Modeling the habitat suitability of *Caulerpa* sp. across the Galápagos Islands

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Abstract

Globally, the number of invasive marine species has increased in recent years, posing a substantial risk both ecologically and economically. Throughout the Galápagos islands, two species of the green macroalgae *Caulerpa*, *C. chemnitzia and C. racemosa*, exhibit invasive tendencies, which may threaten native biodiversity. Characterized by fast growing species that reproduce asexually via fragmentation, the genus *Caulerpa* is known for successful invasion and establishment of populations outside of their natural range. We hypothesized that *Caulerpa* sp. are suitable for a broad geographic range in the Galápagos, with the potential to disperse beyond their current known ranges. Using R packages "terra" and "sdm", we utilized an array of geospatial and presence/absence data to create a habitat suitability model for both species individually, and then ran a comparison of the two models. Findings indicate that the occurrence for both species is highly suitable in locations far beyond their current known range. For *C. chemnitzia*, the highest predictor for habitat suitability was sea surface temperature (AUC: 51.4%), and for *C. racemosa was* chlorophyll concentration (AUC: 44.5%). For both species, we also found that chlorophyll concentration was a high predictor of the model's likelihood of occurrence (AUC: >35%). In addition, proximity to human population was found to be a strong predictor for *C. racemosa* suitability (AUC: >40%) which suggests anthropogenic activity is correlated with occurrence. Although model variable importance differed between species, results indicate that both species are highly suitable to occupy the same niche. This modeling approach serves as a cost-effective and efficient first step for prioritizing management efforts.

Introduction

Due to geographic isolation, native species on remote islands often have fewer predators, rendering them exceptionally vulnerable to non-native species (MacArthur and Wilson 1967, Williamson 1969, Simberloff 1995, Hulme 2009). This makes island archipelagos ideal models for studying the relationships between native and non-native species. Worldwide, the introduction of non-native species to islands has led to an exponential loss of biodiversity (Loope et al. 1988, Carlton et al. 2019). On islands, non-native species heighten interspecific competition for limited resources available (Williamson 1969). Humans are the primary vector for invasive species, and several studies have suggested that non-native species have a greater negative impact on native biodiversity in areas with high human populations (Jeschke and Strayer 2006, Geraldi et al. 2019). The invasional meltdown hypothesis aids in explaining this phenomenon, positing that invasive species facilitate the invasion of subsequent species, leading to cascading negative effects on native species (Green et al. 2011). Globally, the number of invasive marine species has increased in recent years (Hulme 2009). Factors such as climate change, overfishing and increased transport are likely responsible for increased spread of non-native species (Hulme 2009, Keith et al. 2016). In the Galápagos islands, invasive species pose a substantial risk both ecologically and economically (Keith et al. 2016, Carlton et al. 2019).

One green algal genus that poses a substantial threat to the native biodiversity of the Galápagos islands is the Chlorophyta macroalgae, *Caulerpa* (Keith et al. 2016, Keith et al. 2022). Characterized by fast growing species that reproduce asexually via fragmentation, the genus is known for its species successful invasion and establishment of populations outside of their respective natural range (Klein and Verlaque 2008, Guiry and Guiry 2024). In the Galápagos islands, the genus includes two problematic species, *Caulerpa chemnitzia* and *Caulerpa racemosa*, both categorized as cryptogenic with highly invasive tendencies (Franklin and Keith 2019, Keith et al. 2022). *Caulerpa chemnitzia* poses a risk to coral ecosystems due to its fast growing and competitive tendencies (Keith et al. 2022). ENSO warming events are predicted to allow the species to expand their natural range due to high temperatures and low nutrient availability (Keith et al. 2022). The lesser-studied species, *C. racemosa* was first observed in the archipelago in 1899 (Charles Darwin Foundation 2024). *C. racemosa* thrives best in warm water ranging from 18°C to 25°C, in shallow waters (0-5m) with minimal swell exposure (Téran and Keith 2019). Given the behavioral and genetic similarities within the *Caulerpa* genus, it is likely that *C. racemosa* poses similar risks to reefs, and surrounding flora and fauna as *C. chemnitzia*. Although more research is needed to update the "cryptogenic" listing for these species currently, both algae exhibit extremely competitive tendencies, outcompeting native species (Téran and Keith 2019). Extensive studies on *C. racemosa* outside of its native range in locations such as Iran, Cyprus, and Italy, have found that it overgrew and outcompeted native algae, greatly altering the macrobenthic and surrounding ecosystems (Argyrou et al. 1999, Ceccherelli et al. 2001, Buia et al. 2002, Ceccherelli et al. 2002, Balata et al. 2004).

Species distribution modeling (SDM) serves as a vital first step in invasive species management as it is substantially more cost effective than surveying the coastlines of the archipelago. SDM frameworks have demonstrated high predictive power and enable cost-effective management practices. Studies have shown sea surface temperature (SST) and anthropogenic impacts were commonly identified as the most important factors (Jueterbock et al. 2016, Veazey et al. 2019, Blanco et al. 2021). In a 2021 study, anthropogenic factors strongly influenced the probability of occurrence of several invasive macroalgal species (Blanco et al. 2021). Maximum sea surface temperature was identified as the most important factor in limiting the fundamental niche of *Fucus distichus* (Jueterbock et al. 2016). Similarly, a model conducted on the alga *Avrainvillea amadelpha* found sea surface temperature, and shoreline development were the most important predictors of occurrence (Veazey et al. 2019). In the context of *Caulerpa* distribution throughout the Galápagos islands, utilizing SDM approaches for prioritizing sampling sites could provide crucial insights into the current or probable future distribution of the species at a much lower cost. This technique allows for effective management and monitoring of invasive species, helping to mitigate their impact on native biodiversity and ecosystems.

Modeling the habitat suitability of introduced *Caulerpa* species may identify highly susceptible regions that the algae could disperse to. The goal of this project is to leverage SDMs to identify regions highly vulnerable to *Caulerpa* invasion, and to inform management strategies for these algal species. We hypothesize that *Caulerpa* species are suitable for a broad geographic range in the Galápagos, with the potential to spread throughout the archipelago well beyond its current know range. Depth is expected to be the most correlated predictor variable for both species. Additionally, we expect proximity to human population to be a strong predictor for potential distribution. Without affordable and efficient surveying techniques, these species have the potential to continue to disperse throughout the Galápagos islands, while threatening native biodiversity (Keith et al. 2016, Téran and Keith 2019). Our study aims to improve the efficiency of manual surveys by identifying high-suitability regions and to assist in mitigating the impact of *Caulerpa* species on native ecosystems within the Galápagos.

Methods

Data Assembly

***Caulerpa* presence/absence:** Presence and absence points were obtained and concatenated using data from the Ecological Monitoring Program and the herbarium at the Fundación Charles Darwin (Charles Darwin Foundation. 2024). For *C. racemosa*, there were 42 positively identified locations throughout the archipelago, and 65 absence points. For *C. chemnitzia*, there were 90 positively identified occurrence points, and 50 absence points. Due to the assumption of independence made by SDM based on the resolution of the predictor variables (4.6km^2), occurrence records were thinned to include only one presence/absence point per grid which decreased the amount of points the model used (Boria et al. 2014). After thinning occurrence points, C. *racemosa* had 26 presence points, and 42 absence points. *Caulerpa. chemnitzia* had 20 presence and 34 absence points (Fig 1).

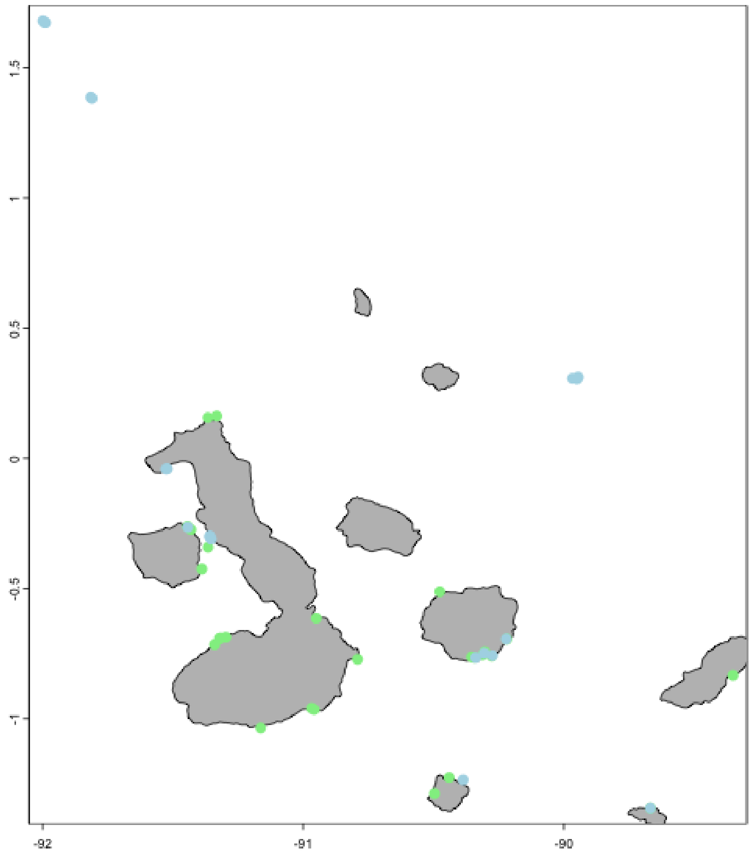
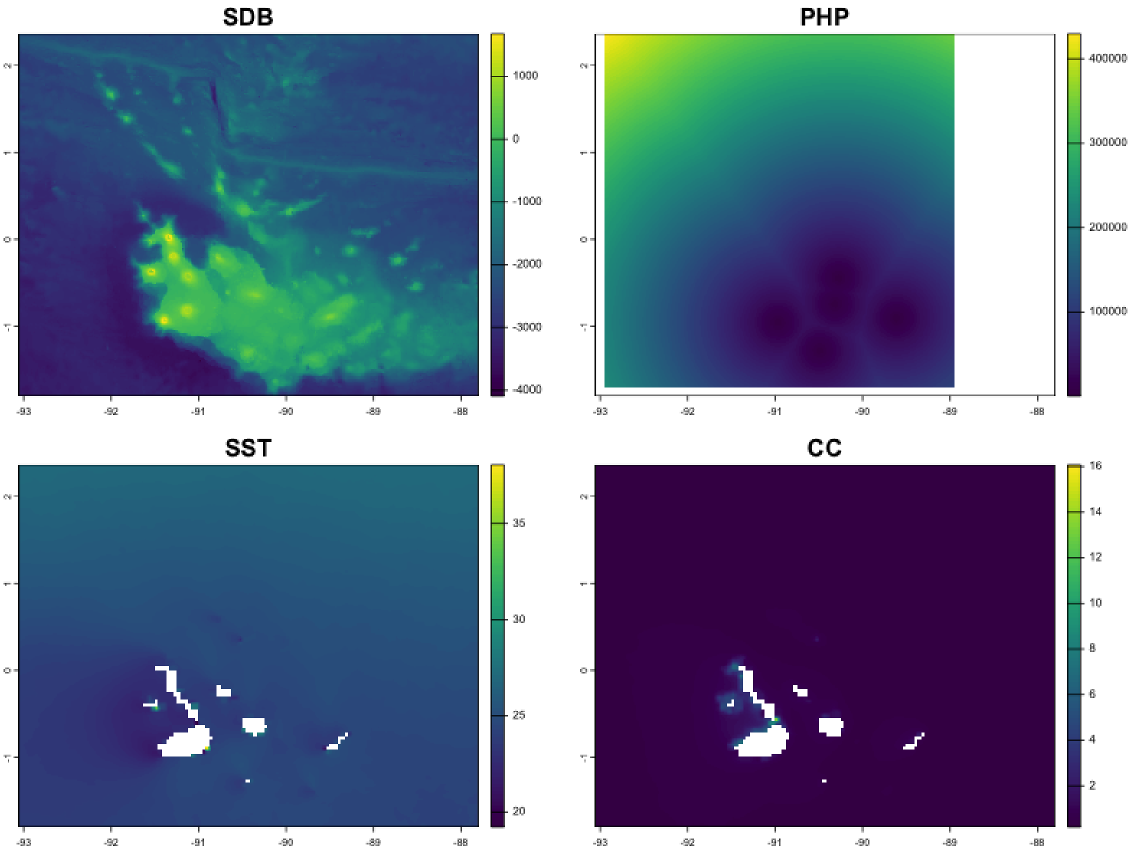


Fig 1: Presence points of *Caulerpa* sp. distribution throughout the Galápagos islands subsequent to thinning points at a resolution of 4.6k^2. Species overlap is seen in many sites within the Galápagos islands.

Predictor variable assembly: Environmental and geographic data were used as predictor variables. Variables selected were: bathymetry (SDB), sea surface temperature (SST), proximity to human population (PHP), visitor sites (VS), particulate organic carbon (POC), chlorophyll a concentration (CC), and photosynthetically available radiation (PAR). Both SDMs used the same predictor variables. SDB data was obtained from GEBCO at 15 arc second resolution (Becker et al. 2009, Smith and Sandwell 1997). POC, CC, SST, and PAR, at a resolution of 4.63km was obtained from MODIS (NASA Ocean Biology Processing Group 2022). Using 2022 census data, and the 2022 annual report of Galapagos, two rasters were created for proximity to human population (PHP) and visitor sites (VS). The PHP raster was created by assigning the centroid of each grid cell the nearest distance to the 5 known populations in the Galápagos. The raster for

VS was created by calculating the summed inverse of the distances to all visitor sites from the centroid of each grid cell at a resolution of 0.05º latitude by 0.05º longitude using the "geosphere" library in R (Caisaguano et al. 2022, Hijams 2022, GeoRef 2024, R Core Team 2024). Using a correlation matrix, variables that were found to be strongly correlated with one another > 70% were removed to ensure we did not overfit the model (Sup Table 1). The variable with more predictive power over the two species was kept. This resulted in visitor sites (VS), particulate organic carbon (POC), and photosynthetically available radiation (PAR) being removed (Sup Fig. 1). All data was processed using the R package "terra" and converted to raster files (Hijmans 2024).


SDB

PHP

SST

CC

Fig 2: Raster plots of the final four predictor variables: bathymetry (SDB), proximity to human population (PHP), sea surface temperature (SST), and chlorophyll a concentration (CC).

Species Distribution Model

We utilized RStudio and the R packages “terra” and “sdm” to create our model (Naimi and Araujo 2016, Hijmans 2024). These packages allowed us to run a variety of SDMs (Generalized Linear Model (GLM), Generalized Additive Model (GAM), Boosted Regression Trees (BRT), BioClim, and Random Forests (RF)) simultaneously. This enabled determining the best fit framework to utilize with respect to our available data. Each model was replicated for 100 iterations using subsampling with data split into 70% training, 30% testing to validate the models’ performances for 100 iterations. The mean outputs of the 100 iterations were then calculated to predict the habitat suitability of each species. Using the mean values of both species outputs, the Pearson correlation coefficient index was calculated to measure the correlation between the predicted suitability between the species. In addition, we used the Overlap Index to measure the degree of overlap between predicted presence/absence of the species.

Results

For *C. chemnitzia*, the highest predictor for habitat suitability was sea surface temperature (AUC: 51.4%), and for *C. racemosa* it was chlorophyll concentration (AUC: 45.5%). For both species, we also found that chlorophyll concentration was a high predictor of the model’s likelihood of occurrence (AUC: >35%). SDB was the lowest predictor for both species (AUC < 5%).

C. chemnitzia

For *C. chemnitzia*, SST and CC make up the majority of predicting variable importance (Fig. 4).

For *C. racemosa*, proximity to human population (PHP) is the highest predictor of habitat suitability (59.3%) with Chlorophyll a as the second highest (31.9%) (Fig. 5).

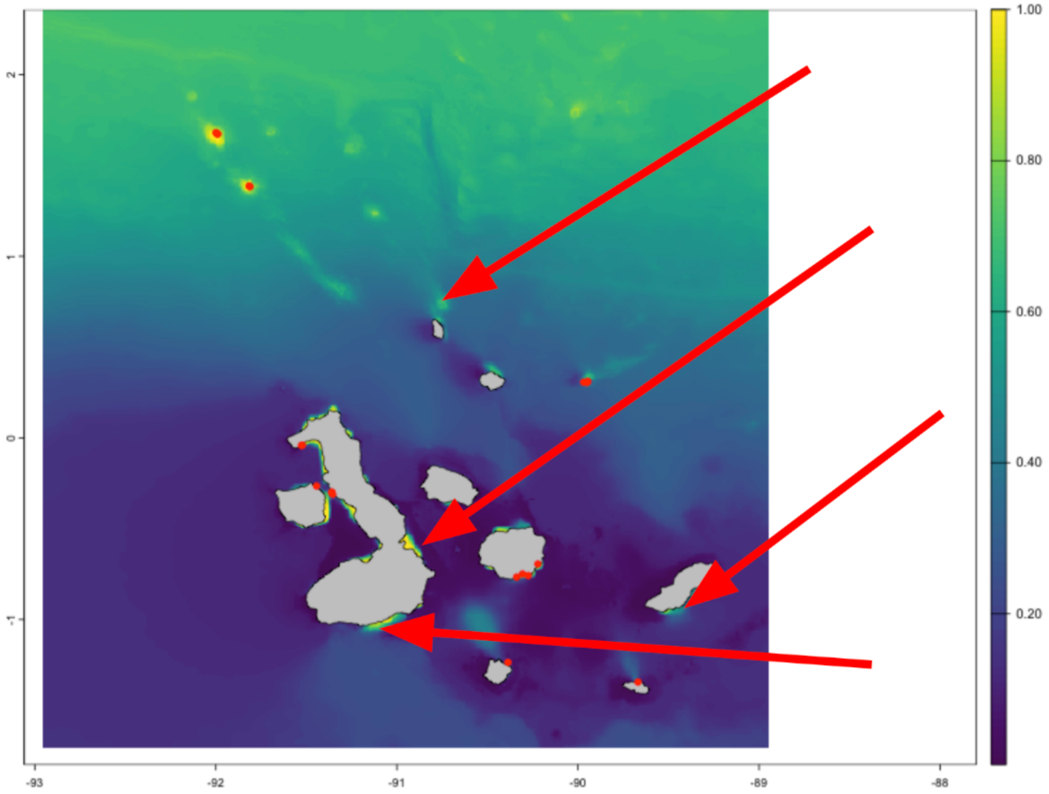


Figure 3: *Caulerpa chemnitzia* model outputs of the four frameworks with known presence points overlaid as red dots. The red arrows represent areas the model predicted to have high suitability with no nearby corresponding known presence point.

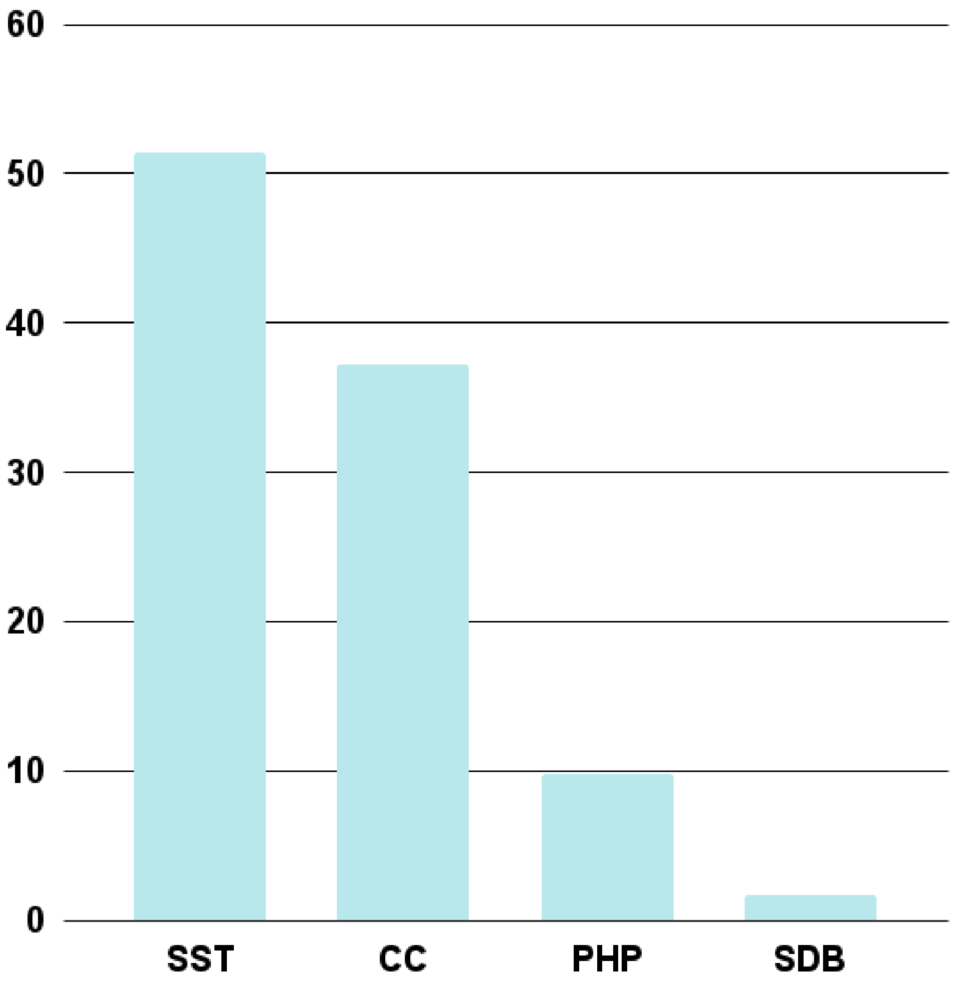


Figure 4: *C. chemnitzia* variables in order of importance (AUC %): sea surface temperature (SST), chlorophyll a concentration (CC), proximity to human population (PHP), sea surface temperature (SST), and bathymetry (SDB).

C. racemosa

For *C. racemosa*, chlorophyll concentration (CC) is the highest predictor of habitat suitability (44.5%) with proximity to human population (PHP) as the second highest (~40%) (Fig. 5).

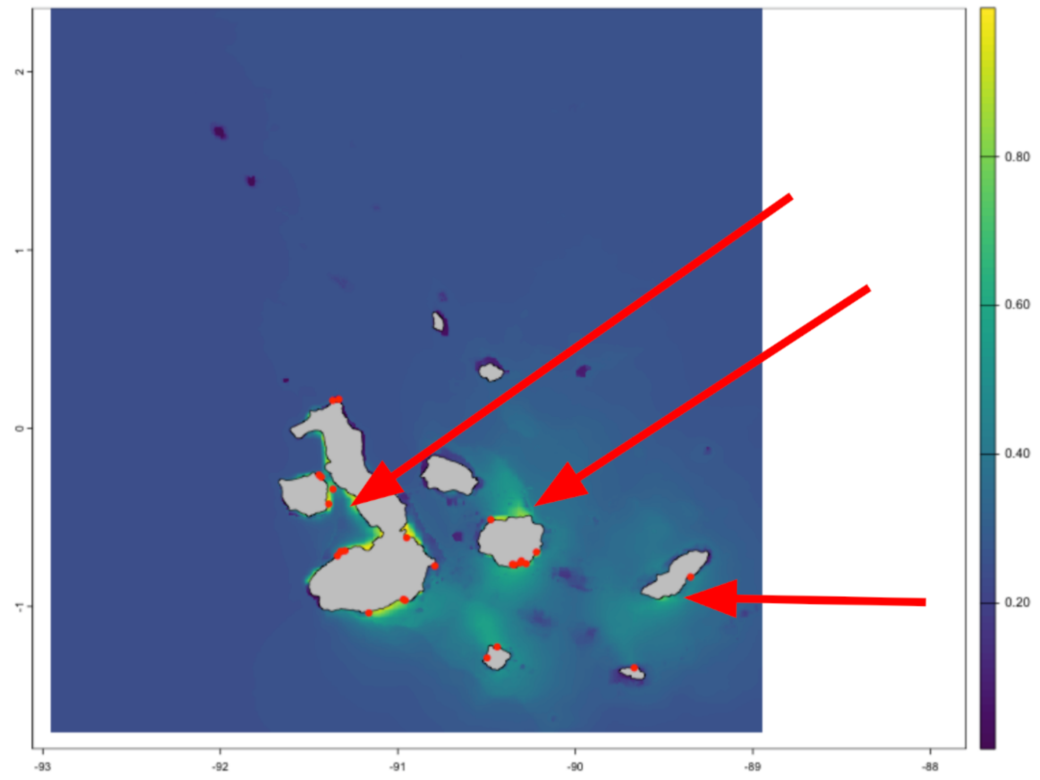


Figure 5: *Caulerpa racemosa* model outputs of the four frameworks with known presence points overlaid as red dots. The red arrows represent areas the model predicted to have high suitability with no nearby corresponding known presence point.

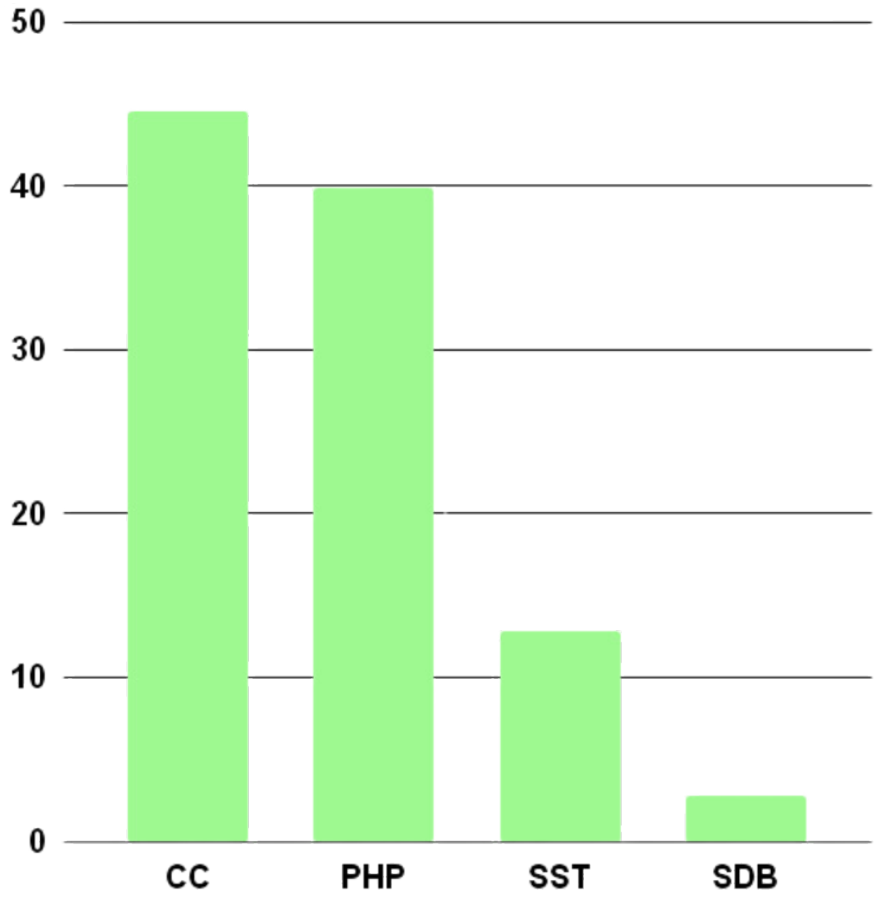


Figure 6: *C. racemosa* variables in order of importance (AUC %): chlorophyll a concentration (CC), proximity to human population (PHP), sea surface temperature (SST), and bathymetry (SDB). CC and PHP make up ~ 85% of the variable importance.

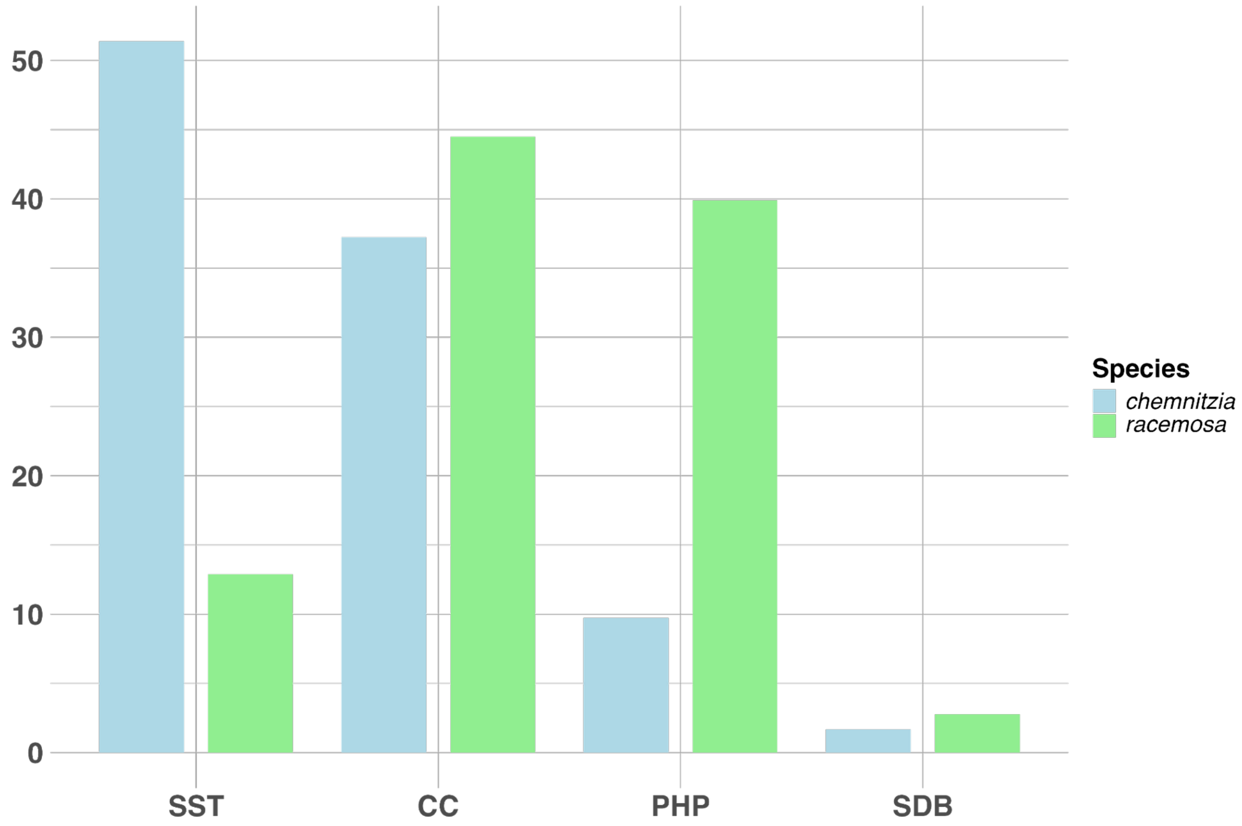


Fig 7: Comparison of variable importance between species, sea surface temperature (SST), chlorophyll a concentration (CC), proximity to human population (PHP), and bathymetry (SDB). Species have differing top predictors, C. *chemnitiza* is SST and C. *racemosa* is CC. Chlorophyll concentration was a high predictor (AUC > 35%) for both species.

Discussion

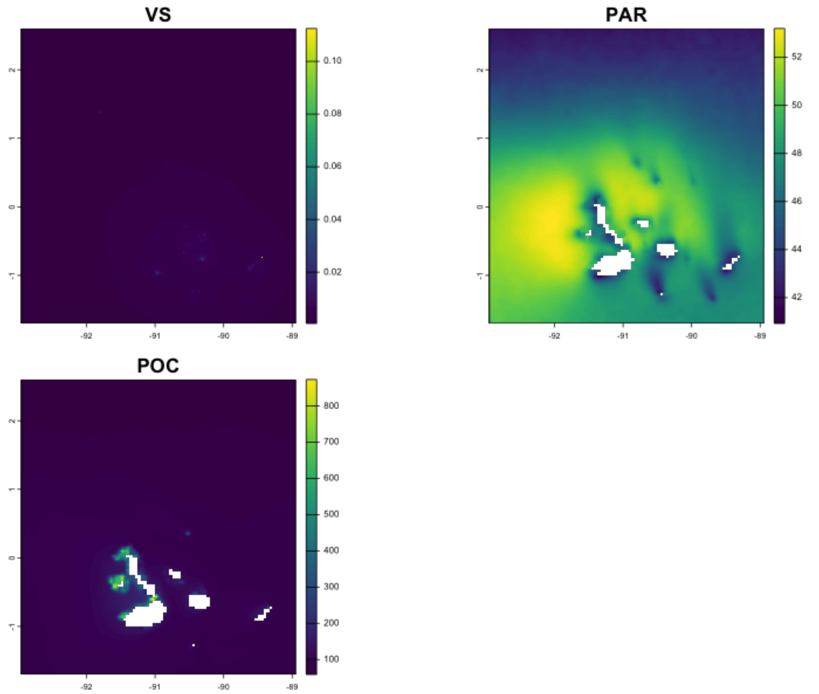
Four model frameworks: Generalized Linear Model (GLM), Generalized Additive Model (GAM), Boosted Regression Trees (BRT), and Random Forest (RF), were utilized to identify the most appropriate model for predicting habitat suitability for these two species, with the respective data. The Generalized Linear Model (GLM) was ultimately chosen for both species due to model outputs and the overall fit (Sup Fig 2 and 3, Sup Table 2 and 3). Notably, the BRT method could not be applied to *C. chemnitzia* due to a lack of presence points after data thinning. One potential solution to this issue could be the inclusion of pseudo-negative points.

Both species were found to be suitable for larger geographic ranges than their currently known distributions, suggesting the potential for range expansion. Our findings indicated several highly suitable sites for each species that currently lack corresponding presence points. This raises the question of whether these species have not yet colonized these areas or if the areas have not been adequately surveyed. Prioritization of surveying highly suitable sites is recommended to mitigate the risk of further dispersal of this alga (Keith et al. 2016, Téran and Keith 2019).

The comparison of variable importance between the species revealed that CC was a high predictor for both species (AUC > 35%). We also determined SDM was not a strong predictor for either species (AUC < 5%) which may be due to the quick, steep changes in bathymetry within the archipelago which is not reflected well in the 4.6km^2 resolution of the data. However, although the variable importance between species differs, the Pearson correlation coefficient index was .899 indicating high linear correlation between the predicted suitability between species. In addition, the Overlap Index was 0.801 which shows a high degree of overlap between predicted presence/absence of the species. These statistics indicate that species could be highly suitable to occupy the same niche as one another, which was not previously thought. Because of this, accurate species ID is necessary to understand the intraspecific relationships these alga have.

All available data presence/absence data were utilized in model creation, alongside the finest resolution predictor variable data. Despite this, the study faced limitations due to the quantity and resolution of available data. This highlights the need for finer resolution open-source spatial predictor variables for the Galápagos islands, as the model may be over predicting due to the resolution of available data. Furthermore, incorporating weighted abundance data rather than just presence/absence data could enhance the model's predictive power and yield more conclusive results. It is important to note that these models predict where the algae are suitable, not their real-time distribution. This modeling approach serves as a cost-effective and efficient first step for prioritizing fieldwork efforts. Overall, this study underscores the need for improved data quality and resolution to better model habitat suitability and predict potential range expansions for these species.

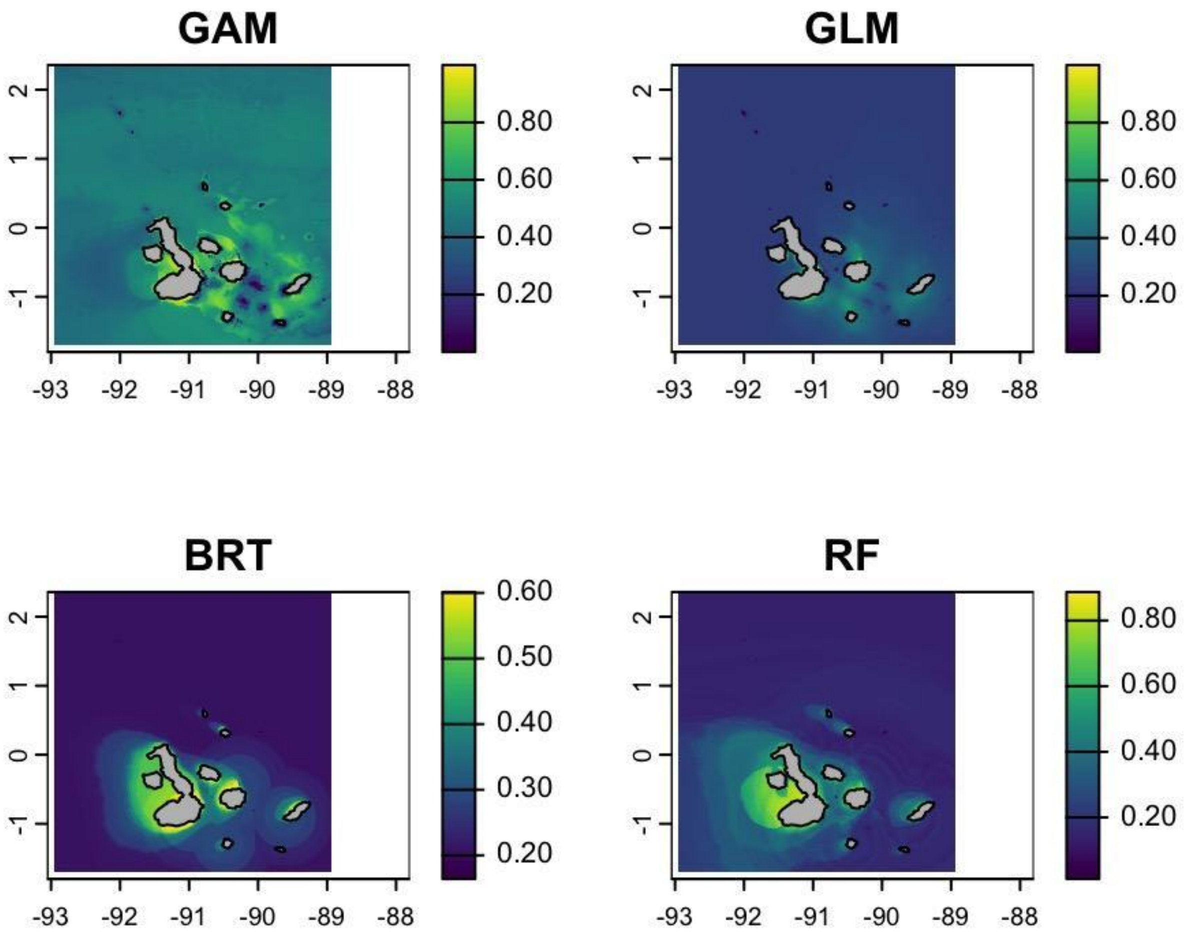
Supplemental



Sup Fig 1: Raster plots of the three predictor variables that were removed from the study because they were correlated > 0.7 to one another. Visitor sites (VS), photosynthetically available radiation (PAR) and particulate organic carbon (POC).

Sup Table 1: Correlation matrix of predictor variables, excluding VS. Highlighted in red are variables that are correlated to one another > 0.7.

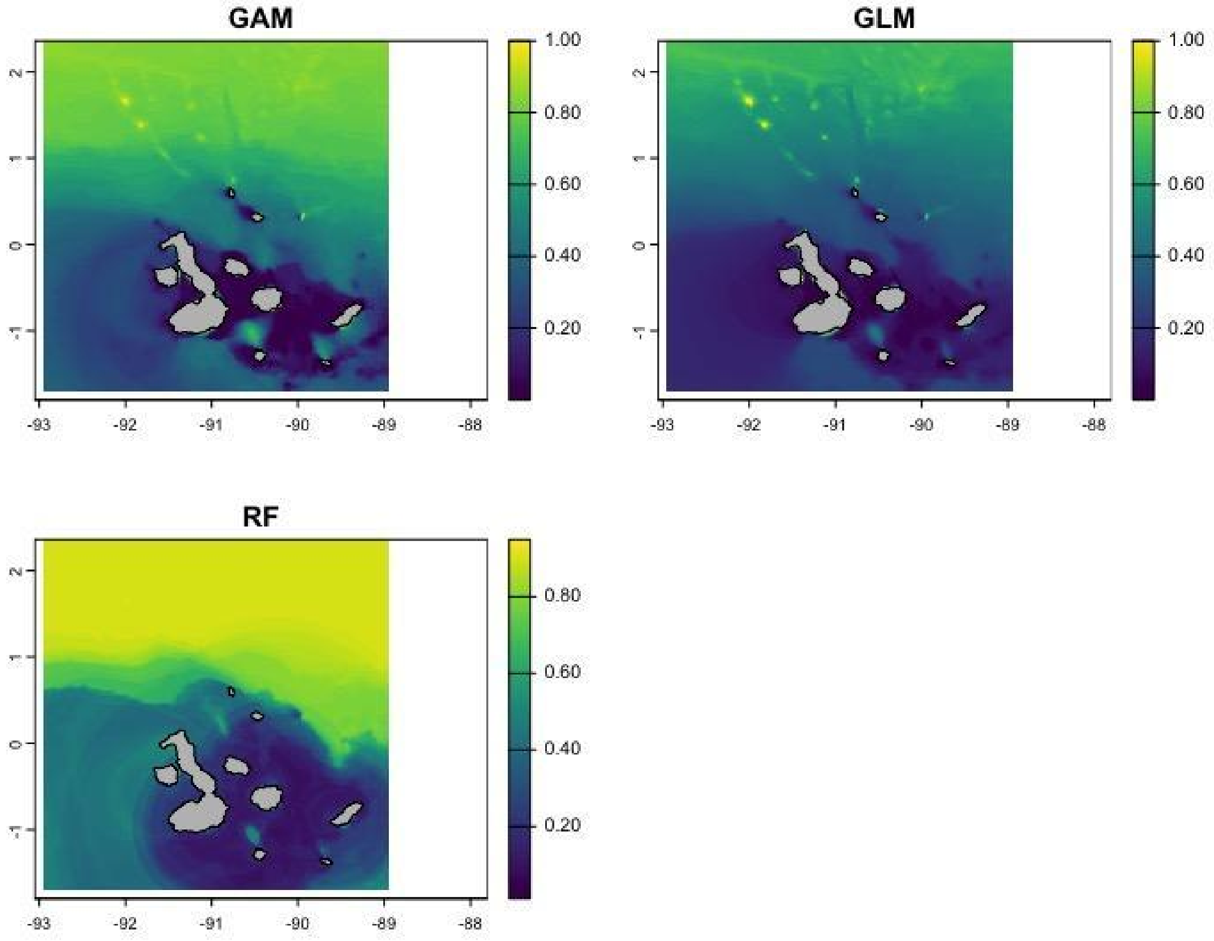
	SDB	**PHP**	**SST**	**POC**	**CC**	**PAR**
SDB	1	-0.4356	0.0446	0.2900	0.2767	-0.2444
PHP	-0.4356	1	0.6875	-0.3048	-0.2667	-0.5136
SST	0.0446	0.6875	1	-0.4295	-0.3928	-0.8205
POC	0.2900	-0.3048	-0.4295	1	0.9246	0.1801
CC	0.2767	-0.2667	-0.3928	0.9246	1	0.1315
PAR	-0.2444	-0.5136	-0.8205	0.1801	0.1315	1



Sup Fig 2: *Caulerpa racemosa* model outputs of the four frameworks.

Sup Table 2: *C. racemosa* framework outputs.

Method	AUC	COR	DEV
GAM	**0.79**	**0.53**	**9.23**
GLM	**0.77**	**0.47**	**1.88**
BRT	**0.88**	**0.61**	**1.07**
RF	**0.87**	**0.62**	**0.93**



Sup Fig 3: *Caulerpa racemosa* model outputs of the four frameworks.

Sup Table 3: *C. chemnitzia* framework outputs.

Method	**AUC**	**COR**	**DEV**
GAM	**0.81**	**0.52**	**8.8**
GLM	**0.88**	**0.64**	**1.92**
BRT	**0.88**	**0.64**	**1.92**
RF	**0.82**	**0.59**	**1.04**

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