plocamium brasiliense* most records occurring between 16 and 24 °C (Figure 3, e-f).

Accordingly to the two evaluation scores used, species distribution models performed fair to good (Table 1). For the full models

built for the variable selection procedure, AUC ranged from 0.75 (± 0.01) to 0.87 (± 0.01) and TSS from 0.44 (± 0.03) to 0.78 (± 0.02). For validation models, the Testing AUC ranged from 0.72 (± 0.05) to 0.88 (± 0.02) whereas TSS ranged from 0.41 (± 0.08) to 0.77 (± 0.09). Finally for the final models minimum AUC was 0.74 (± 0.01) and maximum 0.88 (± 0.01) while TSS ranged from 0.42 (± 0.03) to 0.79 (± 0.02).

Model projections in the future conditions suggested important changes in habitat suitability for all species along the Brazilian coast (Figures 4-6). For most species we observed a general trend of increasing habitat suitability southwards under the A2 scenario. For all species, except for *Dictyopteris jolyana*, habitat suitability will be restricted to only part of the Temperate South America realm under A2 conditions. For the tropical species *Dictyopteris jolyana* the results suggests range extension southwards in both B1 (Figure 4 b) and A2 (Figure 4 c) scenarios, when comparing to the present prediction (Figure 4 a). For *Gelidium coarctatum* the prediction to the B1 scenario (Figure 4 e) suggests increase in habitat suitability in the north comparing to the present (Figure 4 d) and a markedly southwards displacement under A2 (Figure 4 f) to part of the Temperate South America. For the tropical-warm-temperate *Ceramium brasiliense* few changes in habitat suitability were observed when comparing present (Figure 5 a) to B1 prediction (Figure 5 b), however, under the A2 scenario, the habitat suitability is predicted to be displaced to the south (Figure 5 c). For *Cryptonemia delicatula* the B1 scenario predicted increase in habitat suitability in part of the north coast and down south (Figure 5 e), while under the A2 conditions a southward displacement was also predicted (Figure 5 f) when comparing to the present prediction (Figure 5 d). For the warm-temperate species *Levringia brasiliensis* compared to the present prediction (Figure 5 a), the prediction to the B1 scenario suggest a slight change southwards (Figure 6 b) while under A2 conditions the suitability will be strongly displaced to the extreme south (Figure 6 c). For *Plocamium brasiliense* the predictions for B1 conditions suggest an increase in habitat suitability southwards (Figure 6 e) and also a markedly displacement to the extreme south (Figure 6 f) when comparing to the present prediction (Figure 6 d).

Discussion

The minimum sea surface temperature was the main environmental driver explaining the distribution of macroalgae in the coast of southwestern Atlantic, being consistently selected for all species

by independent Species Distribution Modelling methods. SDM performance indicated fair to good accuracy in the predictive maps produced for the modeled species. Projections of SDM predicted minor changes under the scenario B1 with slight southward increases in habitat suitability for most species, however the projections predicted markedly southward changes in habitat suitability under the A2 scenario for all species and regardless of their geographical distribution, confirming our hypotheses that climate change will change habitat suitability for macroalgae. The predicted variation in habitat suitability raises concerns regarding potential changes in macroalgae distribution in SWA suggesting direct and indirect effects to the biodiversity of coastal ecosystems.

Predictors of macroalgae distribution

Minimum sea water temperature was the main predictor being selected and explained at least 50% of the gain contribution for all the modelled species, whereas cloud cover was selected for only one species contributing with more than 30%. Theory suggests in addition to climate, non-climate predictors are also assumed to explain species geographical distributions, especially at small scales (Heikkinen et al. 2006, Austin & Van Niel, 2011). Here, our results are in agreement with the expected importance of temperature for macroalgae distribution, and in addition to the selection of cloud cover support that climate factors act as major drivers of species distributions at broad geographical scales. Sea surface temperature is frequently selected as an important predictor for macroalgae distribution using SDM (Tyberghein et al. 2011, Jueteback et al. 2013, Verbruggen et al. 2013, Gallon et al. 2014, Neiva et al. 2014) being included in spite of other important non-climatic predictors (Martinez et al. 2012). Furthermore, several studies based in direct observations also links changes in macroalgae species distribution to variations in seawater temperature (Hiscock et al. 2004, Lima et al. 2007, Diéz et al. 2012, Johnson et al. 2011, Wernberg et al. 2011a, Wernberg et al. 2011b). In our case, the specific physiological mechanisms involved in driving macroalgae distribution (i.e maximum or minimum temperature) could not be assessed because these two variables are highly correlated. So although we believe temperature is the main driver of macroalgae distribution we could not distinguish if the major distribution driver is the maximum or the minimum temperature.

Sea surface temperature plays a major role in macroalgae distribution and therefore climate change is predicted to cause important shifts in macroalgae distribution worldwide (Bartsch et al. 2012). Additionally, temperature is also recognized as major driver of distribution for other key marine taxa such as corals, mollusks, fishes, mammals, mangroves and seagrasses (Tittensor et al. 2010), so these organisms are also expected to respond to the effects of climate change. However, comparing to terrestrial ecosystems, SDM studies exploring changes in species distributions in marine environments because of climate change are still scarce. For this reason we believe more studies are needed to address these potential effects, particularly in species which are useful proxies for tracking minor changes in environmental conditions such as macroalgae.

Projected effects of climate change

Comparison of present predicted species distributions with projection of SDM into future the two contrasting future scenarios revealed major changes in habitat suitability for all species regardless the geographical distribution. For the tropical brown species *Dictyopteris jolyana* SDM projection suggests large extension in the southern distributional boundaries to new suitable habitats in Temperate South America in Southwestern Brazil and Rio Grande ecoregions under B1 conditions, and in Rio Grande and Uruguay-Buenos Aires Shelf under A2 scenario. For the red species *Gelidium coarctatum* B1 projections suggests both north (colonizing the Amazonian ecoregion) and minor southward increase in habitat suitability, however, under A2 conditions, the species is predicted to be extinct from its entire native range and predicted to be constrained only to the south part of the Temperate South America. For the tropical-warm-temperate species *Ceramium brasiliense* and *Cryptonemia delicatula* projections in B1 scenario also suggest new suitable conditions in north and south. However major southward changes in habitat suitability were predicted for the A2 scenario, restricting the habitats available for this current wide ranged species only to the south half of the Temperate South America at Rio Grande and Uruguay-Buenos Aires shelf ecoregions. For the warm-temperate species *Levringia brasiliensis* and *Plocamium brasiliense* despite of few changes in B1 scenario, our models predict a substantial reduction in the habitat suitability for both species in the Temperate South America realm, with extinction for both species in larger areas. The

Although few SDM studies tackled the potential effects of climate change in macroalgae they also support our predictions of changes in habitat suitability suggesting major distributional shifts and local extinctions in North Atlantic species (Martinez et al. 2012, Jueterbock et al. 2013, Gallon et al. 2014). Moreover, based in modeled summer and winter sea surface temperature, Bartsch et al. (2012) predicts changes potentially leading to an overall poleward shift of the current marine biogeographical regions. In the coast of southwestern atlantic, this projected displacement will be pronounced with the increase of the tropical region southwards reducing the available area of warm-temperate habitats (Bartsch et al. 2012) and concomitantly enabling the colonization of tropical species to these new suitable areas. Our results support the predictions of poleward shifts in habitat suitability for tropical species. This spread of tropical areas polewards has being already observed since the end of the 1980s (Seidel, 2008). Warm-temperate areas are also predicted to spread polewards in southwestern Atlantic (Bartsch et al. 2012). However, the expected reduction of warm-temperate habitats for coastal macroalgae raises important concerns, particularly regarding our warm-temperate species because their geographical distributions are restricted to the north of the Plata River which is a important biogeographic barrier, currently constraining the dispersal of these organisms down south.

Our results suggest that changes in habitat suitability would affect large coastal areas, particularly in the Tropical Atlantic and the north of the Temperate South America realm under the scenario A2. In addition to direct impact in macroalgae populations (i.e local and regional extinctions and contractions in geographical distributions), changes in habitat suitability of habitat forming species may also promote effects at local (eg. community) and regional (eg. ecosystem) scales. Additionally, decline and/or distributional shifts in macroalgae populations may threat the focal species potentially leading to local extinctions over broad coastline areas. These distributional changes can also produce community shifts because their direct effects in biological interactions determining the diversity within assemblages (Hughes, 2000). These shifts can also provoke changes in the trophic cascade such as reduction in food availability for herbivores. For example, the tropical and warm-temperate species *Cryptonemia* spp. and tropical *Gelidium* spp. are important resources in the diet for the green turtle *Chelonia mydas* in Brazil (Santos, 2014), as our warm-temperate species *Plocamium brasiliense* (Reisser et al. 2013). Also, as suggested for our species, climate change can also affect the distributions of other macroalgae

species in a similar way. Assuming this hypothesis, such variations have the potential to produce community shifts in large areas of SWA, particularly in the tropical coast of Brazil, leading to changes in macroalgae species richness and biomass. Finally, in the south of SWA (27° S and southwards) substrate availability is an important limiting factor for colonization by macroalgae species (Oliveira et al., 2002), so most species would not be able to grow in this area.

Study limitations

Because of methodological constraints assessing the potential limitations of our results is a worthwhile exercise. Although using SDM we could not address which temperature is the main driver of macroalgae distribution, climate change is assumed to affect both maximum and minimum seawater temperatures, so we believe our models are able to describe the trends of changes in habitat suitability for the modeled species regardless of which temperature is more important. Also, here temperature was the only selected predictor for all but one species and the only variable with available future prediction. However, in addition to sea surface temperature, climate changes are also predicted to affect frequency of extreme hot and cold days, precipitation, ocean circulation and CO₂ concentration among others (IPCC, 2014), all these variables, and synergetic interaction between them, can also potentially affect marine species, including marine algae.

When projecting changes in species habitat suitability under climate change scenarios using SDM one important assumption is niche conservatism, when species tends to conserve the characteristics of their ecological niche (Wiens & Graham, 2005). Alternatively, species can respond by shifting their niches to tolerate the new conditions (Jezkova et al. 2012). Considering niche conservatism and the widening of tropical region in the study area under future climate scenarios, the polewards shifts trends predicted in this study are expected responses to climate change. Poleward shifts in marine species are well documented in the fossil record (Fields et al. 1993) and in recent marine organisms for distinct taxa (Sorte et al. 2010) including macroalgae (Wernberg et al. 2011b).

Finally, SDM produce estimates of the realized niches of the species, which is a subset of the fundamental niche, therefore the precise range of species tolerance to abiotic conditions cannot be assessed using SDM but with manipulative experiments (see Martinez et al. 2014), which can lead to underestimates of species niche and their projections

in geographical space. In summary, our results are constrained to methodological limitations of SDM studies and as such they must be interpreted with some caution. However, we believe these predictions are reliable, particularly at broad scales, and they are in agreement with the expected pattern described in several direct observed changes in macroalgae distributions related to temperature.

Conclusions

Temperature was the main driver of macroalgae species distributions in Southwestern Atlantic. Under the worst predicted scenario of climate change our projections suggest the habitat suitability for the tropical macroalgae species *Dictyopteris jolyana* can decrease in its current area of distribution, whereas *Gelidium coarctatum* can be extinct of their entire native range. For both species habitat suitability can increase allowing colonization of the south of the Temperate South America. For the tropical warm-temperate species *Ceramium brasiliense* and *Cryptonemia delicatula* the projections predicted extinction in the Tropical region and increase in suitable habitats southwards. The warm-temperate species *Levringia brasiliensis* and *Plocamium brasiliense* can become extinct in most of their current distribution area and be limited to a narrow range. Our results support the observed trend of poleward shifts for marine species in response to climate change. We believe these changes can substantially affect these coastal ecosystems causing extinction of macroalgae populations in the SWA and lead to the tropicalization of the Temperate zone in southwestern Atlantic. Additionally, in the south of SWA (27° S and southwards) substrate availability may constrain the occurrence of macroalgae species. Finally we urge the need of more studies regarding the response of marine species to climate change to increase our understanding of how these ecosystems may respond to climate change and the implementation of these potential changes in species distribution when planning the conservation of the Brazilian coastal habitats.

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Figure legends

Figure 1 – Map of the study area showing part of the coasts of Brazil and Uruguay and detailing the two marine realms (Tropical Atlantic and Temperate South America) three biogeographical provinces and six ecoregions according to Spalding et al. (2007).

Figure 2 – Detail of the environmental layers along the study area. Maximum Cloud Cover (a), Mean Nitrate Concentration (b) and Minimum sea surface temperature (c).

Figure 3 – Histograms showing the number of occurrences of the species *Dictyopteris jolyana* (a) *Gelidium coarctatum* (b), *Ceramium brasiliense* (c), *Cryptonemia delicatula* (d), *Levringia brasiliensis* (e) and *Plocamium brasiliense* (f) according to the Minimum sea surface temperature, the most relevant predictor selected for all models.

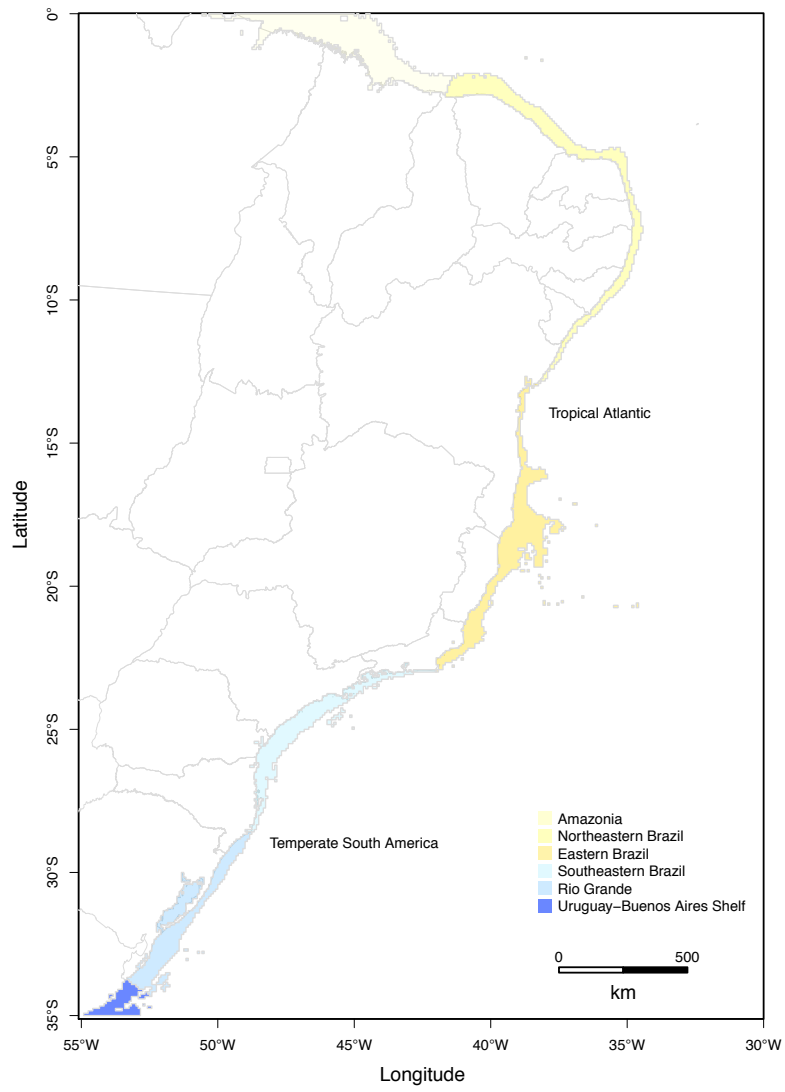
Figure 4 – Projections of SDM for current and future trends of climatic habitat suitability for two species of tropical coastal macroalgae in Brazilian coast. *Dictyopteris jolyana* (a-c) and *Gelidium coarctatum* (d-f). Black lines highlight habitat suitability accordingly to the 10-percentile training presence threshold.

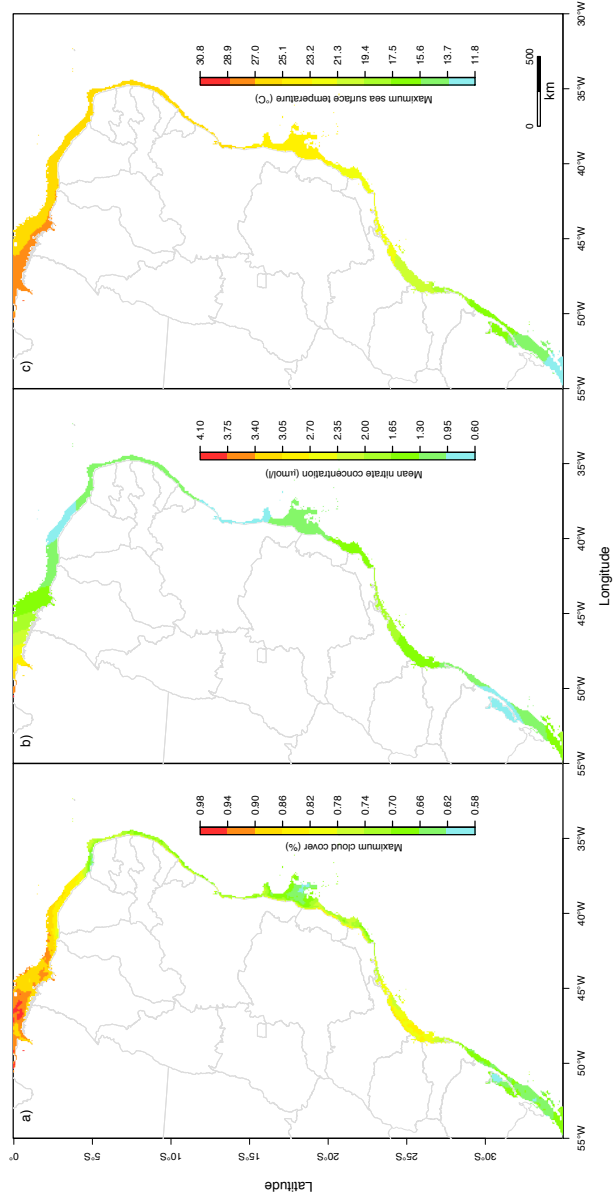
Figure 5 – Projections of SDM for current and future trends of climatic habitat suitability for two species of cosmopolitan coastal macroalgae in Brazilian coast. *Ceramium brasiliense* (a-c) and *Cryptonemia delicatula* (d-f). Black lines highlight habitat suitability accordingly to the 10-percentile training presence threshold.

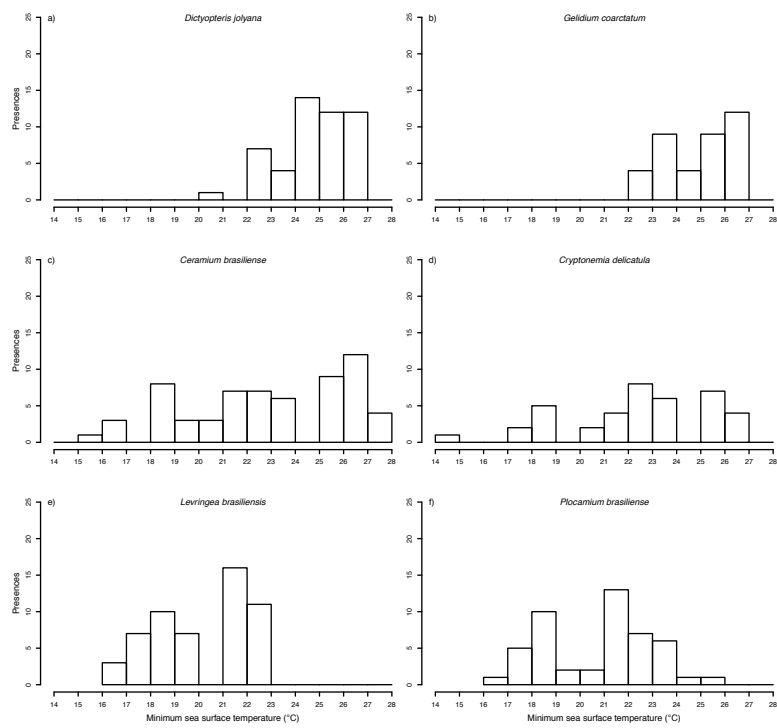
Figure 6 – Projections of SDM for current and future trends of climatic habitat suitability for two species of warm-temperate coastal macroalgae in Brazilian coast. *Levringia brasiliensis* (a-c) and *Plocamium brasiliense* (d-f). Black lines highlight habitat suitability accordingly to the 10-percentile training presence threshold.

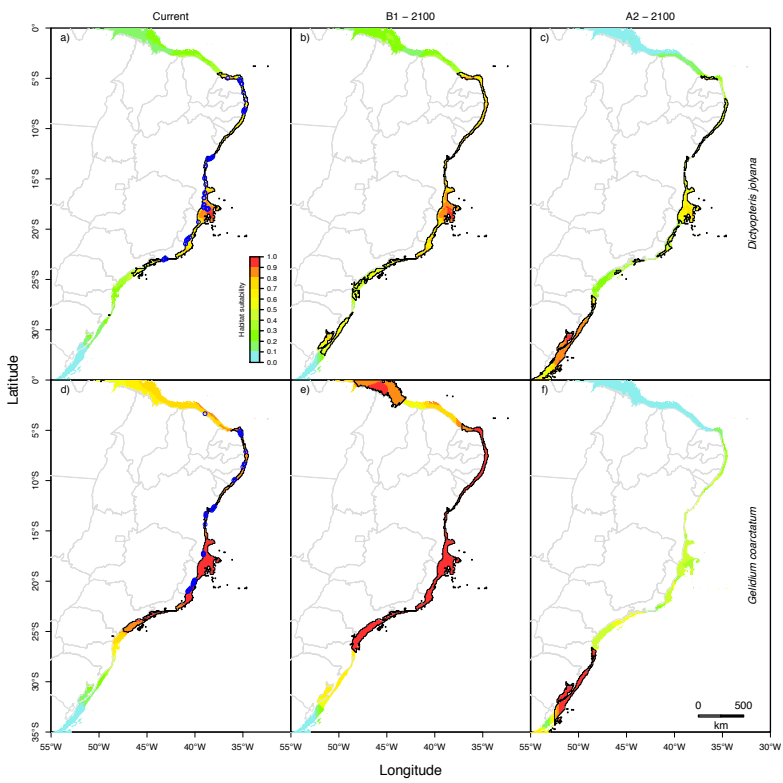
Table 1 – Mean variable contribution for models built with 100% of the data (variable selection procedure, and evaluation scores (AUC and TSS for models built with 100% of the data (Full modes, 80% (model validation and the final models (reduced models. In bold variables selected for the final models. n – number of unique localities used to train the models. ^a variable selected in Linear GLM, ^b variable selected in Linear quadratic GLM.

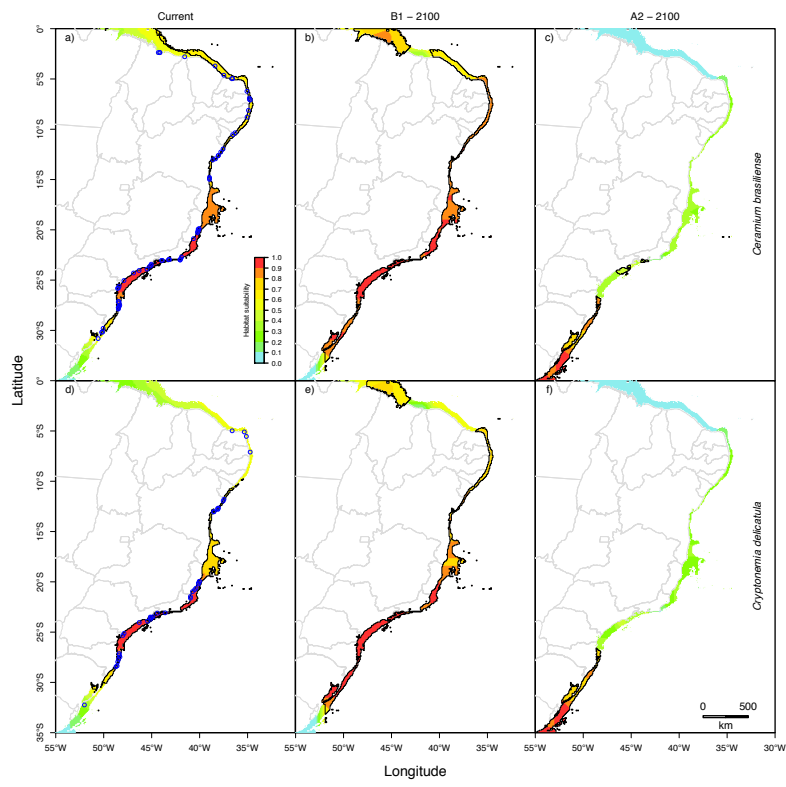
Species	n	Full models				Validation models			Final models	
		cloudmax	nitrate	sstmin	Training AUC	Training AUC	Testing AUC	TSS	Training AUC	TSS
<i>D. jobyana</i>	50	31.6^a	0.7	67.7^{ab}	0.83	0.84	0.84	0.59	0.84	0.64
					0.01	0.01	0.04	0.12	0.01	0.02
<i>G. coarctatum</i>	38	5.5	29.3	65.2^{ab}	0.81	0.8	0.8	0.57	0.81	0.63
					0.01	0.02	0.05	0.14	0.01	0.03
<i>C. brasiliense</i>	63	1.9	47.1	51.0^b	0.75	0.75	0.72	0.41	0.74	0.42
					0.01	0.01	0.05	0.08	0.01	0.03
<i>C. delicatula</i>	39	3.8	39.8	56.4^b	0.8	0.8	0.78	0.52	0.78	0.54
					0.01	0.02	0.06	0.12	0.01	0.04
<i>L. brasiliensis</i>	54	4.8	24.2	71.0^a	0.87	0.88	0.88	0.75	0.88	0.79
					0.01	0.01	0.02	0.11	0.01	0.02
<i>P. brasiliense</i>	48	6.3 ^a	25.2	68.4^a	0.85	0.86	0.86	0.77	0.85	0.74
					0.01	0.01	0.03	0.09	0.01	0.02

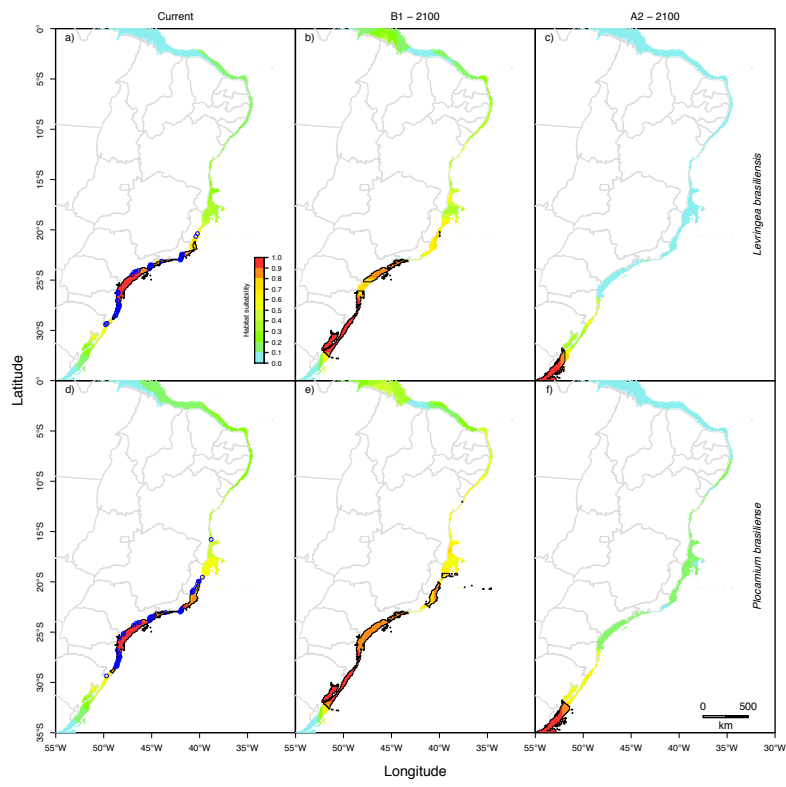












5 CONCLUSÃO GERAL

No caso da bioinvasão do coral sol, os modelos de distribuição de espécie construídos no presente estudo sugeriram que o coral invasor *Tubastraea coccinea* pode vir a ocorrer em praticamente toda zona costeira do Brasil, inclusive dentro da maioria das unidades de conservação costeiras. A sobreposição dos modelos de distribuição das espécies *Mussismilia hispida* e *Tubastraea coccinea* revelou uma grande área propícia à ocorrência de ambas espécies. Considerando o potencial invasivo de *Tubastraea coccinea* observado durante a invasão do Caribe, conclui-se que o coral sol pode promover importantes mudanças na estrutura e composição das comunidades bentônicas de áreas rasas em grande parte da costa do Brasil. Além disso, como a espécie invasora demonstrou-se antagônica à espécie endêmica (que sofre necrose em seus tecidos quando em contato com a invasora), aquela representa uma séria ameaça à *Mussismilia hispida*, podendo ocorrer em grande parte da distribuição geográfica potencial da espécie endêmica e comunidades associadas. Ressalta-se que a espécie *Mussismilia hispida* é uma importante formadora de habitats recifais na costa do Brasil. Recomenda-se, portanto, o investimento em iniciativas de monitoramento e manejo das populações de *Tubastraea coccinea* que já ocorrem na costa do Brasil, e das áreas adjacentes a estas populações.

Em relação ao efeito do viés geográfico amostral nos resultados da análise de priorização especial para conservação, os resultados demonstraram que a análise de priorização é fortemente afetada pelo viés, alocando as prioridades de acordo com o esforço amostral. Contudo, quando o viés é corrigido, os portfólios resultantes são menos enviesados, aumentando a priorização de áreas com menos informação (esforço amostral). Além disso, as curvas de performance da análise de priorização demonstraram uma superestimativa da proporção das distribuições restantes em relação à proporção de perda de habitat quando o viés não foi corrigido. Conclui-se que o viés geográfico pode afetar fortemente a análise de priorização especial, potencialmente levando a uma alocação errônea de recursos de conservação em áreas com maior esforço amostral. Recomenda-se que o viés seja levado em consideração na análise de priorização sempre que os dados disponíveis não forem resultado de esforços de coleta desenhados especificamente para essa finalidade. Reforça-se também a necessidade de investimentos em programas de caracterização da biodiversidade para melhor subsidiar análises de priorização conservação.

Finalmente, os modelos de distribuição de espécies demonstraram que a temperatura foi a principal variável preditora das distribuições de macroalgas da entremarés da costa do Brasil, confirmando o padrão observado em outros estudos. As projeções dos modelos nos cenários futuros sugerem que poderão ocorrer importantes mudanças nas distribuições de todas as espécies (deslocamentos para o sul), independente de suas afinidades biogeográficas. No cenário de maior emissão de CO₂ as mudanças projetadas sugerem que as distribuições de todas as espécies, com uma exceção, serão limitadas a uma pequena parte da costa temperada quente do Atlântico sul oriental. As mudanças projetadas suportam a hipótese de migração de espécies marinhas em direção ao polo. Considerando os papéis ecológicos das macroalgas nesses ambientes, argumenta-se que mesmo mudanças em menores escalas nas distribuições de poucas espécies podem levar a mudanças estruturais em comunidades bentônicas, ameaçando a resiliência desses ecossistemas. Recomenda-se o uso integrado de modelos de distribuição de espécies e modelos mecanicistas baseados em experimentos manipulativos em laboratório para delimitar detalhadamente os limites de tolerância dos organismos às variáveis ambientais mais relevantes para suas distribuições.

Apesar das recentes iniciativas de amostragem de bentos na costa do Brasil em escalas espaciais biogeograficamente relevantes (como, por exemplo, a Rede SISBIOTAMar e a REBENTOS) e também das iniciativas na geração de bancos de dados que consolidem as informações de distribuição já existentes na literatura e em coleções, herbários e museus (como, por exemplo, speciesLink CRIA e o SISBIOTA do Biota FAPESP), para os três grupos de bentos abordados no presente estudo, foi possível observar um acentuado viés geográfico amostral na distribuição das ocorrências, sendo a costa do Estado de São Paulo a região com a maior concentração de registros. Por esse motivo, em todos os casos abordados nesse estudo foi necessário utilizar um método de correção do viés geográfico amostral para construir os modelos. Considerando as lacunas existentes, é recomendável o aumento nos investimentos em inventários da biodiversidade bentônica em largas escalas espaciais na costa do Brasil para garantir a geração de informações necessárias para subsidiar medidas de manejo e Conservação. Adicionalmente, também é importante que além dos dados de ocorrência, exista uma preocupação em coletar dados quantitativos de biomassa e/ou densidade de indivíduos

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