

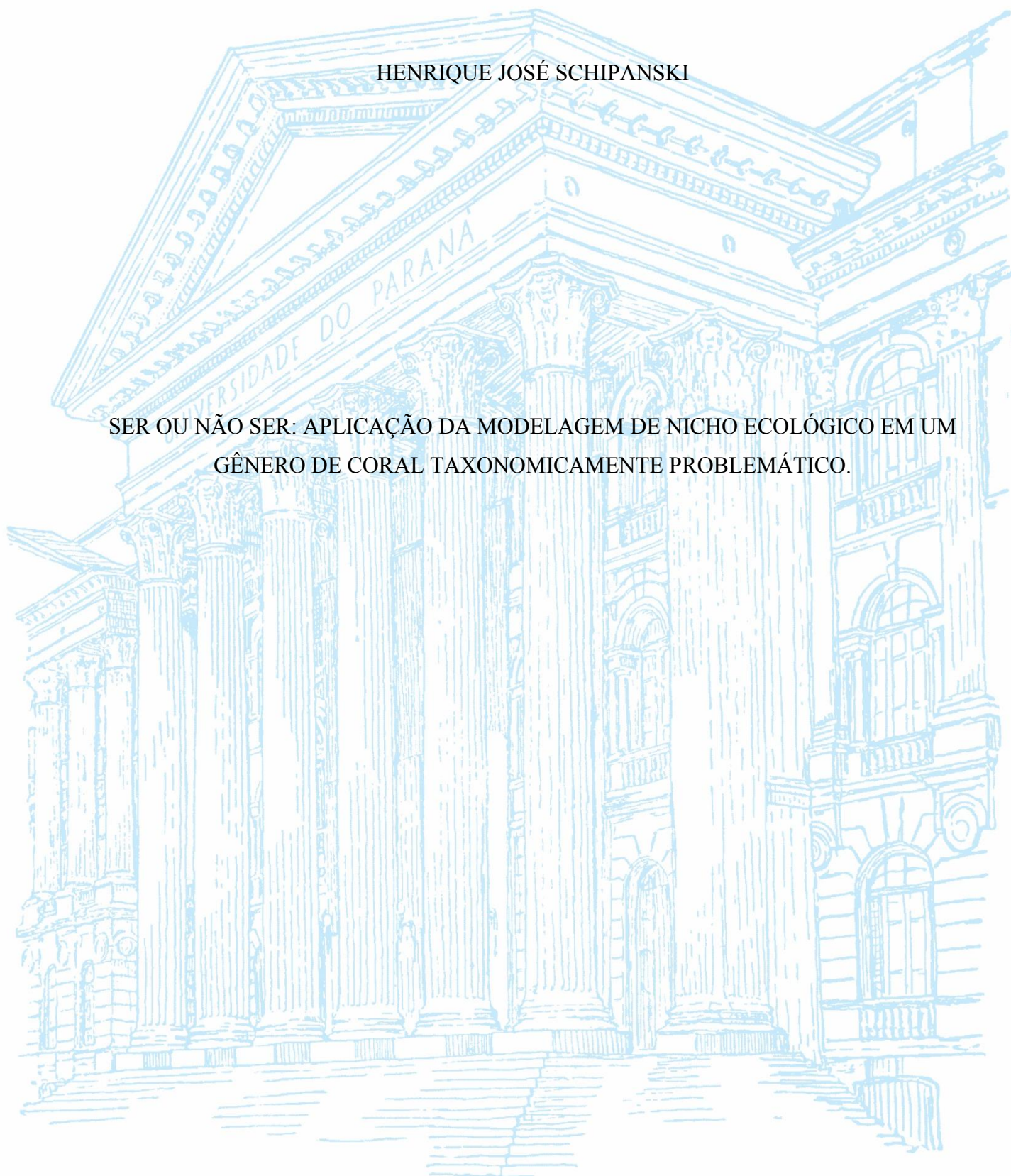
UNIVERSIDADE FEDERAL DO PARANÁ

HENRIQUE JOSÉ SCHIPANSKI

SER OU NÃO SER: APLICAÇÃO DA MODELAGEM DE NICHOS ECOLÓGICOS EM UM
GÊNERO DE CORAL TAXONOMICAMENTE PROBLEMÁTICO.

CURITIBA

2021



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GÊNERO DE CORAL TAXONOMICAMENTE PROBLEMÁTICO.

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FERNANDA THIESEN BRUM

Avaliador Externo (UNIVERSIDADE FEDERAL DO PARANÁ - UFPR)

Assinatura Eletrônica

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MAURICIO OSVALDO MOURA

Avaliador Externo (UNIVERSIDADE FEDERAL DO PARANÁ)

Avenida Cel Francisco H Santos, s/n - CURITIBA - Paraná - Brasil

CEP 81531-980 - Tel: (41) 3361-1641 - E-mail: pgzoo@ufpr.br

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“It's always the living that are haunting my nights”

(David Gilmour)

“Eu prefiro ser essa metamorfose ambulante do que ter aquela velha opinião formada
sobre tudo”

(Raul Seixas)

RESUMO

O gênero *Siderastrea* tem cinco espécies, quatro das quais (*S. glynni*, *S. radians*, *S. siderea*, *S. stellata*) ocorrem no Atlântico, enquanto *S. savignyana* é encontrada no Indo-Pacífico. *S. glynni* foi considerado sinônimo de *S. siderea*. *S. stellata* é supostamente endêmica do Brasil, mas foi recentemente registrada para Parque Nacional de Veracruz, no México. Embora sua distribuição atual englobe o Caribe, Golfo do México e Atlântico Norte, também há um registro do século 19 de *S. siderea* para o Brasil. *S. radians* tem uma distribuição anfi-atlântica e, portanto, é simpátrica a *S. siderea* na maior parte de sua distribuição e a *S. stellata* no Brasil. É difícil distinguir entre essas três espécies devido à grande sobreposição de caracteres diagnósticos quantitativos. Por isso, constituem o “complexo *Siderastrea* do Atlântico”. Se a distribuição dessas espécies fosse associada a diferenças ecofisiológicas, então uma espécie endêmica do Brasil, como *S. stellata*, não deveria ser encontrada no Golfo do México, a menos que as condições ambientais fossem semelhantes entre os dois locais. Uma forma de testar essa hipótese é caracterizar o nicho ecológico de cada espécie e verificar se a distribuição pode ser projetada para áreas onde não há registro de sua presença. Se não houver ampliação da área de ocorrência, as espécies devem ter preferências abióticas distintas e novas ocorrências putativas podem resultar da taxonomia confusa do gênero. Nesse sentido, os objetivos do presente trabalho foram: usar técnicas de modelagem de nicho para projetar os nichos ecológicos fundamentais de (a) *S. stellata* no Mar do Caribe e Golfo do México; (b) *S. siderea* na costa brasileira; (c) ambas as espécies na costa oeste da África e (d) estimar a sobreposição de nicho fundamental entre as três espécies. No Brasil, essas projeções mostraram alta adequabilidade de *S. stellata* (> 70%) no Arquipélago de Abrolhos (18 ° 1'27,82 "S - 39 ° 0'26,91 "W) e grande parte de sua costa nordeste (16 ° 7'10,39" S / 2 ° 37'29,67 "S- 38 ° 38'25,83" W / 42 ° 24'20,04 "W) e também para o Golfo do México, onde a espécie foi recentemente registrada. As projeções para *S. siderea* e *S. radians* demonstraram alta adequação de habitat nas Bahamas, Belize, Florida Keys, na costa nordeste do Brasil e em uma pequena parte da costa da África Ocidental, onde a ocorrência de *S. radians* é conhecida. A análise da sobreposição de nicho mostrou uma alta sobreposição de *S. siderea* e *S. radians* (0,67), mas moderada sobreposição entre *S. stellata* e *S. siderea* (0,40) e entre *S. stellata* e *S. radians* (0,40). Como *S. stellata* e *S. radians* coexistem no Brasil, nossos resultados sugerem que, pelo menos de uma perspectiva puramente ecológica, *S. stellata* poderia de fato ocorrer no Golfo do México e, da mesma forma, *S. siderea* poderia estar presente no Brasil. Assim, o conceito de espécie ecológica não pode resgatar a taxonomia do complexo de seu enigma morfológico.

Palavras-chave: Cnidaria. Scleractinia. Biogeografia

ABSTRACT

The genus *Siderastrea* has five species, four of which (*S. glynni*, *S. radians*, *S. siderea*, *S. stellata*) occur in the Atlantic whereas *S. savignyana* is found in the Indo-Pacific. Molecular systematics revealed that *S. glynni* is a synonym of *S. siderea*. *S. stellata* is supposedly endemic to Brazil, but it was recently recorded for the Yucatán Peninsula in Mexico. Although its current distribution encompasses the Caribbean, Gulf of Mexico and North Atlantic, there is also a 19th century record of *S. siderea* for Brazil. *S. radians* has an amphi-Atlantic distribution and it is thus sympatric to *S. siderea* across most of its distribution and to *S. stellata* in Brazil. It is hard to distinguish among these three species due to the large overlap of quantitative diagnostic characters. For that reason, they make up the so called “*Siderastrea* Atlantic complex”. If the distributions of these species were dictated by their ecophysiological differences, then a species endemic to Brazil, such as *S. stellata*, should not be found in the Gulf of Mexico, unless the environmental conditions were similar between the two locations. One way to test this hypothesis is to characterize each species’ ecological niche and check if its distribution can be projected to areas where there is no record of its presence. If there is no projection, species should be biogeographically distinct and putative new occurrences may result from the confusing taxonomy of the genus. In this sense, the objectives of the present work were to use niche modelling techniques to project the fundamental ecological niches of (a) *S. stellata* onto the Caribbean Sea and Gulf of Mexico; (b) *S. siderea* onto the Brazilian coast; (c) both species onto west Africa’s coast and (d) estimate fundamental niche overlap among the three species. In Brazil, these projections showed high *S. stellata* suitability (> 70%) for Abrolhos Archipelago (18°1'27.82"S - 39° 0'26.91"W) and most of its Northeast Coast (16° 7'10.39"S/2°37'29.67"S- 38°38'25.83"W/42°24'20.04"W) and also for the Yucatán peninsula, where the species was recently recorded. The projections for *S. siderea* and *S. radians* demonstrated high habitat suitability in the Bahamas, Belize, Florida Keys, the Northeast Coast of Brazil and a small part of the coast of West Africa, where only *S. radians* is known to occur. The analysis of niche overlap showed a high overlap of *S. siderea* and *S. radians* (0.67), but moderate, and statistically distinct overlap between *S. stellata* and *S. siderea* (0.40) and between *S. stellata* and *S. radians* (0.40). Because *S. stellata* and *S. radians* do coexist in Brazil, our results suggest that, at least from a purely ecological perspective, *S. stellata* could indeed occur in the Gulf of Mexico and, likewise, *S. siderea* could be present in Brazil.

Keywords: Cnidaria.Scleractinia.Biogeography.

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1 INTRODUCTION

Siderastrea (Blainville, 1830) is a genus composed of five species: *S. radians* (Pallas, 1766), *S. siderea* (Ellis & Solander, 1786), *S. stellata* (Verrill, 1868), *S. savignyana* (Milne Edwards & Haime, 1850) e *S. glynni* (Budd & Guzmán, 1994). *S. savignyana* has been recorded throughout the Indo-Pacific Ocean (Veron, 2000) and *S. glynni* was found to be a junior synonym of *S. siderea* (Glynn et al., 2016). *S. stellata* is restricted to the coast of Brazil where its range partially overlaps with the range of *S. radians* (Neves et al., 2008). The latter species is also found throughout the Caribbean, Gulf of Mexico, Florida and Bermuda, where it occurs sympatrically with *S. siderea*, and also on a small portion of the African Western Coast (Garcia et al., 2017; Monteiro et al., 2013; Morri & Bianchi, 1995). *S. siderea*, *S. stellata* and *S. radians* make up the so called “*Siderastrea* Atlantic complex” due to the overlap of diagnostic, quantitative morphological characters (number of and arrangement of septa, papillae and synapticular rings, corallite diameter etc.), that make the definition of species boundaries subjective (Aldhebiani, 2018) and hence the taxonomy of these species challenging (Menezes et al., 2013, Menezes et al., 2014, Neves et al., 2010).

On the other hand, these congeners do present distinctive reproductive strategies, suggesting that they are reproductively isolated and hence are “good species” according to the biological species concept (de Queiroz, 2005). *S. siderea* is gonochoric (i.e. dioic) and broadcasting (i.e with external fertilization), while *S. radians* is hermaphroditic and presents internal fertilization (Szmant, 1986). *S. stellata* although described as gonochoric (Barros et al., 2003) presents planulation, but this is not observed in *S. radians* neither *S. siderea* (Neves & da Silveira, 2003). Genetic analyses also show that *S. stellata* and *S. radians* populations in Brazil differ with respect to allele frequencies and genotypic variability (Neves et al., 2008). Likewise *S. radians* and *S. siderea* are also genetically distinct (i.e. have exclusive haplotypes and are reciprocally monophyletic) and sympatric in the Caribbean. To date, genetic comparisons between *S. siderea* and *S. stellata* remain little explored (Garcia et al., 2017).

When relying solely on morphological characters, species identification in *Siderastrea* has had, historically, a strong biogeographic component: if the specimen were not identified as *S. radians*, it must be *S. stellata* if collected off the Brazilian coast, or as *S. siderea*, if it was collected elsewhere on the western Atlantic (Laborel, 1974). However, Neves et al., (2010) re-identified a Smithsonian Institute (NMNH) specimen of *Siderastrea* spp. collected by Hartt in the 19th century off Bahia as *S. siderea*, yielding the first record of the species for Brazil.

Additionally, García et al., (2017) reported for the first time the presence of *S. stellata* in the Gulf of Mexico using morphological and genetic data (ITS and ITS2).

One hypothesis that explains this seeming breakup of the canonical biogeographic pattern is human introduction dating back at least to the XIX century. However, oogenesis in *Siderastrea* is long (de Barros et al., 2003; Gelais et al., 2016), hence the establishment of a viable population would require repeated introductions. All species in the genus are slow growing and symbiotic (de Barros et al., 2003; Gelais et al., 2016; Lazar et al., 2011) and data available for *S. stellata* (Neves & da Silveira, 2003) show that larvae are resistant, but very particular in their choice of habitat, taking time to find a suitable place for the settlement and subsequent metamorphosis (Neves & da Silveira, 2003). Therefore rafting, as recently reported on oil platforms by Capel et al. (2019) for the invasive Dendrophylliid *Tubastrea* spp., is unlikely. Planulae of *Siderastrea* remain active for a maximum of two days (Neves et al., 2008) hence transport on ballast water is also unlikely.

Therefore, the recent identification of specimens outside of their putative areas of distribution may be a consequence of the uncertain taxonomy of the *Siderastrea* Atlantic complex that leads researchers to rely more on biogeography than on morphology when trying to identify specimens. Taxonomic characters in corals have long been known to obscure biogeographic patterns, hence such reliance is not entirely unwise. For instance, molecular systematics have shown that Atlantic *Favia fragum* and *Scolymia cubensis* (i.e. morphologically distinct) were phylogenetically closer among themselves than to their Pacific congeners (Fukami et al., 2004). However, if it is true that species may occur outside of their expected areas of distribution, as reviewed above, one would expect suitable habitats for these species to exist outside of their canonical ranges. On the other hand, if those ranges exist because of local adaptation, niche overlap among allopatric species should be minimal (*S. stellata* vs *S. siderea* and *S. radians*). Indeed, ecological segregation in corals has been demonstrated even in sympatric populations and in the absence of barriers to gene flow. This is the case both in soft (e.g. *Briareum asbestinum* - Brazeau & Harvell, 1994; *Eunicea flexuosa* - Prada et al., 2008) and hard corals (e.g. *Agaricia* spp. - Bongaerts et al., 2013; *Favia fragum* - Carlon & Budd, 2002; *Montastraea* spp. - Levitan et al., 2004). If niche segregation leads to no gene flow among populations, they may be considered separate species also according to the ecological concept of species (Kirkpatrick & Barton, 1997; Valen, 1976)

Ecological niche modeling (ENM) is the right tool to test both propositions because it offers the possibility of projecting the distribution of these species where, theoretically, they do not occur, and also the possibility of evaluating niche overlap within a sound statistical

framework. The specific objectives were: (1) to evaluate habitat suitability of the Caribbean Sea and West African coast to *S. stellata* (2) the suitability of Brazilian and West African coast to *S. siderea* and (3) estimate niche overlap between each species pair.

2 METHODS

2.1 OCCURRENCE POINTS

The occurrence points were obtained in primary and "gray" literature (i.e., scientific articles, thesis, dissertations, report, etc.), since data from Global Biodiversity Information Facility (GBIF) had incomplete records that may introduce spatial bias in the analysis (Beck et al., 2014). A total of 3,094 occurrences were collected, of which 1,572 were *S. siderea* records, 1,069 were *S. radians*' and 453 were *S. stellata*'s. Occurrences were subsequently filtered using the *thin* function from the *spThin* package (Aiello-Lammens et al., 2015) and only coordinates separated by at least 10km from the others were retained. A second filter was used to select records in cells with a maximum depth of 60m (Bongaerts et al., 2015), in order to avoid projection to cells whose depths are beyond the recorded range for the genus. A total of 74 occurrence points for *S. stellata*, 166 for *S. radians*, and 172 for *S. siderea* were kept in the final data set (Figure 1; Appendix A).

Sampling sufficiency with respect to spatial coverage of the available literature was evaluated using rarefaction analysis employing 1000 permutations on a presence/absence matrix using the *specaccum* function of R's (R Core Team, 2020) *vegan* package (Oksanen et al., 2019). We used the number of surveyed documents as the predictor and the number of cells with occurrences as the response variable.

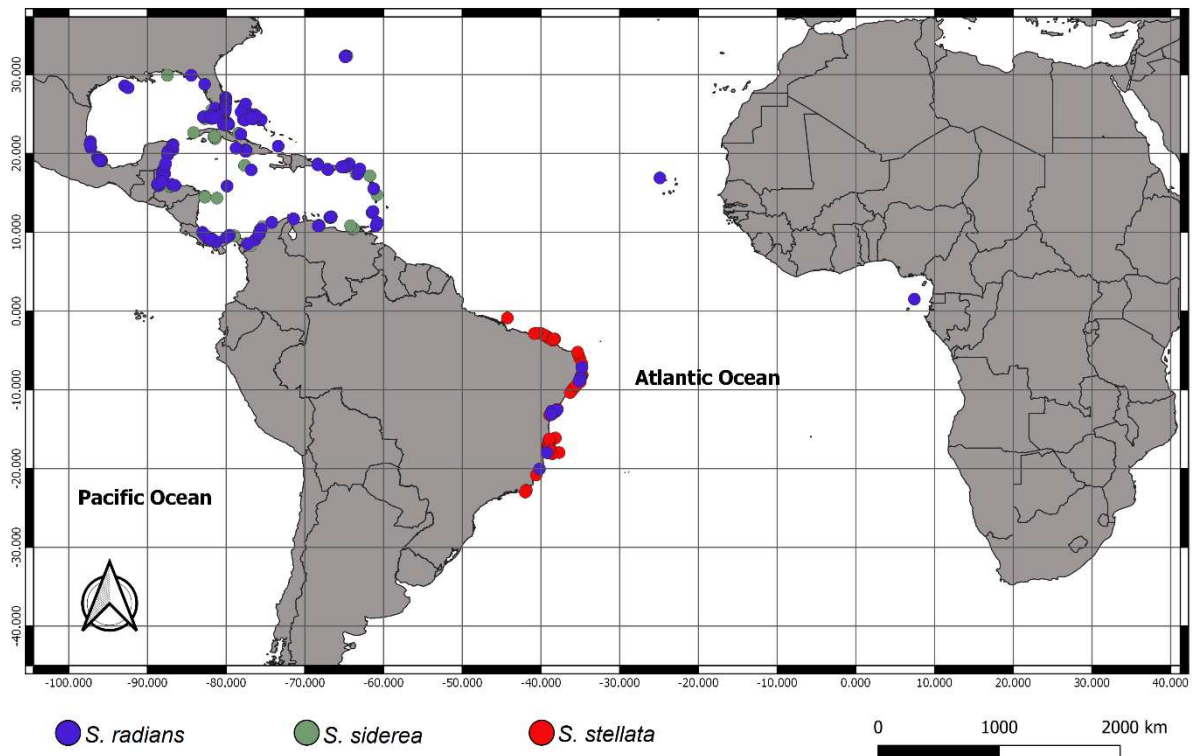


Figure 1: Distribution of occurrence points after (i) spatial and (ii) bathymetry filtering of points. Blue circles represent the occurrence points of *S. radians*. Green circles represent the points of occurrence of *S. siderea*. Red circles represent the occurrence of *S. stellata*.

2.2 ENVIRONMENTAL LAYERS

The environmental layers were obtained from the BIO-ORACLE repository (Assis et al., 2017; Tyberghein et al., 2012), which contains 23 layers in total, with a resolution of 5 arcmin (~9,2 km at the equator). Since the extent for calibration could influence the final results of the model inflating a performance measure, such as the area under the ROC curve (AUC, e.g. Barve et al., 2011; Lobo et al., 2008), layers were trimmed to fit the distribution of *S. stellata* (i.e. 45°-32°W/ 27°S-2°N), *S. siderea* (100°-60°W; 2°S-45°N) and *S. radians* (Africa, Brazil, and the Caribbean- 100°W-30°E; 31°S-34°N).

The environmental variables, chosen considering the biology of the species, were bathymetry (m), average annual temperature (°C), average annual salinity (PSS), chlorophyll A concentration (mg.m⁻³), and diffuse attenuation (m⁻¹). The species do not occur at depths (bathymetry) greater than 60 m, because they are symbiotic, so diffuse attenuation has direct implications on the rate of photosynthesis. Low temperatures decrease calcification rates (Lewis, 1989; Lirman et al., 2002) and high temperatures may cause bleaching (Castillo et al., 2014). Salinity has been reported as a variable that influences coral biology, for example,

changing photosynthetic capacity (Lirman & Manzano, 2009; Manzano & Lirman, 2003; Monteiro et al., 2013). After choosing the variables, it was tested whether they would not be redundant, first by examining a correlation matrix built using the R package *PerformanceAnalytics* (Peterson & Carl, 2019), and retaining only one of the layers whenever pairwise correlation coefficients were smaller than -0.8 or greater than 0.8. All variables were retained to build niche models for *S. radians* (Appendix B); *S. siderea* (Appendix C), and *S. stellata* (Appendix D).

2.3 MODEL BUILDING AND EVALUATION

Niche modelling and projection were performed using presence-only data via Bioclim (Booth et al., 2014), Gower (Carpenter et al., 1993) and Mahalanobis distance (Farber & Kadmon, 2003) and also employing algorithms that rely presence and background points (absence): generalized linear model, or GLM (Guisan et al., 2002), support vector machine, or SVM (Drake et al., 2006) and maximum entropy, or MAXENT (Elith et al., 2011; Phillips and Dudík, 2008). MAXENT has a predictive advantage over all the other methods mentioned (e. g., Elith et al., 2006), but each algorithms has its particularities: Bioclim, Mahalanobis and Gower are models of low complexity and high transparency that perform well when it comes to inferring the potential distribution. However, they sacrifice statistical adjustment and precision by increasing the rate of false positives (commission errors). GLM allows for finer adjustment of environmental parameters, improving the predictive capacity of the model and reducing ecological noise, at the cost of increase complexity and reduced transparency. Its main weakness is the need for extensive scientific knowledge to extract and interpret ecological information (Rangel & Loyola, 2012). Among the chosen algorithms, MaxEnt and SVM have the lowest transparency and highest complexity. They are excellent for describing the species' distributions. However, when the input data is bad they tend to increase the rate of false negatives, although they are unlikely to show commission errors, except in cases such as overfitting (Radosavljevic & Anderson, 2014; Rangel & Loyola, 2012). Occurrence points and environmental layers were used to build the models, first for each species cutout and then for the entire area. As some models need background points, 10.000 random points of were generated for the three cutouts (Barbet-Massin et al., 2012). This procedure was done using the *randomPoints* function of the *dismo* package (Hijmans et al., 2017).

Niche models were validated using 25 pseudo-replicates in which 75% of the data were used for training and 25% for testing the model using the *evaluate* function of the *dismo* package (Hijmans et al., 2017). Subsampling was performed using *dplyr*'s *sample_frac* function

(Wickhan et al., 2020). Because our rarefaction analyses suggest that three species distributions are severely underestimated in published surveys (see section 3.1), we assessed the influence of sampling scarcity on models' predictions by re-validating them using half of the training (i.e. 37.5%) and half of the testing sets (12.5%) for each one of the pseudo-replicates. In order to simplify our downstream generalized linear mixed-model analyses (see below), we computed contrasts (i.e. $C = \text{Full-Halved}$) between the full (75/25) and halved (37.5/12.5) validation sets for each pseudo-replicate and used these contrasts as response variables in those models. If a model is insensitive to sampling, performance statistics should have similar values between the two validation sets in each pseudo-replicate, hence the corresponding contrasts be close to 0.

Three statistics were calculated for each pseudo-replicate in the validation experiment. The first one is the afore mentioned area under the receiver operator characteristic (ROC) curve (AUC), which is independent of classification thresholds (Fielding & Bell, 1997). AUC values range from 0 to 1, with 0.5 representing random predictions, values smaller than 0.5 indicate less predictive power than a random classifier and values ≥ 0.7 indicating appropriate power (Swets, 1988). The second one was true skill statistics (TSS), whose values vary from -1 to +1, where 0 would be equivalent to a random classifier and 0.4 or greater indicate good predictive power (Allouche et al., 2006). TSS is maximized by the sum of sensitivity and specificity (SSS) and it is therefore computed from confusion matrices. Because SSS varies with the classification threshold, it was first computed for each threshold value proposed by using the *threshold* function of the *dismo* package (Hijmans et al., 2017). The threshold that maximized SSS for each pseudo-replicate was stored, with its corresponding TSS score. The third metric was the symmetric extremal dependence index (SEDI, Ferro & Stephenson, 2011), computed using a custom R function. SEDI's computation and interpretation are analogous to TSS, but SEDI scores are not influenced by prevalence: TSS converges to sensitivity regardless of the underlying specificity when prevalence is low (Wunderlich et al., 2019), which is often the case in models that depend on background points such as GLM, SVM and MAXENT.

Niche model algorithms were compared by fitting generalized linear mixed-models (GLMM) to each performance statistic (AUC, TSS, SEDI). Algorithms and species were treated as fixed factors and pseudo-replicates as random factors, nested within species. AUC values are constrained between 0 and 1, hence this response variable was assumed to conform to a beta distribution, whose overdispersion parameter was allowed to vary across predictors (Douma & Weedon, 2019). TSS and SEDI could theoretically vary between -1 and 1, but they were never lower than 0.2 in our validation experiments (see Results). Hence, we also assumed that these statistics were beta distributed. Model fitting was performed via maximum likelihood using the

R package *glmmTMB* (Brooks et al., 2017) and we employed Bayesian information criterion (BIC) to assess the fit of increasingly complex models. In order to evaluate niche modelling performance with respect to sampling, we adopted the same approach described above but using the contrasts between full- and half-set validations as response variable, with the difference that contrasts were assumed to follow a normal distribution. We checked for residual homoscedasticity using *DHARMA* (Hartig, 2020). This R package estimates residuals from data simulated using the selected model and compares those estimates with the residuals obtained when the model is fitted to the real data. Significant deviations from the simulated residual distributions mean that the model is a poor fit to those data. This may be due to missing factors, under or overdispersion, zero- or one-inflated data, etc. The author claims that his approach is much more efficient than trying to infer eventual problems from conventional residual plots. Post-hoc comparisons were performed using least-squares means as implemented by Douma & Weedon (2019).

2.4 NICHE OVERLAP ANALYSIS

Pairwise niche overlap among the three species was estimated according to (Broennimann et al., 2012), with the same parameters adopted by those authors. Briefly, their approach uses the first two axis of a principal component analysis (PCA) applied environmental variables that define the realized niche of the pair of “entities” (species, in our case) being compared. These components define a virtual, two-dimensional environmental space with a fixed number of cells. Species occurrence in those cells are estimated, for instance, from probabilities returned by ENM, which are a function of the same environmental variables used to the define that space. Hence, this approach allows for the definition of a “common environmental ground” on which to measure niche overlap, even if the geographic distributions of both species are disjunct. By applying smoothing functions to PCA scores and occurrence probabilities, this approach expresses both variables as kernel densities bounded between 0 and 1. In the case of the environmental kernel, a value of e_{ij} (where i and j define the cell location in the grid) close to 0 means that the particular combination of environmental variables in a given cell is rare across the range of the two species being compared, whereas 1 means that it corresponds to the most frequent combination. Conversely, for the occurrence kernel (o_{ij}), 0 means that a species is unlikely to occur in a cell and 1 means that occurrence has maximum probability. The occupancy of each cell is calculated as the ratio z_{ij} between o_{ij} and e_{ij} , which is normalized by the maximum ratio found in the grid so that it is also bounded between 0 and 1. These ratios are then used to compute niche overlap using Schoener's D metric (0 means no

overlap and 1 means identical niches - Warren et al., 2008). Statistical significance is estimated by comparing the observed value with the empirically constructed null hypothesis that niche overlap remains constant when species are randomly relocated between their geographic ranges. All occurrences are grouped and divided randomly into two data sets, maintaining the number of occurrences as the original data set, and Schoenner's D is computed. This process is repeated 1000 times and the null hypothesis is rejected if the observed D is smaller than 95% of the null distribution (Broennimann et al., 2012). All of these steps were performed using the ecospat R package (Di Cola et al., 2017).

In order to verify which environmental variables (i.e., values obtained in cells of occurrence points) determine the environmental niche of each species, a linear model was adjusted for each variable, treating species as the factor. Then, the normal distribution and homoscedasticity of residuals of these models were tested, being submitted to an ANOVA one-way test.

3 RESULTS

3.1 SAMPLING SUFFICIENCY

Rarefaction curves showed that the number of cells increases monotonically with the number of publications, without an obvious sign of saturation for any of the three species (*S. stellata* FIGURE 2a; *S. siderea* FIGURE 2b; *S. radians* FIGURE 2c) This indicates that the total sampling effort was not enough to exhaust the occurrence of the species due to insufficient field and not to insufficient bibliographic sampling, since all pages returned by Google Scholar were consulted.

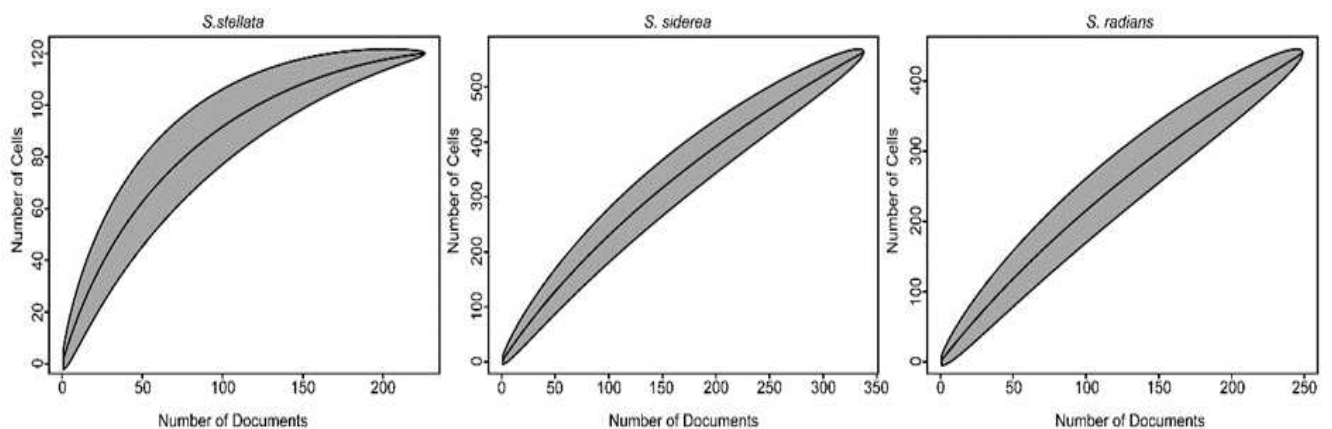


Figure 2: Accumulation curve of cells to *Siderastrea* (*S. stellata*, *S. siderea*, and *S. radians*). The y axis shows the number of cells as the variable response in function publications number.

We sampled every entry returned by Google Scholar when using the keywords (“*Siderastrea*”, “*Siderastrea radians*”, “*Siderastrea siderea*”, “*Siderastrea stellata*” and “coral reefs”), but we did not monitor the time spent in such sampling. To check for sufficiency of bibliographic sampling, we conducted 6 hours of uninterrupted sampling that added 16 new publications for *S. radians*, 47 for *S. siderea*, and 15 for *S. stellata*. Doubling our monitored sampling effort from 3 to 6 hours yielded less than half (24.0% and 12.5%) of the numbers of cells that were sampled in the first 3 hours for *S. siderea* and *S. stellata* (12 vs. 50 and 1 vs. 8, respectively - Table 1). In the case of *S. radians*, doubling the effort more than doubled the number of occurrences (4 new cells vs 3 in the first three hours - Table 1). However these publications increased our initial sampling by just 1,59% (7 new cells vs. 440 in the initial survey - Table 1). Hence, even though our rarefaction analysis indicates that published sampling is too scarce to adequately describe the three species distributions, we considered our literature survey sufficient in the face of available information.

Table 1: Comparison of the number of cells obtained in the initial survey for each subsample. The sum of new cells obtained is much smaller than the initial research, showing that many publications always sample the same locations.

Species	Initial survey	Hours					
		1 st	2 nd	3 rd	4 th	5 th	6 th
<i>S. radians</i>	440	0	3	0	3	1	0
<i>S. siderea</i>	564	34	14	2	11	1	0
<i>S. stellata</i>	120	0	1	7	1	0	0

3.2 FULL DATASET

For all performance statistics, the preferred GLMM included interaction between fixed factors (i.e. methods x species) and variation of the overdispersion parameter across those factors. The only exception was the GLMM fitted using SEDI, which also included overdispersion variation with the interaction term (Appendix E). According to DHARMA, empirical residuals were homoscedastic and in strong agreement with the expectations under the simulations (Appendix F). The only exception as the model fitted to SEDI, whose observed residuals did not correspond to the simulated ones, although homoscedasticity was verified (Appendix Fc).

All performance statistics showed predictive power above critical value (i. e. 0.70 for AUC – Figure 3a; 0.40 for TSS – Figure 3b and SEDI – Figure 3c). The only exception was *S. stellata* SVM for AUC (Figure 3c). Although the median TSS was above the critical value, some pseudo-replicates were way below (Figure 3b). However, for SEDI, neither result was found (Figure 3c). There was strong interaction among fixed factors (models x species) of the GLMM across all performance statistics (AUC, TSS and SEDI). Bioclim and SVM were,

overall, the models with the worst predictive performance, while GLM, Mahalanobis and MaxEnt were the best ones. This was also evidenced by the *post-hoc* least-square means tests (Fig. 3).

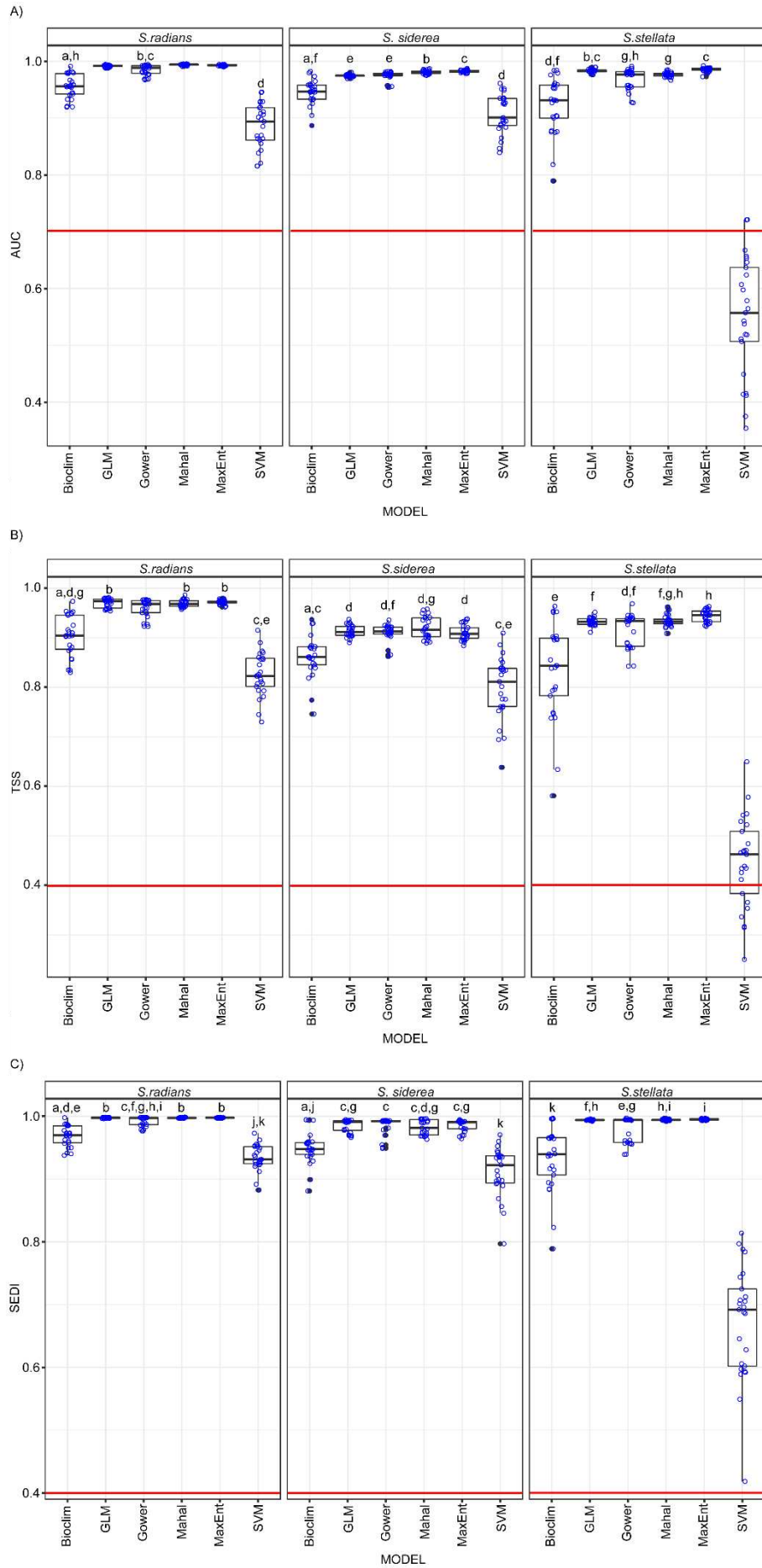


Figure 3: Boxplots for all occurrences using different assessment metrics (i.e. AUC, TSS, and SEDI). The red line indicates the critical prediction value for each metric (0.70 for AUC, 0.40 for TSS and SEDI). Blue circles around the boxplots are the pseudo-replicates. The letters identify the pairs of models that are not statistically different from each other (i.e. $p > 0.05$) according to the *post-hoc* tests of least squares means.

3.3 CONTRASTS

The second part of the analysis focused on analyzing the contrasts between the original and the halved data sets. Contrasts were computed by subtraction (i.e. $C = \text{original} - \text{halved}$). If the contrasts are grouped around 0, this means that performance statistics obtained for halved data sets were not different from the original sets, hence the algorithm is insensitive to sample size. If the distribution mean/median is positive, this suggests that method performance decreases with sample size

For all performance statistics, the preferred GLMM again included an interaction term between fixed factors (i. e. methods x species) and variation of the over dispersion parameter across levels of these factors. The only exception was the GLMM adjusted using SEDI as the response variable, which also included a term allowing for over dispersion variation with the interaction term (Appendix E). According to DHARMA, the experimental residuals were again homoscedastic and in accordance with the simulated expectations (Appendix 7), except for the model employing SEDI, whose observed and simulated residuals were not in full agreement and were not homoscedastic (Appendix Ff).

As in the case of the full data sets, fixed factors again demonstrated strong interaction across performance statistics (AUC, TSS and SEDI), as evidenced from the least-square means analysis (Figure 4). At least half of the methods had contrasts clustered around zero (AUC - Figure 4a, TSS - Figure 4b and SEDI - Figure 4c), meaning that the results obtained with these algorithms are robust to sampling. AUC contrasts were grouped around zero for GLM, Mahalanobis and MaxEnt (Figure 4a). TSS contrasts were concentrated around zero for GLM, Gower, Mahalanobis and MaxEnt (Figure 4b). SEDI's results were similar to TSS's (Figure 4c). In some cases (e.g. Mahalanobis AUC for *S. stellata*; GLM, Gower, Mahalanobis and MaxEnt TSS for *S. siderea*) the median contrast was negative, indicating that halved data sets had better predictive performance than the complete sets (Figure 4). Models susceptible to sampling were Bioclim for all species and SVM in the case of *S. radians* and *S. siderea*. These methods also generated distributions with comparatively large variances, indicating that their results are very dependent on pseudo-replicates and, conceivably, on the particular data set employed in a full analysis (Figure 4).

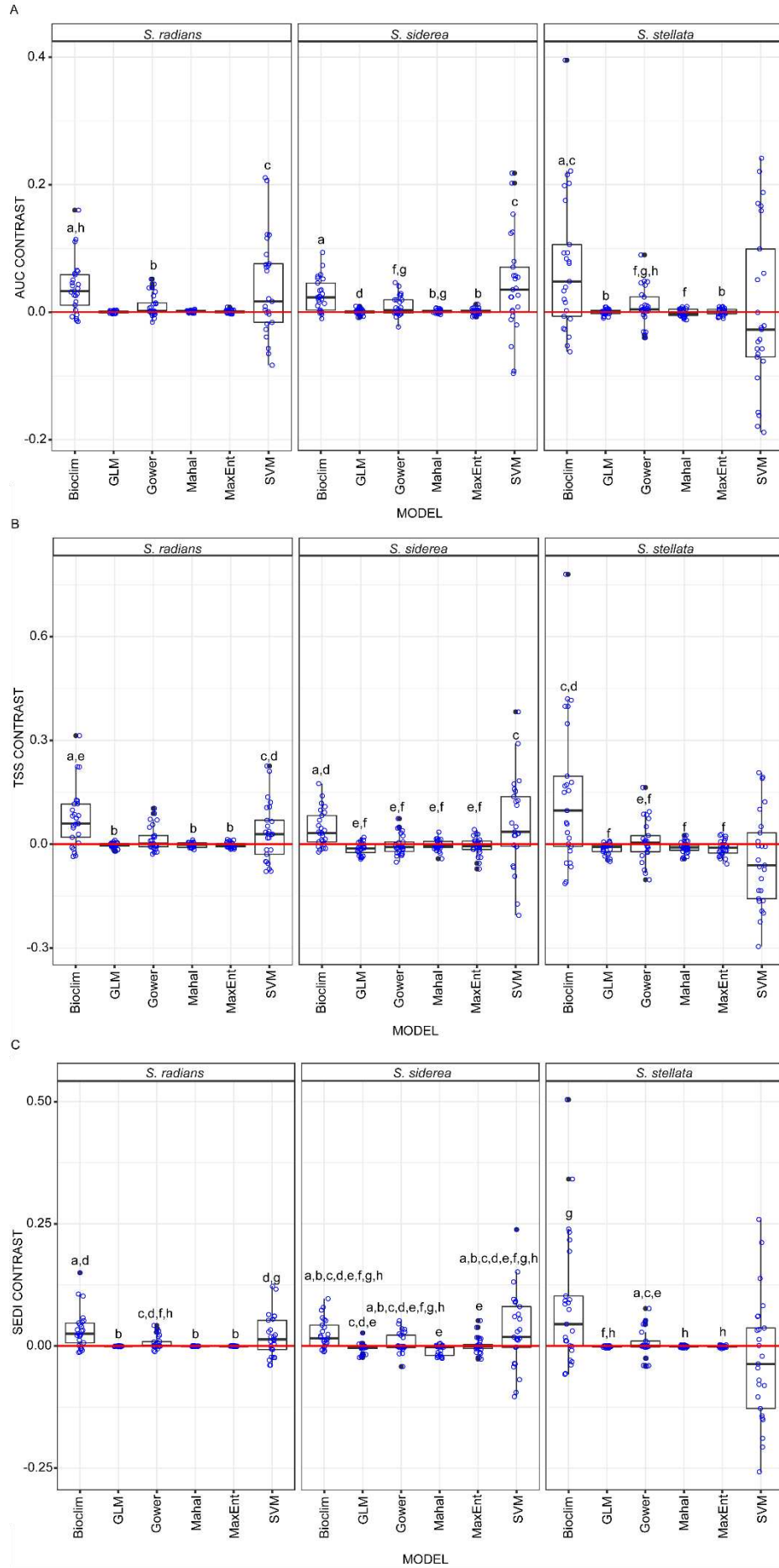


Figure 4: Boxplots for contrasts using different evaluation metrics (i.e. AUC, TSS and SEDI). The red line indicates no contrast for all metrics. Blue circles around the Boxplots are the pseudo-replicates. The letters identify the pairs of models that do not differ (i. e. $p > 0.05$) according to the *post-hoc* test employing least square means.

3.4 POTENTIAL DISTRIBUTION OF SPECIES

Methods chosen for the projections were GLM, Mahalanobis and MaxEnt. The choice of these methods was based on (i) predictive power; (ii) sensitivity to data set choice (expected to be inversely proportional to variance among pseudo-replicates); (iii) robustness to sampling (iv) consistency across performance statistics (Appendix G). GLM, Mahalanobis and MaxEnt estimates were generated by mapping the potential distribution of the three species on a continuous scale of suitability. The continuous maps were binarized by converting the probabilities of the confusion matrix (or true positive and negative rates), into evenly spaced values (cut-off points, found in Appendix H) and combined via committee averaging for the suitability of each cell (Araujo & New, 2007).

In many regions with high suitability ($> 70\%$) for *S. radians* (Figure 5a) its presence has already been reported, e.g. the Florida Keys (Lazar et al., 2011), Bahamas (Chiappone & Sullivan, 1991), Cuba (Gonzalez-Diaz et al., 2003), Belize (Baumann et al., 2018) and the Gulf of Mexico (García et al., 2017). High suitability of *S. radians* were also projected for the Northern and Northeast Brazilian coasts (i.e. Portions of Manuel Luís, Piauí, Ceará, Rio Grande do Norte, Paraíba). However, suitability ranged from high to moderate ($< 62\%$) along Pernambuco and Alagoas. Adequacy was also moderate for regions where *S. radians* are known to occur: Abrolhos (Menezes et al., 2013), Cabo Verde Islands (Moses et al., 2003) and São Tomé Archipelago (Nunes et al., 2011) and in some areas where its was not recorded (i.e. Guinea, Guinea Bissau, Sierra Leone and Liberia).

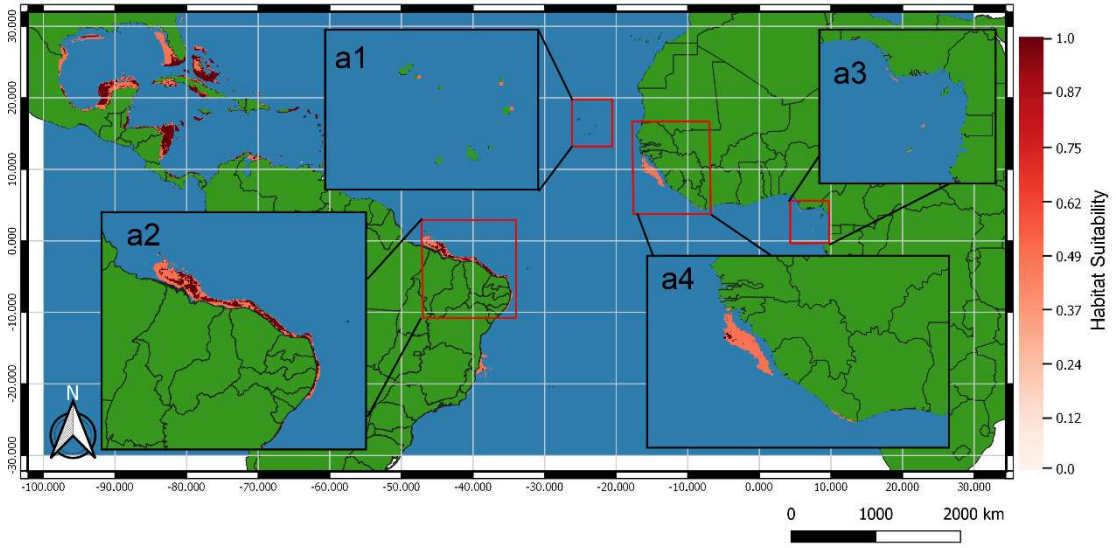
Similar results were found for *S. siderea* (Fig. 5b), i.e., Florida Keys (Kuffner et al., 2013), Bahamas (Voss & Richardson, 2006), Cuba (Gonzalez-Diaz et al., 2003), Belize (Castillo et al., 2011) and Gulf of Mexico (DeLong et al., 2014; García et al., 2017). High suitability (*S. siderea*) was again projected along the Northern and Northeast coasts of Brazil (i.e. Parcel Manuel Luís and parts of Piauí and Ceará) where this species was never found. This scenario is however quite plausible, since this region of Brazil has environmental conditions similar to those found in the Caribbean Sea. The northern coast of Bahia (the place where the colony re-identified by Neves and cols. was collected in the 19th century) was projected as unsuitable for this species (Figure 5b).

Projected suitability for *S. stellata* was high in places where its occurrence is common (Figure 5c): Ceará (Soares & Rabelo, 2014), Rio Grande do Norte (Castro & Pires, 2001),

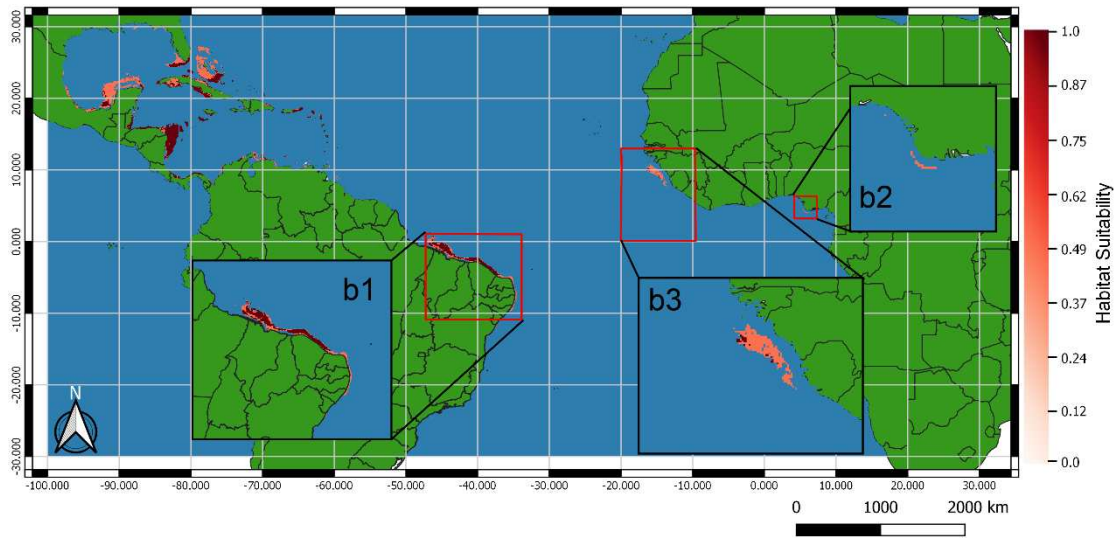
Paraíba (Costa et al., 2008), Pernambuco (Santos et al., 2004), Alagoas (Steiner et al., 2015) and Abrolhos (de Barros et al., 2003). Low suitability (<30%) was projected for Armação dos Búzios, which is peripheral to its geographic distribution (Lima and Coutinho, 2016; Oigman-Pszczol & Creed, 2004). The Gulf of Mexico demonstrated high suitability to the species, although it was highest along the Yucatán peninsula and not Veracruz, where it was recently recorded (Garcia et al., 2017). Low suitability was also projected for the Bahamas and Florida.

In Africa, regions with moderate suitability to *S. radians* (i. e. Guinea, Guinea Bissau, Sierra Leone and Liberia) were also moderately suitable to *S. siderea* and adequacy of the São Tomé Archipelago, close to Nigeria, was low for both species. Unlike for *S. radians*, Cabo Verde was unsuitable for *S. siderea*. Suitability was also low for a small region of Mauritania in the case of *S. stellata* (Figure 5c).

A



B



C

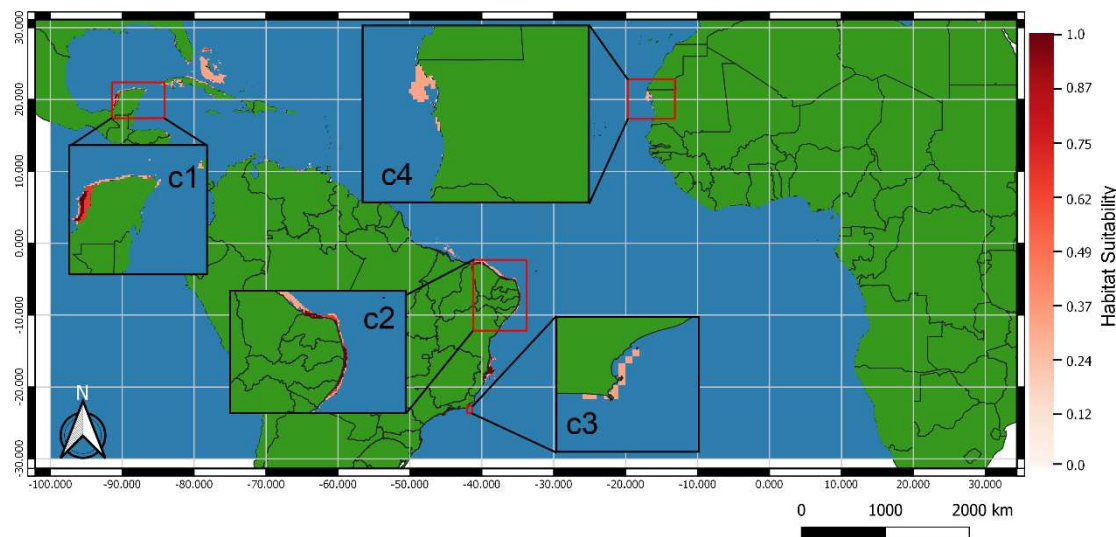


Figure 5: Potential distribution of *S. radians* (A), *S. siderea* (B) and *S. stellata* (C). The potential distribution of all species corresponds to the ensemble of different modeling algorithms (GLM, Mahal and MaxEnt). *S. radians* inserts are a1: Cape Verde Islands; a2: Northeast Brazilian Coast; a3: São Tomé and Príncipe Islands; a4: Region comprising Guinea, Guinea Bissau, Sierra Leone and Liberia. *S. siderea* inserts are b1: Northeast Brazilian Coast; b2: Nigeria, b3: Region comprising Guinea and Sierra Leone. *S. stellata* inserts are c1: Yucatan Peninsula - Gulf of Mexico; c2: Northeast Brazilian Coast; c3: Armação de Búzios; c4: Mauritania. Suitability above 70% (red) is considered high, moderate in the 37% (dark pink) to 62% (orange) range and low if < 37% (light pink).

3.5 NICHE OVERLAP

The observed niche overlap value (Schoenner's D) between *S. stellata* and *S. siderea* was 0,40 or 40% and *S. radians* vs. *S. stellata* ($D = 0,67$ or 67%). The empirically constructed null hypothesis of niche overlap was rejected when *S. stellata* was compared to the *S. siderea* (Figure 6a, $p < 0,001$) and *S. radians* (Figure 6b, $p = 0,003$) but not in the case of *S. siderea* and *S. radians* (Figure 6c, $p > 0,05$).

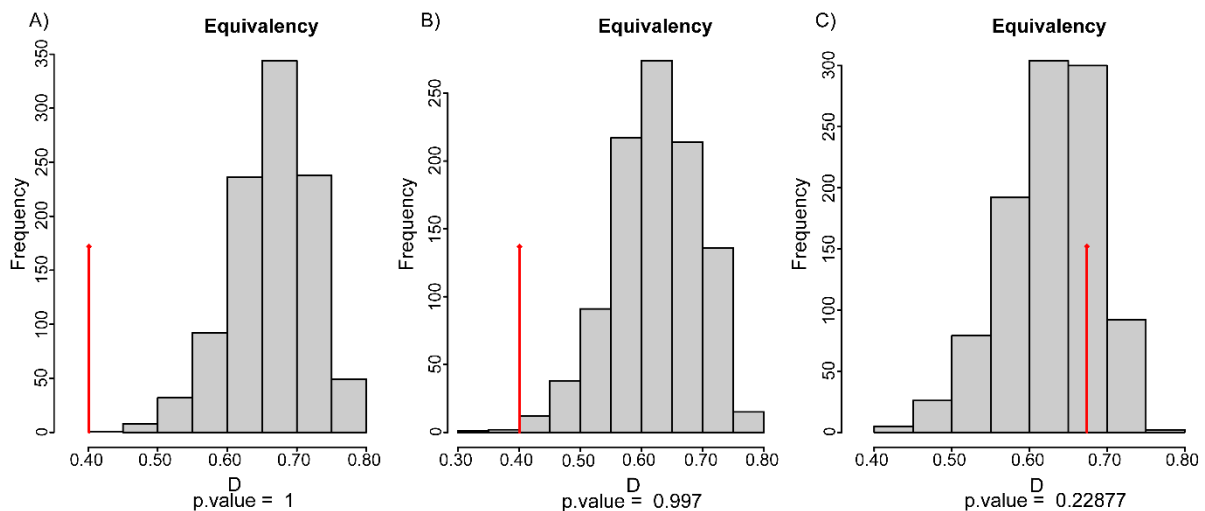


Figure 6: Histograms of simulated data between species (A= *S. stellata* – *S. siderea*; B= *S. stellata* – *S. radians*; C= *S. siderea* – *S. radians*). The red line shows the observed value of the D statistic. P-values reported in the figure correspond to the probability of rejecting the null hypothesis of niche overlap between each pair of species and not to the probability of type I error, as in standard statistical tests.

Due to multiple comparisons, we applied the Bonferroni correction to the significance level (i.e. $\alpha = 0,05 / 5 = 0,01$) when comparing environmental variables grouped by species. Four out of five environmental variables showed significant differences (Figure 7) between species (Bathymetry; $F = 9.20$; $p < 0.01$; Salinity: $F = 50.77$ $p < 0,01$; Temperature: $F = 12.13$; $p < 0.01$; Chlorophyll., $F = 12,04$, $p < 0,01$; $df. = 2$ in all cases). However, no significant differences were observed for diffuse attenuation ($F = 0,28$, $p = 0.75$).

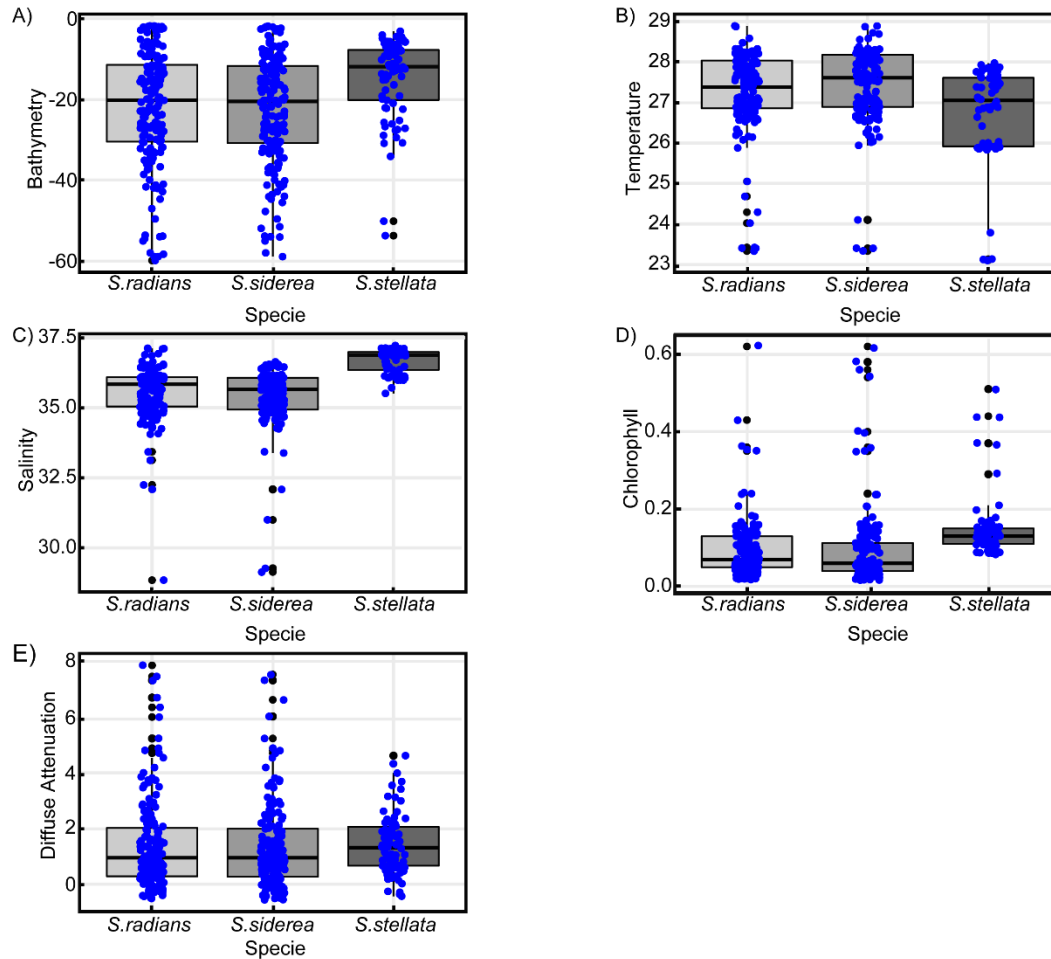


Figure 7: Boxplots indicate significant differences between species for the variables of (a) bathymetry, (b) temperature, (c) salinity, and (d) chlorophyll. Indicating that *S. stellata* has distinct environmental preferences from *S. siderea* and *S. radians*.

4 DISCUSSION

To our knowledge, this is the first study that use ENM to estimate the occurrence of non-invasive coral species outside of their known ranges. Our rarefaction analysis shows that sampling of species in the Atlantic *Siderastrea* complex is rather incomplete and hence their canonical ranges may have been established due to a combination of insufficient sampling and confusing taxonomy. Our niche projections were based on an ensemble of models chosen after rigorous assessment of their relative performances and projected ranges were rather restricted. Still, these projections indicated high suitability of the Yucatán Peninsula as *S. stellata* habitat. This result corroborates the recent record of *S. stellata* in the Gulf of Mexico. However, this species has been reported in the Veracruz system (Garcia et al., 2017), which lies ~600 km from the projected sites. Likewise, our projections suggest that *S. siderea* may indeed occur along the Northeastern Brazilian coast, but not in Bahia, as previously reported (Neves et al., 2010). Additionally, our projections suggest that both *S. siderea* and *S. stellata* may occur along the African coast, where only *S. radians* was recorded.

4.1 DATA QUALITY AND MODEL SELECTION

There was no cells saturation for any species (*S. radians* - Figure 2a; *S. siderea* - Figure 2b; *S. stellata* - Figure 2c). Since all results returned by combining keywords ("*Siderastrea*", "*Siderastrea radians*", "*Siderastrea siderea*", "*Siderastrea stellata*" and "coral reefs") were consulted (Google Scholar) and few new cells were obtained after supervised sampling (Table 1), it is concluded that obtaining new cells will depend on a greater sampling effort in the field. A single publication used this type of data in rarefaction analysis (Zattara & Aizen, 2021), but this work analyzed whether the decline of bees was being reflected in the number of occurrences published in GBIF (Zattara & Aizen, 2021). Thus, this is the first work to use this approach to check if a certain number of occurrences are sufficient for niche modelling in corals. Although an adequate response to the purposes previously stipulated was not obtained, this analysis contributes towards stating that new places should be sampled in the future, although it is known that this is conditioned to a greater incentive for research. The answer to the previous question (i.e. is the number of occurrences sufficient to model the potential distribution of the species?) was obtained by comparing two situations. First, the predictive performance of all performance statistics was evaluated using the complete set of occurrences. Subsequently, this process was repeated with half the occurrences and contrasting the results of the different moments. Regardless of the set of occurrences, GLMM indicated a strong interaction between species and method. Thus, the use of the metric was little dependent on the set, indicating that the number of occurrences was sufficient. This conclusion is supported when the predictive performance of *S. stellata* is similar to that of *S. siderea* with *S. siderea* having more than twice the occurrences about *S. stellata* (75 for *S. stellata* and 172 for *S. siderea*). Likewise, works involving corals exhibit a large gap in terms of occurrence records and have similar predictive performance, regardless of the data source used (Table 2). For example, a study that used 11 records (Carlos-Junior et al., 2015a) showed similar predictive performance ($AUC > 0.90$) to that which used 149 (Riul et al., 2013). The comparisons can be extended to the TSS, although most publications have used only AUC as a way of evaluating the model (Table 2). When using 8789 records (Descombes et al., 2015) it showed a lower TSS (0.81) in relation to Boavida et al. (2016) who used 103 records (TSS = 0.90). Comparisons between the cited publications (Carlos-Junior et al., 2015a; Boavida et al., 2016; Descombes et al., 2015; Riul et al., 2013) with other relevant ones (Carlos-Junior et al., 2015b; Davies & Guinotte, 2011; Jones et al., 2019; Martin et al., 2014; Rengstorf et al., 2013) are found below (Table 2).

Besides that, Pearson et al., (2007) showed that five occurrence sites are acceptable to model the distribution of a species. This result was also found for octocorals (Quattrini et al., 2013). The SEDI metric of the present work showed a value greater than 0.90 for MaxEnt in all species; this was found by a recent work (Sandoval - Castillo & Beheregaray, 2020) that used 210 occurrence points for the genus *Pseudobatos*. The reason why only one study used SEDI is that it was only recently suggested for ecological niche modeling (Wunderlich et al., 2019). Before, its main objective was to predict meteorological phenomena (Ferro & Stephenson, 2011). All the results presented above and the comparison with other studies indicates that the number of occurrences was adequate for the purpose of the study. It is unlikely that the high values displayed by the evaluation statistics are the product of over fitting because MaxEnt's main characteristics are to exhibit high statistical adjustment and to be extremely accurate (Rangel & Loyola, 2012). If that were the case, the distribution area provided by this method would be larger than that observed (Radosavljevic & Anderson, 2014).

Table 2: Information about records, source of data, methods used, and use of evaluation metrics in different publications.

Publication	Number of records	Source	Method	AUC	TSS
Boavida et al., 2016	103	Papers, grey literature, field works	Boosted Regression Tree	-	0.90
Carlos-Junior et al 2015a	11	Papers, grey literature,, GBIF, WORMS e SpeciesLink	MaxEnt	0.96	-
Carlos-Junior et al 2015b	132	Papers, grey literature, GBIF, WORMS e SpeciesLink	MaxEnt	0.92	-
Davies & Guinotte, 2011	2.270	Papers, grey literature, museum records, cruise records	MaxEnt	0.97	-
Descombes et al., 2015	8.789	ReefBase	GLM	-	0.81
Guinan et al., 2009	247	Caracol expedition and ROV videos	GARP	1.00	-
Jones et al., 2019	295	Ocean Biogeographic Information System (OBIS)	Bioclim, Random Forest, Maxent	0.80, 0.96,0.98	0.68, 0.86, 0.89
Martin et al., 2014	11.174	Papers and grey literature	MaxEnt	0.80	-
Rengstorf et al 2013	243	Papers, grey literature, field works	MaxEnt	0.97	-
Riul et al., 2013	149	Papers, grey literature, OBIS, GBIF,	ANN, CTA,GAM,GBM, GLM, MARS,MAXENT , RF, SRE	0.99*	0.95*

* AUC e TSS by ensemble methods

Although the number of occurrences was sufficient in both sets, the GLMM demonstrated a strong interaction between the fixed factors (i.e. methods x species). This, basically, indicated that the methods were divided into two groups (Figure 3); (i) good predictive performance, composed of GLM, Mahal and MaxEnt and (ii) regular predictive performance, composed of Bioclim, Gower and SVM. They are considered regular because, although they showed satisfactory predictive performance, they also varied a lot in the pseudo-replicates regardless of the evaluation metric (Figure 3). Thus, depending on the sub-sample the use of the metric was lower; in addition, these methods were dependent on the complete set of data (i.e. demonstrated positive contrasts). As far as it is known, this is the first work that uses 37.5% to calibrate the model and 12.5% to validate and contrast these results with the 75/25 set. Consequently, no work has evaluated the sensitivity and specificity of the models with half of the sampling.

The choice of the method must be based on the ecological hypothesis that will be tested and on the predictive performance (Hortal et al., 2012; Rangel & Loyola, 2012; Soberon & Nakamura, 2009). However, it seems that works involving corals simply neglect the ecological assumption of the method, giving more importance to the aspect of predictive performance (Carlos-Junior et al., 2015a). When using MaxEnt to predict the potential invasion of *Tubastraea tagusensis* in Brazil, this method did not demonstrate suitability for Brazil with data from the native area of the species (Carlos-Junior et al., 2015a). As expected MaxEnt, if calibrated correctly, will not expand this area beyond the range of the species, as it tends to reduce commission errors (Radosavljevic & Anderson, 2014) unless the input data is completely skewed (Rangel & Loyola, 2012). However, the absence of the species in places where it occurs in Brazil was attributed to an expansion of the species' niche (Carlos-Junior et al., 2015a). This kind of dantesque interpretation could be avoided by choosing a method that would respond to the species' environmental preferences, and not to an exaggerated attachment to the results presented by the evaluation metric (Rangel & Loyola, 2012). Such that, when an invasive species of known presence (*Tubastraea coccinea*) is designed for places where it occurs (Brazil and the Caribbean), MaxEnt correctly indicates areas of high suitability (Carlos-Junior et al., 2015b). Sometimes, the projection indicates areas where the species does not occur, even using methods that have high precision, such as the *Boosted Regression Tree* (Boavida et al., 2016; Couce et al., 2013). However, the projection remains very dependent on the occurrence data used, indicating that knowledge about the species' biology is paramount in obtaining solid results (Boavida et al., 2016). Likewise, the use of a mixture of methods proved to be extremely useful to predict potential areas of invasion of *Tubastraea coccinea* to places

where their presence was unknown in Brazil (e.g. Abrolhos, north and south coast) helping in future environmental issues (Riul et al., 2013).

This does not mean that one must always use a mixture of methods or only those that respond to abiotic factors, but one must take into account the assumptions of the method, scale used, and objectives that one aims to achieve. For example, the use of MaxEnt on a small scale was very good for predicting the distribution of three species of octocorals (*C. gracilis*, *Callogorgia Americana americana* and *C. a. delta*) in the Gulf of Mexico (Quattrini et al., 2013) and deep-sea corals (*Lophelia pertusa*) in Ireland (Rengstorf et al., 2013). Likewise, the use of a single method that only responds to environmental preferences (ENFA) generated a broader niche (high rate of false positives or commission error) for *Lophelia pertusa* than it really was when it was extrapolated to global scales (Davies et al., 2008).

Here, MaxEnt and GLM were used to avoid commission errors. The projection of different species to places where they do not occur in the present study was an indication of responses to abiotic factors. These factors were only captured because methods that respond to environmental variations were used (GLM and Mahal). This mixture of methods (GLM, Mahalanobis, and MaxEnt) allowed solid inferences. Thus, it is unlikely that the results presented are the product of statistical bias (points of occurrence, choice of variables, and methods). So, our findings suggested that the distribution of the *Siderastrea* spp.) is the product of environmental factors (Section 4.2 - Niche Overlap) possibly due to historical processes (Section 4.3 - Biogeography of *Siderastrea* spp.).

4.2 NICHE OVERLAP

Although the three species have demonstrated suitability for some regions of the West Coast of Africa, it is believed that the potential distribution of *S. radians* should be even greater in Africa, because the occurrence data showed a large bias. For example, in the Caribbean ~940 records were sampled, while in Africa only 121. However, in addition to being restricted to specific archipelagos such as Cabo Verde and São Tomé (e.g. Nunes et al., 2011), their numbers were probably reduced due to the filters used (Figure 1). This same bias has already been reported in the north of the African continent (Martin et al., 2014). The results showed that *S. stellata* has environmental preferences that differ from the others, resulting in a distinct niche (Figure 6). In fact, environmental preferences have long been recognized as an important component in the evolution of Scleractinia (Barbeitos et al., 2010; Kitahara et al, 2010). Here the results showed significant differences between species for (i) chlorophyll concentration, (ii) temperature, (iii) bathymetry, and (iv) salinity (Figure 7).

In Brazil, reefs that are located in shallow bathymetry (5-20m) nutrient uptake are influenced by ocean currents (Johns et al., 1998). For example, the northern coast of Brazil (e.g. Ceará) where *S.stellata* is registered (Soares & Rabelo, 2014) is under the influence of the Northern Brazil Current (Johns et al., 1998). Such a current causes constant suspension of sediments that make the water darker and less prone to the propagation of light, hindering the photosynthetic activity of the symbionts (Bongaerts et al., 2015; Johns et al., 1998). The diffuse attenuation for the Caribbean species did not differ in relation to *S. stellata* (Figure 7e). This raises the question of how this is possible, with Caribbean waters not so prone to sedimentation. The explanation for this question may be in comparing the bathymetry of the Brazilian endemic with Caribbean species. These are found in waters that differ significantly in terms of *S.stellata* depth (Figure 7a) and depth has an important influence on light propagation (Huston, 1985), perhaps for this reason *S. siderea* and *S. radians* have demonstrated high suitability for this region of Brazil (Figure 5), although *S. radians* has already been found in conditions of high sedimentation in Biscayne Bay in Florida (Lirman et al., 2002).

As seen in (Figure 7d) the chlorophyll concentration was significantly high in *S. stellata* compared to the Caribbean, possibly this result was influenced by the large algae coverage (macroalgae and filamentous algae) on the Brazilian coast (Aued et al., 2018). The averages annual temperature in *S. stellata* was also significantly lower (Figure 7b). It has been reported for *S. radians* (occurring in Brazil) that low temperatures decrease the rate of photosynthesis, interfering with the rate of calcification and its consequent growth (Lewis, 1989; Neves et al., 2008). However, this result is explained by the presence of *S.stellata* in Búzios (de Barros et al., 2003). In the Southeastern Brazil town of Armação dos Búzios (22 ° 44'0.87 "S - 41 ° 52'0.23" W), where they are exposed to constant resurgence, colonies thrive well (or even better) than colonies found in Abrolhos Archipelago (18 ° 1'27.82 "S - 39 ° 0 '26.91" W) or Northeastern Brazil (16 ° 7'10.39 "S / 2 ° 37'29.67" S- 38 ° 38'25.83 "W / 42 ° 24'20.04 "W) where oceanographic conditions are much more favorable to coral growth (Lima & Coutinho, 2016). This would explain why its suitability for this region has been moderate (Figure 5c), as it is a completely different niche compared to most of the Brazilian coast where its occurrence is documented. This suggests local adaptation to ecological conditions, which is a peripheral region in the distribution of the genus (Kirkpatrick & Barton, 1997; Tunala et al., 2019).

Salinity was also significantly higher for *S.stellata* (Figure 7c) and the question of this finding is how *S.stellata* has greater salinity in relation to the Caribbean since Brazil is full of rivers (e.g. Rio Amazonas, Rio São Francisco, and Rio Doce) that flow into the ocean (da Silva et al., 2010; Filizola & Goyot, 2011; Oliveira & Quaresma, 2017). The answer is that these

regions exhibit little or no suitability for *S.stellata* (Figure 5c), that is, *S. stellata* really prefers places with higher salinity.

A question that arose from a more in-depth analysis of these variables was: “How does diffuse attenuation (Figure 7e) in *S. stellata* not differ from *S. radians* and *S.siderea*, as these are not conditioned to turbid waters like *S.stellata*?”. This result is no longer conflicting when it is observed that the concentration of chlorophyll A (Figure 7d), in *S.stellata* was much higher than in *S.siderea* or *S.radians*. This means that phytoplankton is more abundant in the Brazilian sites where *S. stellata* occurs than concerning its Caribbean counterparts. A second question that may arise from this is: "But how can there be a more pronounced eutrophication process in *S. stellata*, since its temperatures are lower?". The answer derives from the orientation of the layer, as it takes into account the surface temperature (Figure 7b), and not the temperature related to bathymetry gradients (i. e. greater depths). Another explanation for the first question is that the places where *S.siderea* and *S.radians* were found are much deeper (Bathymetry) than in relation to the places where *S.stellata* was, so the light attenuation will be greater for these species as well (Figure 7a). Another question that emerges is “But if the temperature is conditioned to the orientation of the layer, how can it be lower for *S.stellata* since the species occurs at latitudes that are close to the equator?”. The answer is that, although *S. stellata* occurs at latitudes close to the equator, it also occurs in Armação de Búzios (22 ° 44'0.87 "S - 41 ° 52'0.23" W), this being a peripheral region of the geographical distribution that is constantly exposed to resurgence events (average annual temperature is around 18 - 19° C - Lima and Coutinho, 2016) and thrives as well or better where the temperature is higher (for example: Abrolhos - 18 ° 1 ' 27.82 "S - 39 ° 0'26.91" W). In this sense, the results indicate that different environmental parameters (Figure 7) shaped the ecological speciation of the genus.

This section presents good arguments in favor of speciation mediated by environmental factors. How these factors are related to geological, hydrological and climatic phenomena are discussed in the following section.

4.3 BIOGEOGRAPHY OF ATLANTIC *Siderastrea* spp.

Menezes (2018) when using all molecular markers (ITS, CAG, and SRP54), utilizing a relaxed normal log molecular clock, showed that the divergence of *Siderastrea* spp. occurred ~127Myr (95% HPD = 27,1 – 311,8Myr). Although the ocean is usually a homogeneous environment (i.e., geographical barriers are scarce), making allopatric speciation (reproductive and geographical isolation) less frequent than that observed on the continent (Palumbi, 1994), they're still two barriers that could have influenced this species separation.

The meso-Atlantic barrier (bathymetry) separates Africa from America, its origin is dated ~85Myr, with a minimum distance (in a straight line) of 2,800km, acting as a substantial barrier in larvae of marine organisms' dispersion (Luiz et al., 2011). For example, it has been documented that *Diadema antillarum* has a restricted gene flow since their larvae cannot disperse through this obstacle (because of long distances), even the larvae on the American coast cannot establish themselves on the African coast as the larvae on African coast cannot establish themselves in America. (Lessios et al., 2001). Additionally, the sea current may be involved in the dispersion of *Siderastrea* spp, it requires a long time to complete its cycle - e. g., north equatorial countercurrent exhibits a 3-month seasonal cycle - (Fonseca et al., 2004; Urbano et al., 2008). Another recent example, involving *Felimare picta* (that has many subspecies with Amphi-Atlantic distribution) which is inactive making its dispersion capacity reduced in all stages of development, but, even though, occur on both coasts (Almada et al., 2016).

Menezes (2018) by choosing only the ITS molecular marker, recovered two distinct groups: *S. siderea* and *S. radians*; thus, discarding endemic *S. stellata*. The divergence (using all markers) between these groups occurred ~29,02Myr (95% HPD = 15,6 -59,8Myr). However, our findings differ from this result. It was clear that *S. stellata* has very different salinity preferences from *S. radians* and *S. siderea*, and possibly the divergence that was classified as *S. siderea* - *S. radians* actually is *S. stellata* – *S. radians* (considering our results and the date of divergence from Menezes' study). It has long been known that there is a great distance (2,300 km) between the reefs of the Caribbean and Brazil, being a substantial barrier to dispersion, as it is composed of turbid and low salinity waters (Nunes et al., 2011). This barrier is formed by low salinity waters from Amazon, Orinoco, and other rivers in South America. The Amazon and Orinoco rivers reached their current drainage configuration around the Upper Miocene (Hoorn et al., 1995), indicating that the low salinity and the high sedimentation had their genesis 10Myr and, as previously described, the divergence between *S. siderea* or *S. radians* with *S. stellata* occurred before the complete formation of this barrier. As seen in Figure 7c, species have a narrow niche related to salinity, so it is less likely that allopatric speciation is recent. This could explain the partial overlap of the potential niche of *S. stellata* with *S. siderea* and *S. radians*.

Although reproductive isolation is outside the scope of the present study, several pieces of evidence reinforce the standards described above. These events could have generated interactions between the species and abiotic factors, such as salinity, playing a role in speciation and fixing pre-zygotic isolation (e.g., Knoltown, 1993; Knowlton et al., 1997; Levitan et al.,

2004; Prada et al., 2008; Prada et al., 2014; Tomaiuolo et al., 2007). Doebeli (2005) showed that the evolution of the assortative mating mechanisms (a tendency of individuals with similar phenotypes to mate more than expected at random) could, in theory, bring adaptative speciation, even if based on ecologically neutral female preferences and male traits. Thus, not only do mating sites recombine freely, as there is recombination between mating preferences and their environmental preferences. The fertility and volume of the female gamete of *S. siderea* decreased significantly with the increase of latitude on a small spatial scale (~200km to 25° from 27°). The fertility of *S. siderea* is probably affected by a higher temperature variation in seawater (Gelais et al., 2016). *S. stellata* shows latitudinal and temporal differences between the populations of Búzios and Abrolhos. This variation was attributed to the photoperiod in these areas. In Abrolhos, larval release occurs close to the summer solstice, when the photoperiod is longer (de Barros et al., 2003). In *S. radians* the chance of juveniles to survive is also affected by differences in habitat, for example, their position in relation to larger colonies; the further away from the chance in obtaining resources increases (Vermeij, 2005). Thus, these three species are considered different according to the ecological (Valen 1976) and biological (Queiroz, 2005) concepts of species.

5 CONCLUSIONS

From a purely ecological perspective, the results showed that *S. radians*, *S. siderea*, and *S. stellata* can be sympatric on the Brazilian coast and Gulf of Mexico, just as *S. radians* and *S. siderea* can be sympatric in Africa, both places show conditions for these species, meeting the basic precept of the ecological concept of species. However, this concept cannot bring back the taxonomy of the complex based on its morphological enigma, as another historical process could be involved in the ecological speciation of *Siderastrea*, which is far from the scope of this work.

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APPENDIX A - FILTERED OCCURRENCES

Longitude	Latitude	Specie
-35.0094	-8.50944	S_stellata
-38.9747	-17.898	S_stellata
-38.6333	-12.7167	S_stellata
-35.15	-8.9	S_stellata
-38.567	-18.117	S_stellata
-38.8739	-17.3503	S_stellata
-39.0508	-17.6053	S_stellata
-39.0483	-17.7864	S_stellata
-38.6903	-17.9069	S_stellata
-39.1353	-17.4219	S_stellata
-39.1683	-17.0983	S_stellata
-39.1269	-17.0039	S_stellata
-44.2667	-0.88333	S_stellata
-37.9833	-12.5667	S_stellata
-38.7968	-3.53542	S_stellata
-38.17	-16.117	S_stellata
-38.6014	-17.7214	S_stellata
-41.9296	-22.8828	S_stellata
-38.8957	-3.50543	S_stellata
-38.9883	-18.0203	S_stellata
-39	-16.665	S_stellata
-39.0807	-16.8799	S_stellata
-38.9015	-13.2007	S_stellata
-38.5043	-3.72722	S_stellata
-39.9777	-2.8462	S_stellata
-39.0365	-3.40877	S_stellata
-39.267	-3.21697	S_stellata
-39.4391	-3.14632	S_stellata
-39.55	-3.07912	S_stellata
-39.6498	-3.02306	S_stellata
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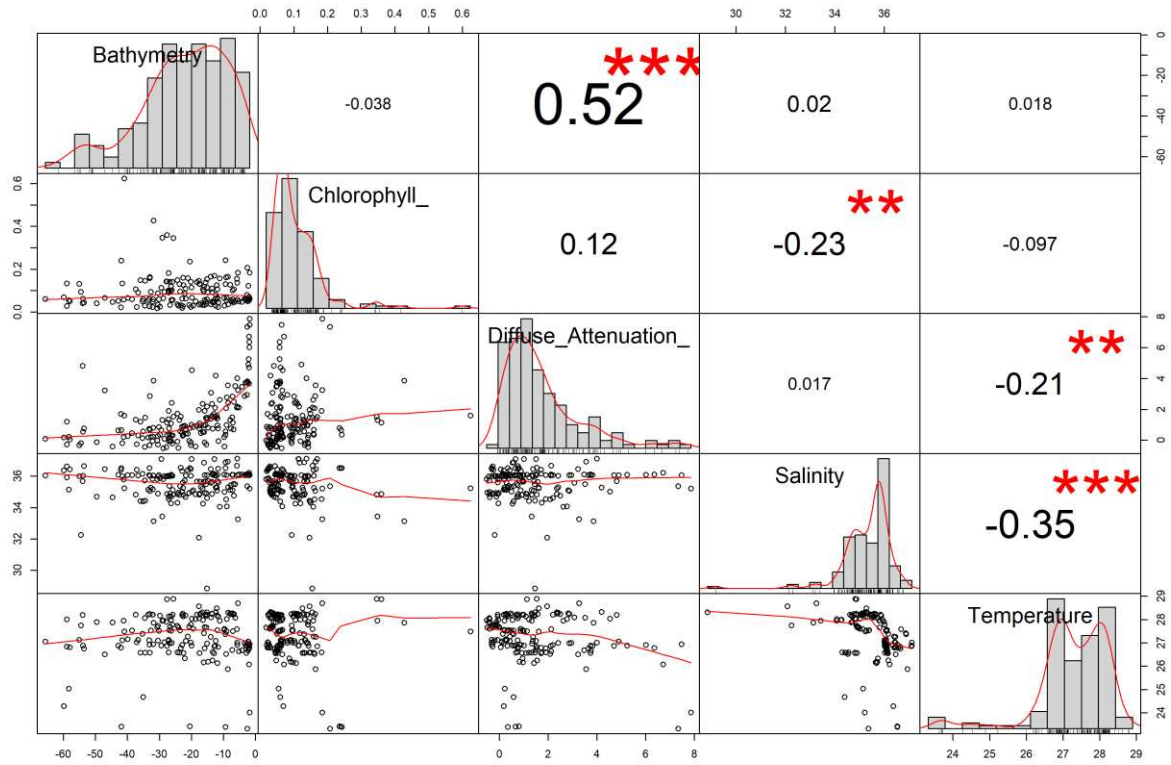
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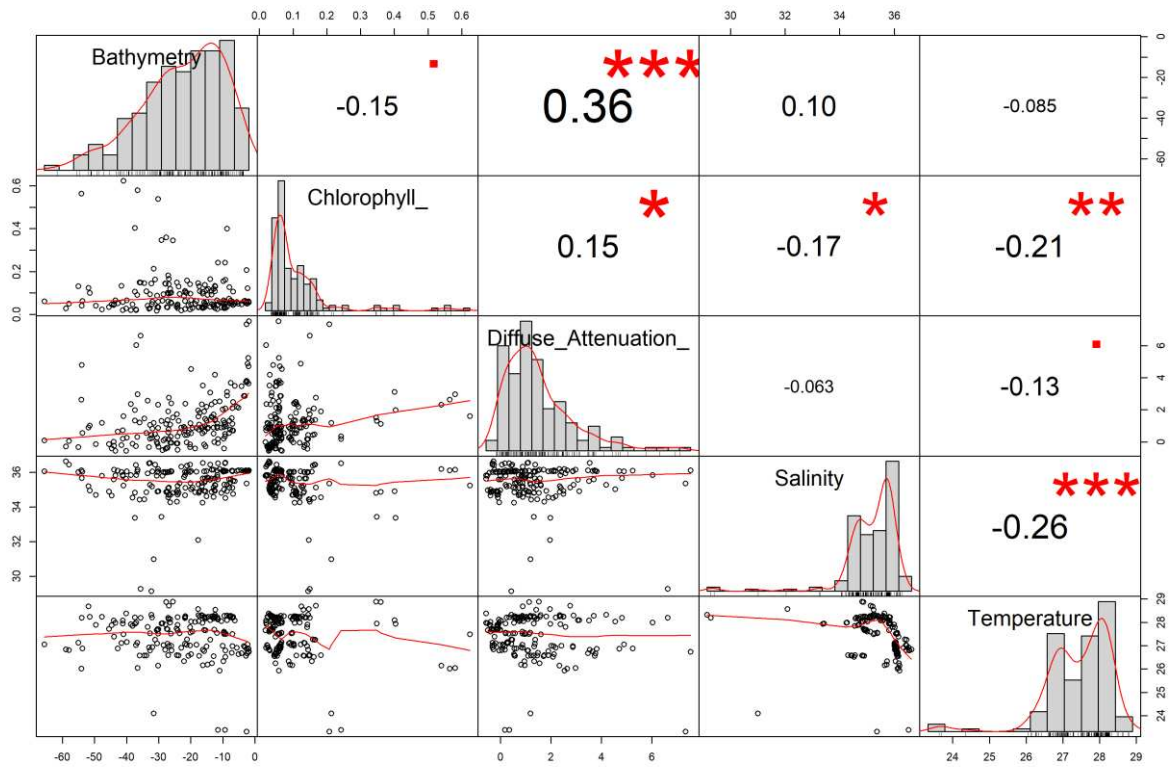
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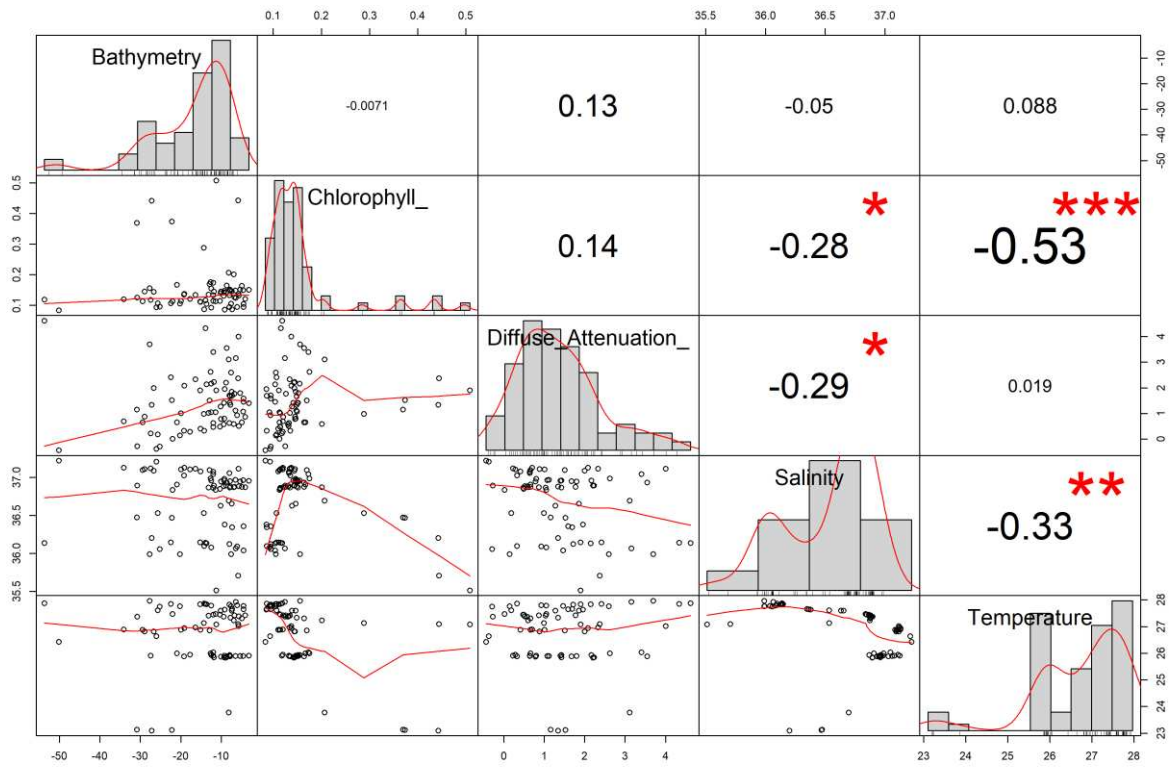
**APPENDIX B - CORRELATION GRAPH OF THE ENVIRONMENTAL VARIABLES
OF *S.radians***



**APPENDIX C - CORRELATION GRAPH OF THE ENVIRONMENTAL
VARIABLES OF *S.siderea***



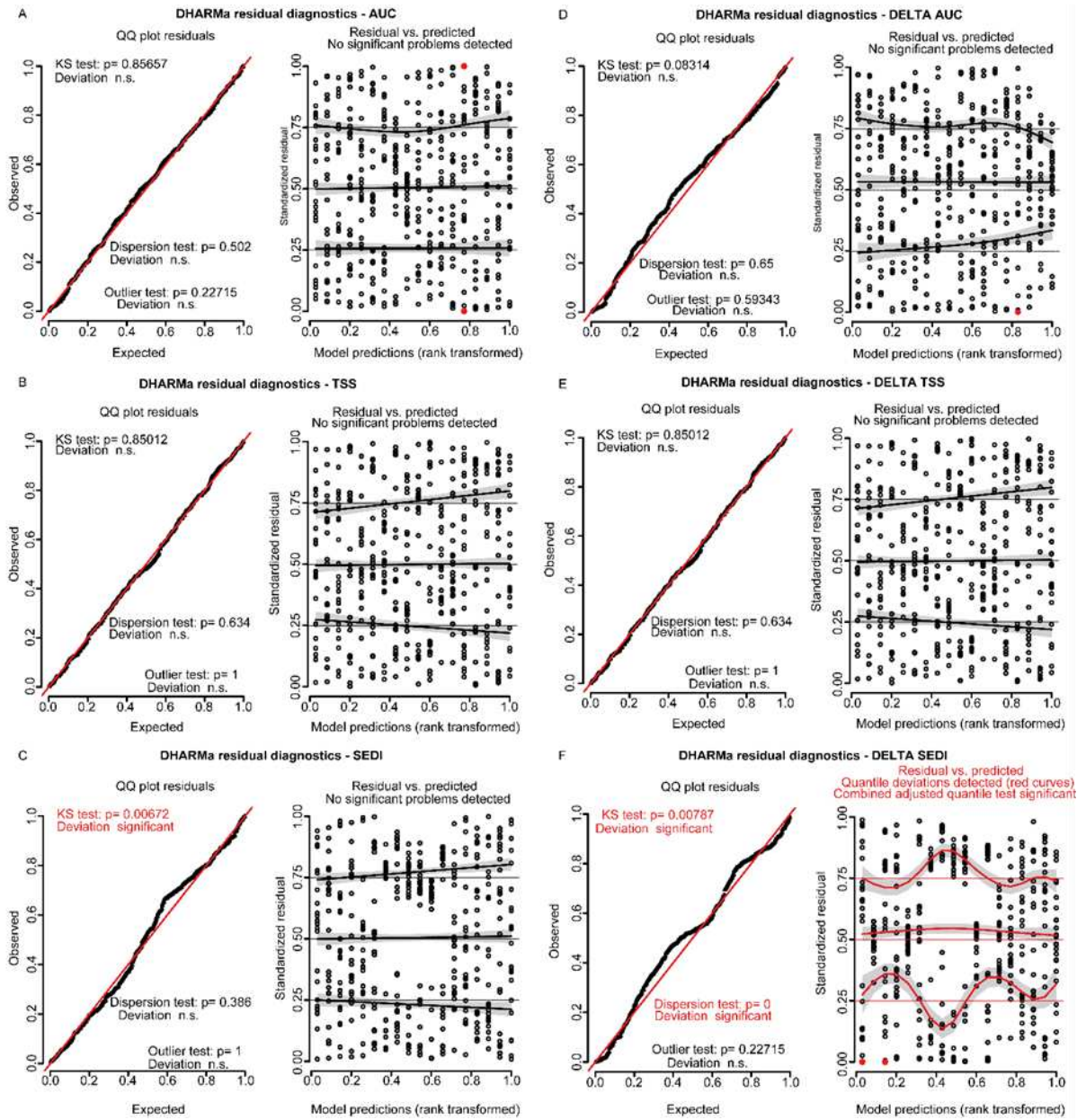
**APPENDIX D - CORRELATION GRAPH OF THE ENVIRONMENTAL
VARIABLES OF *S.stellata***



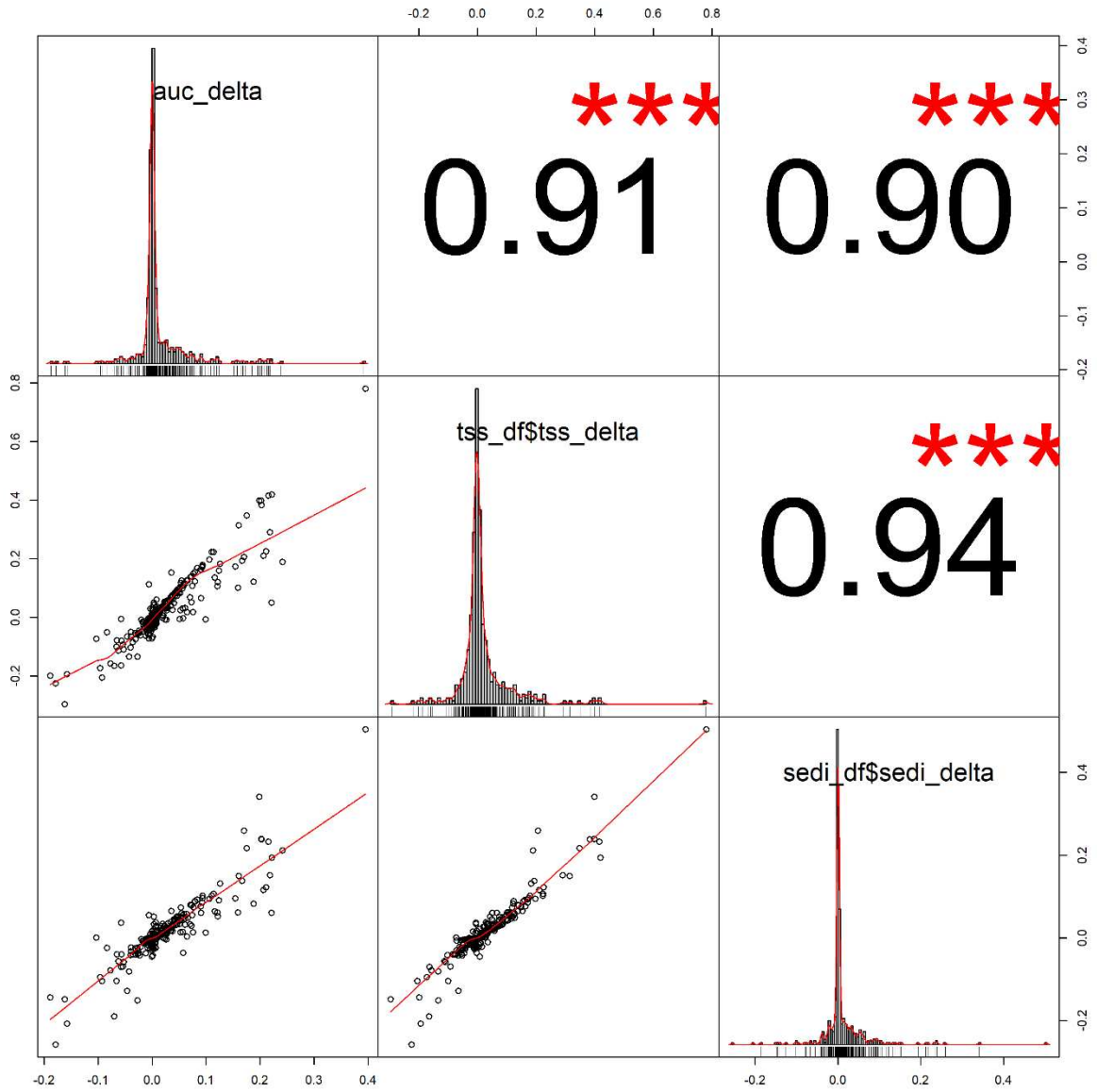
APPENDIX E - BIC FOR GLMMS

Model	Set	Metric	BIC
complet~specie+model+(1 replica_nest)	All Occurences	AUC	973,1
complet ~ specie*model + specie + model + (1 replica_nest)	All Occurences	AUC	576,6
complet ~ specie*model + specie + model + (1 replica_nest) with overdispersion for model	All Occurences	AUC	57,2
complet ~ specie*model + specie + model + (1 replica_nest) with overdispersion for model + specie	All Occurences	AUC	0
complet~specie+model+(1 replica_nest)	All Occurences	TSS	601,6
complet ~ specie*model + specie + model + (1 replica_nest)	All Occurences	TSS	288,9
complet ~ specie*model + specie + model + (1 replica_nest) with overdispersion for model	All Occurences	TSS	157,7
complet ~ specie*model + specie + model + (1 replica_nest) with overdispersion for model + specie	All Occurences	TSS	0
complet~specie+model+(1 replica_nest)	All Occurences	SEDI	683
complet ~ specie*model + specie + model + (1 replica_nest)	All Occurences	SEDI	479,9
complet ~ specie*model + specie + model + (1 replica_nest) with overdispersion for model	All Occurences	SEDI	436,7
complet ~ specie*model + specie + model + (1 replica_nest) with overdispersion for model + specie	All Occurences	SEDI	0
delta~specie+model+(1 replica_nest)	Contrasts	AUC	1668,2
delta ~ specie*model + specie+ model + (1 replica_nest)	Contrasts	AUC	1289,8
delta ~ specie*model + specie + model + (1 replica_nest) with overdispersion for model	Contrasts	AUC	79,4
delta ~ specie*model + specie + model + (1 replica_nest) with overdispersion for model + specie	Contrasts	AUC	0
delta~specie+model+(1 replica_nest)	Contrasts	TSS	1153,7
delta ~ specie*model + specie+ model + (1 replica_nest)	Contrasts	TSS	288,9
delta ~ specie*model + specie + model + (1 replica_nest) with overdispersion for model	Contrasts	TSS	53,1
delta ~ specie*model + specie + model + (1 replica_nest) with overdispersion for model + specie	Contrasts	TSS	0
delta~specie+model+(1 replica_nest)	Contrasts	SEDI	1745,1
delta ~ specie*model + specie+ model + (1 replica_nest)	Contrasts	SEDI	1246,2
delta ~ specie*model + specie + model + (1 replica_nest) with overdispersion for model	Contrasts	SEDI	347,3
delta ~ specie*model + specie + model + (1 replica_nest) with overdispersion for model + specie	Contrasts	SEDI	0

APPENDIX F – DHARMA Residuals



APPENDIX G – CORRELATION CHART BETWEEN METRICS



APPENDIX H - CUTTING THRESHOLDS FOR BINARIZATION

