

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

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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

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suitability 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 meta-analysis 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, Vaclavík & 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

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

Predictor	Unit	Variable	Justification for predictor
Mean calcite concentration	mol m ⁻³	Calcite	Calcite (and aragonite) are needed for coral skeleton accretion (Gattuso et al. 1998)
Min. chl a	mg m ⁻³	Chlomin	
Max. chl a	mg m ⁻³	Chlomax	
Max. cloud cover	%	Cloudmax	
Min. diffuse attenuation	m ⁻¹	Damin	
Max. diffuse attenuation	m ⁻¹	Damax	
Mean nitrate concentration	µmol l ⁻¹	Nitrate	Reef corals are adapted to nutrient deficient, clear water conditions (Hallock & Schlager 1986)
Max. photosynthetically available radiation	Einstein m ⁻² d ⁻¹	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	Practical salinity scale	Salinity	Corals are sensitive to wide ranges in salinity (Muthiga & Szmant 1987)
Mean silicate concentration	µmol l ⁻¹	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)

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 pseudo-absences 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 co-occurrence 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 ($34^{\circ} 42' W$; $18^{\circ} S$). Lower probabilities were found in the extreme north (from $\sim 1^{\circ} 15' S$ to $3^{\circ} N$). 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 $5^{\circ} S$) and below the southern ($25^{\circ} S$) 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.

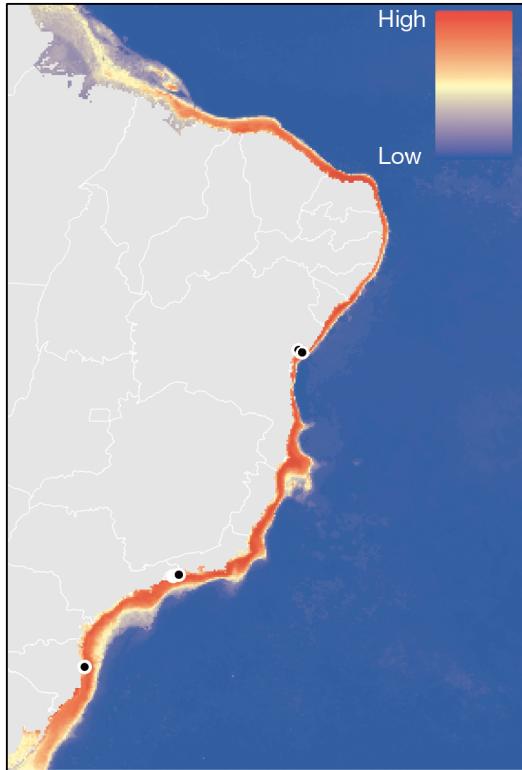


Fig. 1. Climatically suitable environments for *Tubastraea coccinea* along the Brazilian coast in the southwest Atlantic. (●) Unique localities along invaded range used to train the model

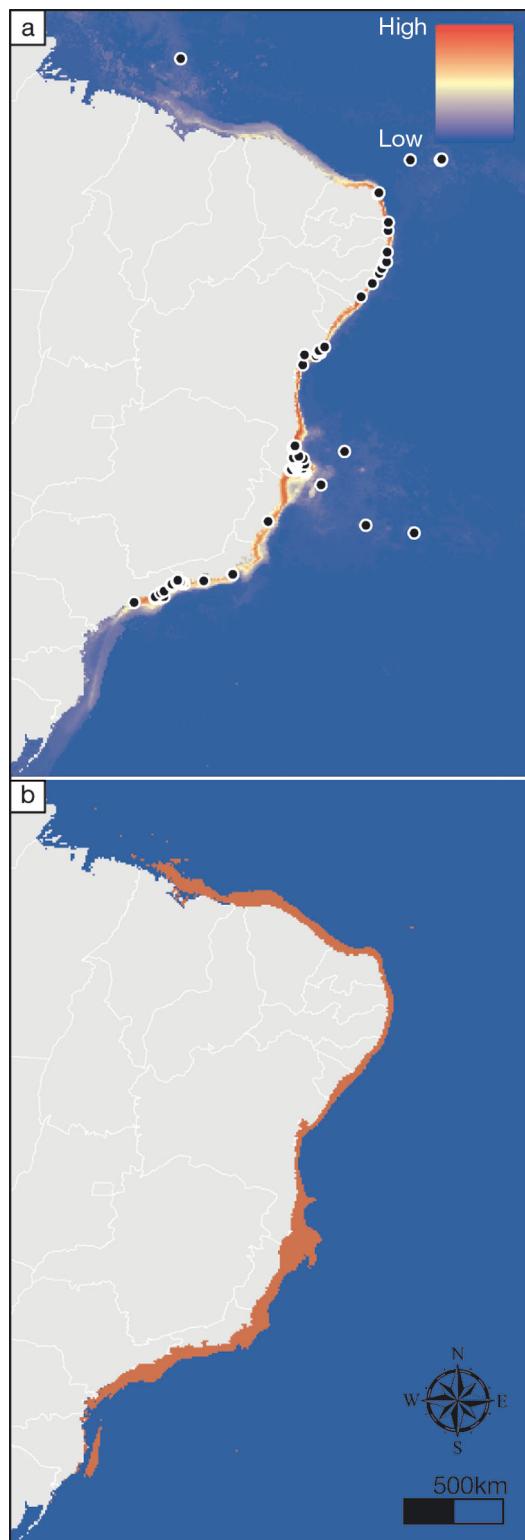


Fig. 2. (a) Climatically suitable environments for *Mussismilia hispida* and (b) regions with suitable environments for *M. hispida* and *Tubastraea coccinea* along the Brazilian coast in the southwest Atlantic. (●) Unique localities used to train the model of *M. hispida*

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 *Mussismilia* is endemic to Brazil and *M. hispida* along with its congeners *M. brasiliensis* 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 taxons.

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 envi-

ronmental 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 costal environments.

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