Importance of Anthropogenic Determinants of *Tubastraea coccinea* Invasion in the Northern Gulf of Mexico

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Abstract: *Tubastraea coccinea* is an invasive coral that has had ecological, economic, and social impacts in the Atlantic Ocean, the Caribbean Sea, and the Gulf of Mexico (GoM). *Tubastraea coccinea* is considered a major threat to marine biodiversity, whose occurrence in its non-native range has been associated with artificial structures such as oil/gas platforms and shipwrecks. A recent species distribution model identified important determinants of *T. coccinea* invasion in the northern GoM and projected its potential range expansion. However, the potential effects of anthropogenic factors were not considered. We used boosted regression trees to develop a species distribution model investigating the importance of oil/gas platforms and shipping fairways as determinants of *T. coccinea* invasion in the northern GoM. Our results indicate that maximum salinity, distance to platform, minimum nitrate, and mean pH were the first to fourth most influential variables, contributing 31.9%, 23.5%, 22.8%, and 21.8%, respectively, to the model. These findings highlight the importance of considering the effects of anthropogenic factors such as oil/gas platforms as potential determinants of range expansion by invasive corals. Such consideration is imperative when installing new platforms and when decommissioning retired platforms.

Keywords: biological invasions; coral reefs; marine biodiversity; oil/gas platforms; rigs-to-reefs program; species distribution models

1. Introduction

Coral reefs provide USD 3.4 billion per year in ecosystem services in the U.S. [1], and invasive marine species have negatively impacted these ecosystem services [2]. Biological invasions often result in a reduction in biodiversity, loss of native and commercial species, and changes in the structure and function of communities and ecosystems [3,4]. Rising globalization has increased the number of anthropogenic structures in marine environments, while coral species colonize manmade reefs [5,6]. In the Gulf of Mexico (GoM), the “rigs-to-reefs” program, conducted under the auspices of the Bureau of Safety and Environmental Enforcement, converts decommissioned offshore oil and gas rigs into artificial reefs [5]. Oil/gas platforms facilitate the dispersal of coral larvae and may be accelerating the range expansion of invasive corals in the northern GoM [6].

*Tubastraea coccinea* is an invasive coral that has had ecological, economic, and social impacts in the Atlantic Ocean, the Caribbean Sea, and the GoM [7]. It is commonly known as orange cup coral or sun coral [8–10]. *Tubastraea coccinea*, whose occurrence in its non-native range is mainly associated with artificial structures such as oil/gas platforms and shipwrecks, is considered a major threat to marine biodiversity [6,11–13]. A recently developed species distribution model identified important determinants of *T. coccinea* invasion in the northern GoM and projected its potential range expansion [14]. Five environmental factors, including two variables from the top surface layer of the ocean...
(mean pH and mean calcite) and three variables from benthic layers adjacent to the seabed (maximum current velocity, minimum iron, and minimum dissolved oxygen), contributed >99% to the overall model [14,15]. However, the potential effects of anthropogenic factors were not considered.

In this paper, we use boosted regression trees to develop a species distribution model investigating the importance of anthropogenic determinants of \textit{T. coccinea} invasion in the northern GoM. Specifically, we focus on the potential effects of oil/gas platforms and shipping fairways as determinants of the invasion.

2. Materials and Methods

2.1. Focal Species

\textit{Tubastrea coccinea} is an azooxanthellate coral native to the Indo-Pacific reefs, where it was first described near Bora Bora Island in French Polynesia [16]. It was first reported on offshore oil platforms in Brazil in the 1980s [17]. It is easily identified by its red-to-orange body and orange-to-yellow tentacles, although colonies of \textit{T. coccinea} can vary in size and color [18]. \textit{Tubastrea coccinea} is not considered a reef-building coral [8]. Colonies are composed of a spongy calcareous base with protruding calcareous cups known as corallites [17]. Each corallite contains a single polyp [14], which can be up to 11 mm in diameter and can extend up to 4 cm from the spongy calcareous base [8]. In the GoM, \textit{T. coccinea} rarely occurs at depths >78 m [19]. \textit{Tubastrea coccinea} have been reported as fouling organisms on oil/gas platforms [20].

2.2. Study Area

The GoM occupies 1.5 million km$^2$ and contains thousands of species from over 40 phyla [21]. Our research focuses on the northern GoM along the coasts of Texas, Louisiana, Mississippi, Alabama, and Florida (Figure 1a). The gulf coastal waters adjacent to these five states contribute greatly to ecosystem goods and services. On average, they contribute over USD 2 trillion per year to the gross domestic product, excluding additional income produced by non-market regulating, cultural, and supporting services [22].

![Figure 1. Maps of (a) the study area, which includes the exclusive economic zone of the United States within the northern portion of the Gulf of Mexico, and (b) the records of \textit{Tubastrea coccinea}, oil/gas platforms, and lanes of heavy shipping fairways within the northern Gulf of Mexico.](image-url)
2.3. Data Collection

We obtained *T. coccinea* occurrence data from Derouen et al. [14] (Figure 1b). Derouen et al. [14] collected data from the Ocean Biogeographic Information System [23], the Global Biodiversity Information Facility [24], and the Web of Science [25]. They identified nine environmental variables as being physiologically and/or ecologically relevant for marine organisms in general [15,26] and for *T. coccinea* in particular [14]. Seven were benthic variables (maximum current velocity, minimum dissolved oxygen, minimum light at the bottom, maximum salinity, minimum iron, minimum nitrate, and maximum primary productivity) and two were surface variables (mean calcite and mean pH) (Table 1). These variables were determined to be independent using Pearson’s correlation coefficient (electronic supplementary material 2 of Derouen et al. [14]). We downloaded data on these nine variables as TIFF raster files from Bio-ORACLE. We downloaded a map of the GoM study area as a marine region shapefile, which included the exclusive economic zone and International Hydrographic Organization sea area, from a website (marineregions.org) managed by the Flanders Marine Institute [27]. Derouen et al. [14] provide further details on the collection and processing of these environmental data. In addition to the environmental data, we downloaded a CSV containing georeferenced locations of oil/gas platforms in the GoM from the Bureau of Safety and Environmental Enforcement Data Center [28], and obtained the routes of associated shipping fairways from ESRI [29] (Figure 1b).

### Table 1. Units and descriptive statistics for the nine environmental variables and the two anthropogenic variables.

| Variable                           | Unit       | Maximum  | Mean      | Minimum   |
|------------------------------------|------------|----------|-----------|-----------|
| Benthic                            |            |          |           |           |
| Maximum current velocity           | m−1        | 1.2980   | 0.1915    | 0.0319    |
| Minimum dissolved oxygen           | mol m−3    | 210.0137 | 181.9234  | 119.4268  |
| Minimum light at bottom            | -          | 19.0054  | 1.4978    | 0         |
| Maximum salinity                   | PSS        | 36.7947  | 35.6285   | 30.8558   |
| Minimum iron                       | µmol m−3   | 0.0073   | 0.0011    | 0.0004    |
| Minimum nitrate                    | mol m−3    | 27.5709  | 12.4456   | 0.0000    |
| Maximum primary productivity       | g m−3 day−1| 0.1313   | 0.0114    | 0         |
| Surface                            |            |          |           |           |
| Mean calcite                       | mol m−3    | 0.0560   | 0.0026    | 0.0001    |
| Mean pH                            | -          | 8.2139   | 8.1195    | 7.9690    |
| Anthropogenic                      |            |          |           |           |
| Distance to nearest oil platform   | m          | 782,115  | 167,220   | 25        |
| Distance to nearest shipping       | m          | 309,949  | 81,067    | 10        |
| fairway                            |            |          |           |           |

2.4. Data Processing and Analysis

We overlaid the occurrence data on the map of the study area to produce a *T. coccinea* occurrence map. Each of the nine environmental variables were joined with the occurrence map in QGIS 3.20 (Odense). We overlaid a georeferenced grid containing 0.083° × 0.083° cells on the joined (*T. coccinea* occurrence plus nine environmental variables) map to calculate the potential predictor variables at the centroids in each cell. We overlaid the oil/gas platform points and shipping fairways on the study area map. We then used the GRASS plugin tool, v.distance, to calculate the nearest cell centroid (in m) to each platform and the nearest cell centroid to each shipping fairway (Table 1). We conducted our analysis using boosted regression trees following the procedure described by Derouen et al. [14]. Specifically, the optimal model was determined (1) by altering the learning rate and tree complexity until the predictive deviance was minimized without over-fitting, and (2) by limiting our choice of the final model to those that contained at least 1000 trees, following the recommendations of Elith et al. [30]. Once the optimal combination of learning rate and tree complexity was found, model performance was evaluated using a tenfold cross-validation procedure with re-substitution. For each cross-validation trial, 60% of the dataset was randomly selected for model fitting, and the excluded 40% was used for testing, following the recommendation of Wang et al. [31]. We derived our optimal model in R.
3.6.0 [32] using the gbm package version 1.5–7 [33]. We calculated the relative influence of each potential determinant variable in the model and constructed partial dependence plots for the most influential variables. We used the optimal model to calculate the probabilities of \( T. coccinea \) occurrence in the northern GoM and superimposed these probabilities on the map of the northern GoM using ArcGIS Pro 2.8.3 [34].

### 3. Results

Analyses of 500 combinations of tree complexity (ranging from 3 to 7) and learning rates (ranging from 0.001 to 0.01) produced models with between 450 and 3100 trees. The optimal model had a tree complexity of 5, a learning rate of 0.003, and a total of 1050 trees. The AUC score was 0.920 ± 0.022 (“very good” ability to discriminate between species presence and absence). Four variables were included in our final species distribution model, with two benthic variables contributing 54.7%, one anthropogenic variable contributing 23.5%, and one surface variable contributing 21.8% to the overall model (Figure 2).

Maximum salinity, distance to platform, minimum nitrate, and mean pH were the first to fourth most influential variables, contributing 31.9%, 23.5%, 22.8%, and 21.8%, respectively. Partial dependence plots indicated that \( T. coccinea \) occurrences were associated with benthic conditions characterized by maximum salinity between 36.21 and 36.61 PPS (Figure 3a) and minimum nitrate between 0.000053 and 1.17 mol m\(^{-3}\) (Figure 3c), anthropogenic factors characterized by a distance to platform between 380 and 9958 m (Figure 3b), and surface conditions characterized by mean pH less than 8.06 m (Figure 3d). These results suggest the potential for range expansion of \( T. coccinea \) in the northern GoM is the highest along the Texas and Louisiana coasts between 90° W and 95° W, where the estimated probabilities of occurrence (\( P \)) were relatively high (0.7 < \( P \) ≤ 0.8) (Figure 4). Considering our entire study area, approximately 93.51%, 6.12%, 0.29%, and 0.08% of the cells fell within the \( P \) ≤ 0.5, 0.5 < \( P \) ≤ 0.6, 0.6 < \( P \) ≤ 0.7, and \( P \) > 0.7 categories, respectively.

![Figure 2](image2.png)

**Figure 2.** Relative contribution (%) of the four variables used in our final model.

![Figure 3](image3.png)

**Figure 3.** Partial dependence plots for the four variables, (a) maximum salinity, (b) distance to nearest oil platform, (c) minimum nitrate, and (d) mean pH, included in the final model. The y-axis represents the logit scale used for the indicated variable; hash marks at the top of the plot indicate deciles of each variable.
4. Discussion

Species distribution models and ecological niche models have been increasingly used to address a variety of ecological issues involving endangered species, invasive species, and emergent infectious diseases [35–37]. Many approaches, ranging from statistical methods to machine learning methods, have been developed and applied. Moreover, data-related issues (including data availability and limitation, inclusion of independent variables, and scaling data) remain a fruitful area of debate [38,39]. Indeed, providing reliable predictions of a potential habitat for *T. coccinea* now and in the future remains a challenge. Variables affecting *T. coccinea* spread operate at different spatial scales, resulting in data limitations and modelling challenges [40,41]. Coral range projections have been made for more than a decade [42], including four recent studies focused on *T. coccinea* [14,43–45]. Even though these four studies all focused mainly on the impacts of benthic and surface variables on the distributions of *T. coccinea*, their results differed somewhat due to the limited availability of occurrence data, the different research regions from which the data were collected, and, hence, the inclusion of different independent variables in the different models [46–48]. The relative importance of independent variables may also vary with the stage of invasion [40,49]. The selection of specific independent variables may have markedly changed the model development and likelihood estimates [41], which is a general problem related to structural uncertainty in the quantitative representation of natural systems [50,51]. In our study, the possibility always remains that we failed to include some important independent variables, and that the relative importance of those variables we included depends on the current state of the system [35,40]. The availability of additional data on the biological process (e.g., coexistence and competition) and environmental variables (e.g., suspended sediments and current direction), as well as the functional relationships between the variables and the stage of invasion, would likely enhance the prediction precision [52–54].

Our results highlight the importance of considering the effects of anthropogenic factors such as oil/gas platforms and shipping fairways as potential determinants of range expansion by invasion corals. We found distance to oil/gas platforms to be among the most important determinants of *T. coccinea* invasion in the northern GoM, contributing on the same level as more commonly considered benthic and surface variables in terms of relative importance in our species distribution model. Below, we first compare our
results with those of Derouen et al. [14] and comment briefly on the environmental factors included in our final model. We then conclude by offering some thoughts on the inclusion of anthropogenic factors in species distribution models of invasive corals.

Our estimated probabilities of *T. coccinea* occurrence indicated a potential distribution that differs noticeably from that reported by Derouen et al. [14] in that it did not include areas along the Gulf coast of Florida (Figure 4). Our highest probabilities of occurrence (\( p > 0.7 \)) were clustered in two areas along the Texas and Louisiana coasts, between approximately 90° W and 94° W. Derouen et al. [14] estimated that such high probabilities (\( p > 0.7 \)) extended farther along the Texas and Louisiana coasts, from 88° W to 97° W. Derouen et al. [14] identified three benthic variables (maximum current velocity, minimum iron, and minimum dissolved oxygen) and two surface variables (mean pH and mean calcite) as the most important determinants of *T. coccinea* invasion (collectively contributing >99% to their overall model). Our results concur that both benthic and surface environmental conditions are important determinants of invasion. However, consideration of anthropogenic factors, which led to the inclusion of distance to gas/oil platforms in our model, changed the identity and relative importance of the environmental factors included in the final model. Our model included none of the environmental variables included in the model of Derouen et al. [14], except for mean pH, and reduced the overall contribution of environmental variables by almost one-quarter (to \( \approx 76\% \)). Statistically, it is not surprising that the addition of a new variable changed the relative influence of variables included in the original set. Nor, from an ecological perspective, is it surprising that the relative importance of specific environmental variables shifted, given the complex interactions among environmental factors and coral physiology. Derouen et al. [14] comment on the physiological/ecological relevance of each variable included in their model, and we do the same in the following paragraphs. What, perhaps, is surprising is the omission of anthropogenic factors from species distribution models focused on coastal marine environments—a point to which we will return in our concluding remarks.

Maximum salinity was the most influential variable in our model, contributing 31.9%. Throughout the study area, maximum salinity ranged from 30.86 PSS to 36.79 PSS (Table 1), while *T. coccinea* was associated with maximum salinity at the higher end of that range (between 36.21 and 36.61 PPS). As a structuring factor in marine ecosystems, salinity affects the distribution of corals [55]. In the models of Derouen et al. [14] and Riul et al. [43], both of which included only environmental variables, salinity was found to be less important. The model of Santos et al. [56], which included a variable representing distance to oil/gas platforms, found salinity to be associated with *Tubastrea* spp. occurrence, although the presence in their study was associated with lower rather than higher salinity. Corals have a low tolerance to large changes in salinity, although studies have shown that some corals are able to withstand moderate salinity fluctuations [57]. Low salinity may cause reduced photosynthesis and bleaching [57,58], and stony corals, such as *T. coccinea*, are assumed to be quite sensitive to freshwater compared to other marine invertebrates [59]. High salinity may lead to increased thermotolerance [60], but *T. coccinea* has not yet been subjected to such testing, and more studies investigating the effect of salinity fluctuation on coral fitness are needed [57].

Minimum nitrate was the second most influential environmental variable in our model, contributing 22.8% to the overall model. Minimum nitrate throughout the study area ranged from 0.00 to 27.57 mol m\(^{-3}\). *Tubastrea coccinea* was associated with minimum nitrate levels between 0.000053 and 1.17 mol m\(^{-3}\). Nitrate is a limiting nutrient for marine organisms, and the input of fixed nitrogen into reef ecosystems sustains primary production and overall net productivity [61]. Corals may increase nitrogen fixation in response to increased temperatures and dissolved organic carbon availability [62], which could provide corals with a potential mechanism to persist in variable environments [61]. Corals prefer oligotrophic water, and an excessive nitrogen supply can result in phosphate starvation, which can increase the vulnerability of corals to heat and light stress [63].
Mean pH was the third most influential environmental variable in our model, contributing 21.8% to the overall model. Mean pH throughout the study area ranged from 7.97 to 8.21. *Tubastraea coccinea* was associated with a mean pH less than 8.06. Mean pH was the most influential variable in the model of Derouen et al. [14], and those authors found that *T. coccinea* was associated with a somewhat similar range of mean pH (less than 8.12). pH is an important physicochemical in marine ecosystems [64], directly affecting calcification rates [65]. *Tubastraea coccinea* has shown little response to changes in pH in previous studies [66]. When under heat stress, invasive *T. coccinea* in the GoM are more stress-resistant to changes in pH than their endemic Indo-Pacific counterparts [67], which may give *T. coccinea* a competitive advantage [66].

The anthropogenic factor included in our model, distance of oil/gas platforms to the nearest centroid, contributed almost one-quarter (23.5%) of the explanatory power of the model. The distances to oil/gas platforms throughout the study area ranged from 25 to 782,115 m. *Tubastraea coccinea* was associated with a distance to platform between 380 and 9958 m (Figure 3b). There are ≈1862 oil/gas platforms in the GoM [28], which provide hard substrates for benthic community colonization and development [68]. Within the northern GoM, *T. coccinea* was first discovered on seven oil/gas platforms, and these platforms likely served as stepping stones that facilitated further spread [12]. Coral larvae can disperse hundreds to thousands of kilometers to settle [69], and *T. coccinea* populations have been utilizing oil/gas platforms to expand their geographic range in the northern GoM [6,12].

Our model and the model of Derouen et al. [14] both estimated the highest probabilities of *T. coccinea* occurrence to be along the coasts of Louisiana and Texas. Derouen et al. [14] suggested that this distribution may be explained by gulf currents transporting planulae, and they identified maximum current velocity as the main contributor to their model. With the addition of distance to oil/gas platforms as a variable, we found maximum current velocity to be unimportant in our model. Derouen et al. [14] also suggested heavy shipping traffic could be a possible influential variable, although they did not investigate its potential effect on their model. We explicitly included distance to shipping fairways as a potential determinant of invasion, but it was not an important contributor to our model.

The take-home message from the comparison of these two models is not that one model is superior to the other in any absolute sense. Certainly, the roles of both current flows and the distribution of oil/gas platforms in the range expansion of *T. coccinea* are ecologically interpretable, as are the roles of the other variables included in each model. Rather, the take-home message is that the inclusion of anthropogenic variables as potential determinants of occurrence can alter the relative importance of environmental variables and can enrich the ecological interpretation of species distribution models. Other studies have also emphasized the importance of including anthropogenic factors in species distribution models of corals [11].

Regarding the management implications of our results, we concur that the installation of new oil/gas platforms will require a priori risk assessments and that the decommissioning of retired platforms should take into consideration non-native species dispersal, especially that of *T. coccinea* [70]. In the United States, federal legislation requires that all offshore platforms be removed within a year after production has ended [71]. The Bureau of Ocean Energy Management (BOEM) has created the “rigs-to-reefs” program, which encourages owners to donate oil/gas platforms to the program. The donated platforms are either left in place or toppled and towed to an artificial reef site located in the U.S. Exclusive Economic Zone (EEZ) [19]. *Tubastraea coccinea* thrives on artificial substrates [12], and significantly higher densities of *T. coccinea* have been found on toppled rigs-to-reefs platforms than on standing platforms [19]. Careful consideration is essential both prior to and after the creation of an artificial reef regarding its possible facilitation of the invasion of non-native species such as *T. coccinea* [5].
5. Conclusions

Our results highlight the importance of considering the effects of anthropogenic factors as potential determinants of range expansion by invasive corals. Considering the invasive nature of *T. coccinea* and its impact on natural and artificial reefs, the documentation of its present distribution and the identification of likely areas of potential range expansion are of paramount importance. Oil/gas platforms in particular can act as a vector for the range expansion of *T. coccinea* within the northern GoM. The installation of new oil/gas platforms will require a priori risk assessments, and the decommissioning of retired platforms should take into consideration non-native species dispersal, especially that of *T. coccinea*. Such considerations are imperative within programs such as the “rigs-to-reefs” program in the United States.

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