



Distribution of macroalgae epiphytes and host species from the Cuban marine shelf inferred from ecological modelling

Abdiel Jover^{a,e,*}, Asiel Cabrera^a, Alieex Ramos^a, Maurício H. Vancine^b, Ana M. Suárez^c, John Machell^d, José Lucas Pérez-Lloréns^e

^a Departamento de Biología y Geografía, Universidad de Oriente, Patricio Lumumba s/n, Santiago de Cuba, CP 90 500, Cuba

^b Instituto de Biociências, Departamento de Biociências, Laboratório de Análise e Síntese em Biodiversidade, Universidade Estadual Paulista (UNESP), Av. 24-A, 1515, Bela Vista, Rio Claro, São Paulo, 13506-900, Brazil

^c Centro de Investigaciones Marinas, Universidad de La Habana, Calle 16, No. 114, e/ 1ra y 3ra, Miramar, La Habana, CP 11300, Cuba

^d Pennine Water Group, University of Sheffield, Sir Frederick Mappin Building, Mappin Street, Sheffield, S1 3JD, United Kingdom

^e Instituto Universitario de Investigación Marina (INMAR), Universidad de Cádiz (Campus Universitario de Puerto Real, Puerto Real, Cádiz, 11510, Spain

ARTICLE INFO

Keywords:

Ecological modelling
Marine variables
Algae-algae interactions
Niche breadth
Niche overlap
Generalist species

ABSTRACT

Ecological Niche Modelling (ENM) is a tool widely used in ecology to determine environmental conditions and the potential distribution of species. In this article we assess the potential distribution, tolerance limits and similarity niche of macroalgae epiphytes and hosts from the Cuba marine shelf. Using different methods (BIOCLIM, Gower, Maxent and SVM) we have modelled the niche for each species. The final prediction map of distribution was made using the ensemble prediction technique. The similarity of ENMs was quantified by Schoener D and Hellinger I distance. The predictive power of all models was reasonable, since the values of the area under the curve (AUC) were greater than 0.9. The host macroalgae most closely related to the spatial distribution pattern of potential abundance of epiphytic macroalgae are *Styopodium zonale* (Kendall correlation, $r^2 = 0.886$) and *Digenea simplex* (Kendall correlation, $r^2 = 0.777$). Environmental variables that contributed mostly (30 %) to the ecological niche models were: the average maximum salinity per year (35.5–36 PSU); the average minimum flow velocity per year ($0.2 \text{ m}\cdot\text{s}^{-1}$) and the average minimum light at ground level per year ($10\text{--}60 \text{ E}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$). The results show that epiphytic macroalgae and their most common hosts are generalist species (niche width 0.8) with high overlap in their niche (Schoener D > 0.7; Hellinger I distance = I > 0.6).

1. Introduction

Epiphytic marine macroalgae are multicellular algae (encrusted, leaf-like or branched forms) that live on another photosynthetic organism (Hurd et al., 2014; Taylor, 2019). Epiphyticism is common in marine benthic communities where macroalgae adhere to the surface of host algae (Gauna et al., 2015; Zheng et al., 2015), seagrasses (Karsten et al., 2000; Borowitzka et al., 2006), or mangrove roots (Hogarth, 2015). These primary basic species (algae, mangroves) provide habitat for the macro-algae epiphytes and increase the richness and diversity of the ecosystem (Thomsen et al., 2018; Gribben et al., 2019).

Epiphytes are important for understanding the structure, composition and functioning of marine ecosystems. For example, they can reduce water movement within seagrass meadows (Borowitzka et al., 2006) and minimize damage from desiccation stress (Penhale and

Smith, 1977; Bruno et al., 2003). In addition, the specific composition of epiphytes can become a source of nutrients for the growth of seagrasses when the biomass of the epiphyte becomes higher than that of its host (Penhale and Smith, 1977; Mazzella and Alberte, 1986). Epiphytes contribute significantly to the productivity of this ecosystem, both vertically (as part of the trophic structure) and horizontally (abundance and heterogeneity within the trophic levels) (Borowitzka et al., 2006). Additionally, they alter conditions and resources at the micro-scale level, which provide food and shelter (Álvarez-Álvarez et al., 2020), and protect other algae under acidifying marine conditions (Guy-Haim et al., 2020).

The taxonomic composition and diversity of epiphytic macroalgae depend largely on the properties of host macroalgae such as longevity, surface area, size and morphological architecture (Creed, 2000; Álvarez-Álvarez et al., 2020). In tropical habitats, the richness and

* Corresponding author at: Departamento de Biología y Geografía, Universidad de Oriente, Patricio Lumumba s/n, Santiago de Cuba, CP 90 500, Cuba.
E-mail address: ajover@uo.edu.cu (A. Jover).

<https://doi.org/10.1016/j.aquabot.2021.103395>

Received 24 February 2020; Received in revised form 11 March 2021; Accepted 16 April 2021

Available online 22 April 2021

0304-3770/© 2021 Elsevier B.V. All rights reserved.

abundance of epiphytes are related to a larger surface area (and biomass) to be colonized (Ortuño-Aguirre and Riosmena-Rodríguez, 2007). In addition, the secondary metabolism of host macroalgae is also important for epiphyte-host interactions (Leonardi et al., 2006), although there is a rather low specificity of such interactions in marine environments (Diez et al., 2013; Harder, 2014).

Ecological niche models (ENMs) relate species occurrence data to environmental variables to predict areas that favor the potential occurrence of these species (Guisan and Zimmermann, 2000; Roloff and Haufler, 2002; Guisan and Thuiller, 2005). Such models are used to predict potential areas of current occurrence or the impact of climate change on the distribution of species (Tognelli et al., 2009). Overall, predictive models are a useful tool for studies of ecology and biogeography (Anderson and Martínez-Meyer, 2004; Coudun et al., 2006).

Currently, various tools and methods are available to preserve ecological niche models and the potential distribution of species (Diniz-Filho et al., 2009; Guisan and Rahbek, 2011; Lessin et al., 2018). The method most commonly used in the scientific literature is MaxEnt, despite criticism of its misuse and the production of outdated models (Kaky et al., 2020). One of the methods used to avoid the problems indicated is ensemble modeling methods, in which individual models are combined to produce a predictive output (Thuiller et al., 2004; Marmion et al., 2009). Ensemble modeling (also known as consensus modeling or ensemble prediction) has gained momentum in ENMs over the last ten years and involves combining predictions from individual ENM models into a binary prediction map. Usually, they are based on average model predictions weighted by an evaluation metric (Kaky et al., 2020).

These modeling methods predict the ecological suitability for a species according to its ecological niche (Phillips et al., 2006). There are two assumptions about ecological environmental variables that are used to build these models: 1) there must be a temporal correspondence between the location/sites of occurrence of a species and the value of the environmental variables (Anderson and Martínez-Meyer, 2004) and; 2) the variables should influence the distribution of the species on a relevant scale determined by the geographical extent and size of the location/site (Pearson et al., 2004). The appropriate choice of environmental variables for modeling niches also influences the degree to which the model can be generalized to other regions outside the study area or other periods (Phillips et al., 2006). Another factor that determines the precision of the models is the accuracy of the coverage of species occurrence (Anderson et al., 2003).

Regarding ENMs, we use in our study a so-called Grinnellian niche interpretation (Jackson and Overpeck, 2000). According to Soberón (2019) “Grinnellian niches” essentially imply two things. Firstly, niche spaces are composed of scenopoetic variables (Hutchinson, 1978). Scenopoetic variables are ecological variables that do not interact with others, and change very slowly. Secondly, they are naturally aimed at analyzing biogeographical questions, using realistic geographical regions that are explicitly defined and subdivided by a discrete grid of expansion (Shmida and Wilson, 1985). These ideas imply different concepts of ecological niches, which are summarized in Jiménez et al. (2019). The fundamental niche (NF) is the totality of environmental conditions in which values of fitness (without interactions or immigration subsidies) can sustain populations. The existing niche (N*F) is the subset of the conditions of the NF that are actually available to a species when it occurs within its dispersal range (the accessible area M) at a given time (Jackson and Overpeck, 2000; Peterson et al., 2011). Finally, the realized niche (NR) is that part of N*F not affected by negative interactors, such as competitors.

Modeling niches in aquatic systems are limited because environmentally relevant variables are very rare or even non-existent in raster format for most regions of the world (Wiley et al., 2003; McNyset, 2005; Chen et al., 2007). Groundbreaking studies in aquatic systems “borrowed” environmental variables from terrestrial measurements, e.g. surface temperature and precipitation (Iguchi et al., 2004;

Domínguez-Domínguez et al., 2006). In 2011, the first set of ocean surface environmental variables was became available at the global level (Tyberghein et al., 2012). These variables are currently being validated through research on different temporal and spatial scales and then correlated with the surface and benthic environment for possible different future climate scenarios (Assis et al., 2018b).

In marine ecosystems, studies on ENM and Species Distribution Models (SDMs) on local scales are only available for the North Atlantic Ocean (Robinson et al., 2017; Melo-Merino et al., 2020). According to these authors, most research focuses on correlative studies, and the most studied groups were fish, mollusks and marine mammals. In this review, macroalgae represent the fourth most studied group and it highlights the work on habitat-forming species (Assis et al., 2018a, 2018b; Buonomo et al., 2018). These studies are limited to the coasts of Western Europe. For algae, the studies refer to the current distribution patterns of the species (Verbruggen et al., 2009; Yesson et al., 2015; Martínez et al., 2018), invasive species (Marcelino and Verbruggen, 2015; Murphy et al., 2016; Veazey et al., 2019) and the effects of climate change (Jueterbock et al., 2016; de la Hoz et al., 2019; Westmeijer et al., 2019).

In the Caribbean Sea, knowledge about the composition, abundance and distribution of epiphytic macroalgae is rare and limited to specific studies (la Rosa and Suárez, 1990; Fricke et al., 2011; Ramírez et al., 2011; Diez et al., 2013). One solution to this information deficit is to estimate the distribution of epiphytic macroalgae using ranges of tolerance to environmental variables. ENMs can be used to quantify environmental preferences that allow the establishment of areas with suitable environments for the species (Yesson et al., 2015). At low latitudes, such as the Caribbean Sea, the distribution of macroalgae is limited by a number of factors including environmental tolerance (Keith et al., 2014). We hypothesized that both the epiphytic as well as the host macroalgae on the Cuban marine platform would be expected to be generalist species with similar environmental tolerance ranges and niches. Therefore, the overall objective of this study is to estimate the potential distribution of the most common macroalgae epiphytic and host species in the Cuban marine Shelf (CMS) using correlated ecological niche models and niche overlap.

2. Material and methods

2.1. Selection of presence data

The georeferenced data of the epiphytic and host macroalgae are from a review of the scientific literature published up to December 2018. Scopus and Google Scholar were used to perform the systematic analysis. In this review, the Boolean operators were restricted to AND OR. The search strings were: (1) (“Seaweed” OR “Algae” OR “Macroalgae”) AND (“Epiphyte” OR “Epibiont”); (2) (“Seaweed” OR “Algae” OR “Macroalgae”) AND (“Host” OR “Basibiont”). The basibiont is considered a substrate organism (Harder, 2008), so this term was included as a keyword in the search for the systematic overview. In the systematic review, proof of presence was obtained from 35 journal articles, a book section and a book. The searching and selection procedure of the bibliographic sources from which the data were taken is explained in Jover et al. (2020c). In addition, epiphyte data were added that are available in the collections of the Centro de Investigaciones Marinas (Universidad de La Habana) and Ficoteca Cubana y Antillana (Universidad de Oriente).

Where macroalgae with epiphytic life forms or host life forms have been reported, only occurrence data have been taken from the literature or collection. Once the epiphytes and hosts were identified, those that were more frequently recorded in the literature (with 20 or more records) were selected. A total of 552 records were used in the models after eliminating multiple records of the same species in the same coordinate and eliminating duplicate records by pixel. A total of 404 data sets were obtained for 10 epiphytic macroalgae and 148 data sets for three hosts. The locations for each species (coordinates) were projected onto the

corresponding maps using the program QGIS 2.18.11, and using the geographic coordinate system. All data sets used in this study are available in FigShare (Jover et al., 2020a).

2.2. Selection of the predictor variables

We obtained 74 oceanographic variables from the online platforms Bio-ORACLE (Tyberghein et al., 2012) and MARSPEC (Sbrocco and Barber, 2013). The variables represent minimum and maximum values and mean values of minimum and maximum values per year in the period 2000–2014. The data of the environmental variables were processed at a spatial resolution of 30 arc-seconds (about 0.86 km² in Ecuador) on Geographic Coordinates.

A reduction of the variables used in the final models was performed, eliminating those variables that showed a high degree of Spearman correlation (greater than 0.75 or less than -0.75) (Fig. S1). This analysis was performed to eliminate redundant environment variables. The correlations were performed with the Hmisc package (Harrell, 2019) of the R program (R Core Team, 2019). To select the variables that provided the most information, the threshold was set at 0.75 (Fig. S1). Variance Inflation Factor (VIF) was determined to exclude bioclimatic multicollinearity among the variables. It is assumed that if the VIF is greater than 5.0, these climatic variables will unsettle the model and make it difficult to identify an optimal set of explanatory variables (Mateo et al., 2011). To obtain a set with an adequate VIF (Table S1), all variables were analyzed with the "HH" package of R (Heiberger, 2018). The resulting variables were used in the distribution models of host macroalgae. For the models of epiphyte species, the potential distribution of host macroalgae was included as variables.

2.3. Modeling process

A model was generated for each host and epiphytic macroalgae using the ensemble prediction method. In this method, the results obtained with different algorithms are combined to obtain a single algorithmic consensus model per species (Araújo and New, 2007; Diniz-Filho et al., 2009). According to these authors, the combined use of different algorithms allows the creation of more robust and reliable distribution models, considering the uncertainty between methods. The following algorithms were used in the construction of the modeling ensemble: Bioclimatic Envelope (BIOCLIM) (Busby, 1991), Generalized Linear Models (GLM) (Lee et al., 2018), Maximum Entropy (MAXENT) (Phillips et al., 2006; Phillips and Dudík, 2008), and Support Vector Machines (SVM) (Tax and Duin, 2004).

Firstly, for the assessment of ENMs, the species occurrence data were randomly divided into calibration and assessment sets comprising 75 % and 25 % of the data sets respectively. Secondly, 40 models (10 replicates x 4 methods) were generated for each species of epiphytic macroalgae and each host. Then, the results of the model were transformed into binary maps using the maximum sensitivity and specificity as threshold values (Liu et al., 2013). Using the "maximum sensitivity and specificity" as a threshold leads to similar results when using data sets with presence / absence or only with presence (Liu et al., 2016). Finally, a consensus map for each macroalgal species was constructed by averaging the prediction ensemble (Araújo and New, 2007).

Each model was statistically evaluated using the AUC (Area Under the Curve) statistics and True Skill Statistic (TSS). The AUC values vary from 0 to 1, although the closer to 1, the better the prediction of occurrence (Mateo et al., 2011). The values of TSS vary from -1 to 1. Negative and near-zero values are typical for models that are no different from randomly generated models; values close to 1 indicate good models, while values above 0.5 are assumed to indicate suitable models (Allouche et al., 2006). The models were generated using the raster, rgdal, USDM, dismo, kernlab, rJava, viridis and tidyverse packages of the program R (R Core Team, 2019).

The modeling processes were performed using two types of models.

The first type we call abiotic models (AV models) and the second type biotic models (AV + BV models). In the abiotic models, six environmental variables for host and epiphyte macroalgae were used. In the biotic models, six environmental variables and the habitat suitability of the three host macroalgae for ENMs of epiphytes were used.

2.4. Maps of potential species richness

The method of Stacked Species Distribution Models (SSDM) was also used to study the spatial distribution pattern of potential epiphytic and host macroalgae richness (Guisan and Rahbek, 2011). The Lowest Presence Threshold (LPT) was used as the cut-off threshold to transform each continuous frequency into binary maps (0 for absence and 1 for presence) (Pearson et al., 2007). We obtained the predicted number of species occurrence (richness) of hosts and epiphytic macroalgae in each pixel summing all species binary maps. The main limitation of this method is that it tends to overestimate species richness by ignoring biotic constraints (Calabrese et al., 2014; Gavish et al., 2017). It is, however, the simplest method to produce maps of species richness (Trotta-Moreu and Lobo, 2010).

In addition, Kendall correlation analyses were carried out between the habitat suitability values of the host macroalgae, the potential richness of the host macroalgae and the potential richness values of the epiphytic macroalgae. The aim of these correlations was to determine the relationship between the distribution of host macroalgae and the potential wealth of epiphytic macroalgae. The correlation was performed with the "Corrplot" package of R v3.6.3 (Wei and Simko, 2017).

2.5. Environmental tolerance range, breadth and niche overlap

The ecological requirements for epiphytic and host macroalgae were examined based on three analyses. The first was to extract the tolerance values of each environmental variable using the reaction curves generated in MAXENT (Phillips and Dudík, 2008). The reaction curves show the quantitative relationship between the logistic probability of presence and the environmental variables (Ma and Sun, 2018).

The second analysis was used to know whether the epiphytic macroalgae are generalists or specialists, relative to niches. This analysis was determined by niche breadth and LOESS regressions. The niche breadth of each species was estimated using the habitat distribution models established for the epiphytic and host macroalgae studied. The niche breadths were determined using the standardized Levins index from the ENMTools package in R (Warren et al., 2010). The niche breadth is a means of calculating the range of suitable environmental variables for a species and provides a value between 0 and 1, with larger values for more general species with wider environmental tolerances and smaller values for more specialized species with narrower environmental tolerances (Levins, 1968). The regression scatterplot of LOESS was constructed using the ade4 package in R (Dray and Dufour, 2007).

The third analysis was performed to determine the niche overlap of host and epiphytic macroalgae by Schoener D and Hellinger I index. The range Schoener D (Schoener, 1968) can vary from 0 (niche models have no overlap) to 1 (identical niche models), and the Hellinger I distance derivative (Van der Vaart, 1998) can vary from 0 (no overlap) to 1 (identical niche models). These indices were calculated with the ENMTools package in R (Warren et al., 2010). They ("Levins", "D" and "I") do not use cut-off criteria, but instead use continuous values of habitat suitability estimated by the models.

3. Results

3.1. Ecological niche models and contribution of environmental variables

A review of the scientific literature yielded more than 20 valid presence records for modeling the species distribution of 13 macroalgae in the CMS (Table 1). Epiphytic species with the highest number of

Table 1

Number of presence occurrences used in the model of potential distribution of macroalgal epiphytes and hosts in the Cuban marine shelf.

Macroalgae	Number of presence records
Epiphytes	
<i>Amphiroa fragilissima</i> (Linnaeus) J.V.Lamouroux	45
<i>Hydrolythion farinosum</i> (J.V.Lamouroux) Penrose & Y.M. Chamberlain	40
<i>Jania adhaerens</i> J.V.Lamouroux	33
<i>Gelidium pusillum</i> (Stackhouse) Le Jolis	25
<i>Herposiphonia secunda</i> (C.Agardh) Ambronn	58
<i>Laurencia caraibica</i> P.C.Silva	53
<i>Canistrocarpus cervicornis</i> (Kützting) De Paula & De Clerck	28
<i>Caulerpa cupressoides</i> (Vahl) C.Agardh	22
<i>Caulerpa sertularioides</i> (S.G.Gmelin) M.Howe	24
<i>Anadyomene stellata</i> (Wulfen) C.Agardh	76
Hosts	
<i>Hypnea musciformis</i> (Wulfen) J.V.Lamouroux	27
<i>Digenea simplex</i> (Wulfen) C.Agardh	38
<i>Styopodium zonale</i> (J.V.Lamouroux) Papenfuss	83

presence records (50) were *Anadyomene stellata*, *Herposiphonia secunda* and *Laurencia caraibica*. *Styopodium zonale* was the host macroalga with the highest number of proven occurrences. The potential distribution of epiphytic and host macroalgae was accurately predicted, as the values of the area under the curve (AUC) were greater than 0.9 and the true ability statistics (TSS) were greater than 0.8 (Table 2).

The predictive maps were generated by a logistic output by assigning each pixel a potential of occurrence in areas of habitat incompatibility ($p = 0$) and habitat suitability ($p = 1$). The maps showed the geographical area where each cell is 30 arcseconds and has a habitat suitability value between 0 and 1, for distribution models of epiphytes based on abiotic variables (AV models) (Fig. S2), and models with biotic + abiotic variables (AV + BV models) (Fig. S3). In all maps, probability values of 0.50 were used to define the specificity threshold as a "suitable" habitat.

Distribution models showed values for the probability of occurrence of more than 60 % for nine epiphyte species on the north and south-east coast of Cuba (Fig. S2). Only *Hydrolythion farinosum* showed a more restricted potential distribution on the north-west and southeast coast. Except for the epiphyte *Canistrocarpus cervicornis*, all models showed habitat suitability in the coastlines around the islands and cays. Both models, AV and BV + AV, showed a similar probability distribution

Table 2

Percentage of relative contribution of the environmental variables that most contribute the ecological niche models, Area under the Curve (AUC), and True Skill Statistic (TSS) of the epiphytic and host macroalgae models in the Cuban marine shelf.

Macroalgae	Predictor variables									AUC	TSS
	Current	D.O.	Light	NO ₃	Salinity	SiO ₄	Hmusc	Dsimp	Szona		
Epiphytes											
<i>Amphiroa fragilissima</i>	13.5	22.1	9	4.5	50.7	0.2	1.3	22.4	75.5	0.95	0.86
<i>Hydrolythion farinosum</i>	13.3	2.5	12.3	27.7	41.5	2.6	1.6	3.1	89	0.96	0.86
<i>Jania adhaerens</i>	12.3	3.1	15.6	16.6	52.3	0	3.1	54.1	40.6	0.95	0.82
<i>Gelidium pusillum</i>	37.2	3.7	10.4	10.5	38	0.2	0.6	5.5	91.4	0.94	0.82
<i>Herposiphonia secunda</i>	13.9	15.1	13.4	4.4	51.7	1.5	3.3	69.6	24.4	0.93	0.8
<i>Laurencia caraibica</i>	3.1	4.7	11.1	5	75.9	0.2	0.8	8.5	88.4	0.94	0.8
<i>Canistrocarpus cervicornis</i>	61.4	0.6	9	7.6	17.5	3.9	25.9	9.4	63.1	0.94	0.8
<i>Caulerpa cupressoides</i>	11.7	5.8	9.1	18.1	55.2	0	2.2	2	92.9	0.95	0.83
<i>Caulerpa sertularioides</i>	56	0.3	12.7	7.7	21.6	1.4	35.8	4.3	57.5	0.94	0.81
<i>Anadyomene stellata</i>	10.8	13.7	10.4	3.2	61.6	0.2	0.8	19.9	76.9	0.96	0.85
Hosts											
<i>Hypnea musciformis</i>	65	0.6	8.8	7.2	16.5	1.9	–	–	–	0.92	0.83
<i>Digenea simplex</i>	7.5	22.2	15.8	9.9	43	1.6	–	–	–	0.91	0.81
<i>Styopodium zonale</i>	11.3	13.9	10.9	3.9	59.6	0.3	–	–	–	0.91	0.8

Values of greater contribution in bold. Hmusc = distribution of *Hypnea musciformis*, Dsimp = distribution of *Digenea simplex*, Szona = distribution of *Styopodium zonale*. Where: Current: Minimum records average of currents speed per year, D.O.: Minimum records average of dissolved oxygen per year, Light: Minimum records average of light in the bottom per year, NO₃: Maximum nitrate concentration, Salinity: Maximum records average of Salinity per year, SiO₄: Maximum silicate concentration.

pattern (Fig. S3). In general, the probability of occurrence of epiphytic macroalgae is reduced when biotic variables are included into the models. This phenomenon can be observed both in widespread epiphytic macroalgae such as *Amphiroa fragilissima* (Fig. 1A and C) and in more narrowly defined epiphytes such as *H. farinosum* (Fig. 1B and D).

Maps for host macroalgae also show the geographical area where each cell is 30 arcseconds with a habitat suitability value between 0 and 1 (Fig. 2). In the CMS, the host macroalgae *Styopodium zonale* was the macroalga with the largest distribution area, followed by *Hypnea musciformis*. Like the epiphytic macroalgae, the host species showed habitat suitability in the coastlines around the islands and cays.

In AV models the percentage contribution of environmental variables was different for epiphytic and host macroalgae (Table 2). The abiotic variables with the highest contribution in the models were: 1) the average records for maximum salinity per year ($n = 13$: 10 epiphytes and three hosts); 2) the average records for maximum current velocity per year ($n = 11$: nine epiphytes and two hosts); and 3) the average records for maximum light (bottom) per year ($n = 9$: seven epiphytes and two hosts). The percentage contribution of the previous variable to the models was greater than 10 %.

In BV + AV models for distribution models of the epiphytic macroalgae, the hosts *Styopodium zonale* and *Digenea simplex* were the most important biotic variables in ten and four models respectively (Table 2). *Hypnea musciformis* contributed only with values greater than 25 % in the distribution models of *Caulerpa sertularioides* and *Canistrocarpus cervicornis*. In models that combined both types of variables, the percentage contribution of the biological variables was greater than that of the abiotic variables.

3.2. Maps of potential species richness

The potential species richness of the host macroalgae (Fig. 3A) showed a different distribution pattern between the areas of the CMS. In the littoral areas of cays and islands they represent suitable habitats for the three macroalgal hosts studied. However, the areas with the highest probability for coexistence of two of the macroalgal hosts are limited to the Gulf of Guacanayabo (20° 28' 00" N, 77° 30' 00" W) and the Gulf of Ana María (21° 24' 46" N, 78° 49' 02" W) on the south coast of Cuba. The potential areas on the north coast for two hosts are only recorded to the west of the Cuban archipelago, while only one species of host macroalgae is recorded in the Gulf of Batabanó (22° 15' 00" N, 82° 30' 00" W) on the southwest coast of Cuba.

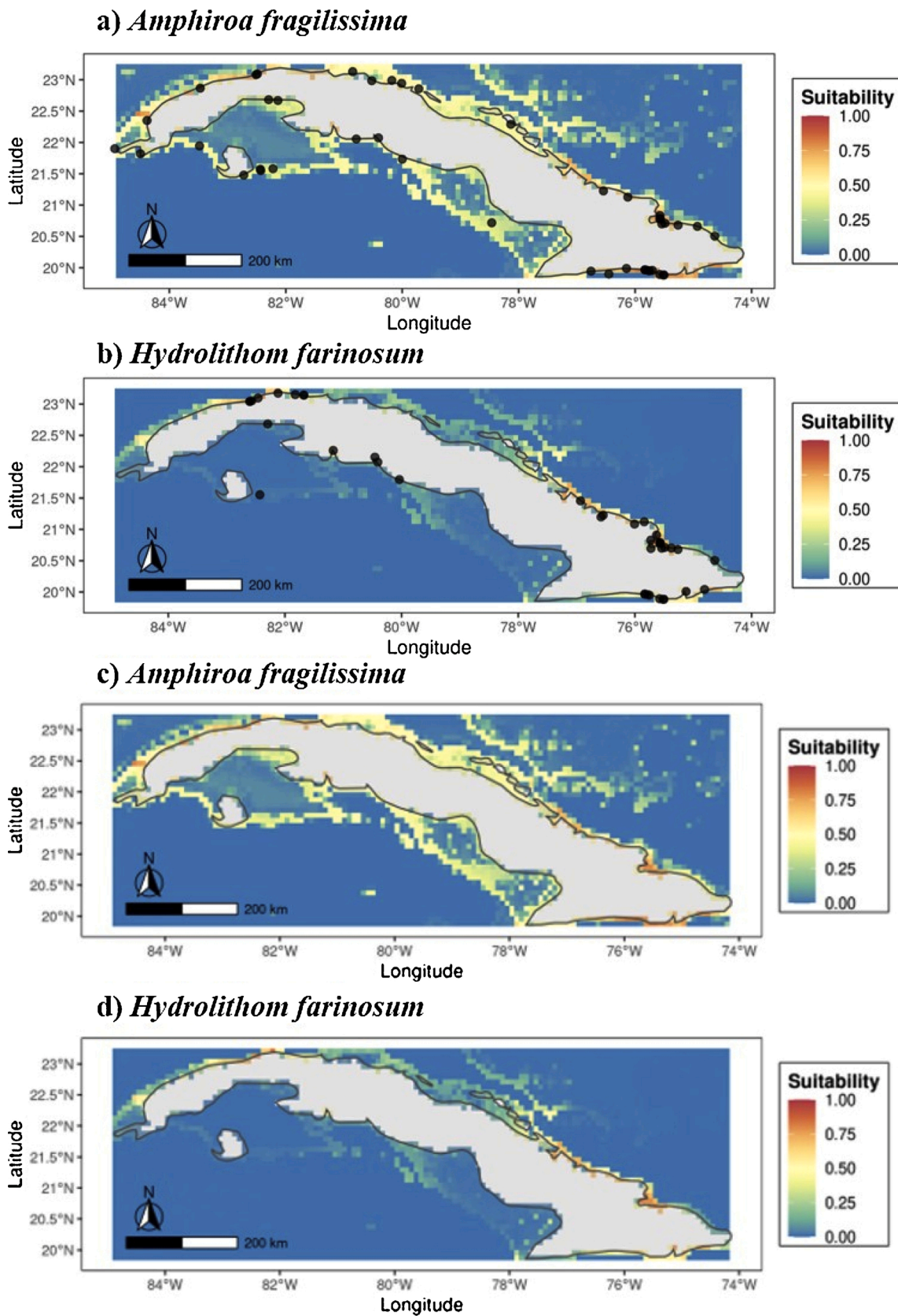


Fig. 1. Potential distribution of habitat suitability above 0.5 of the epiphytic macroalgae in Cuban marine shelf using abiotic variables (A-B) and biotic variables (C-D) in ecological niche modelling. Black points indicate occurrences used to train and test the models.

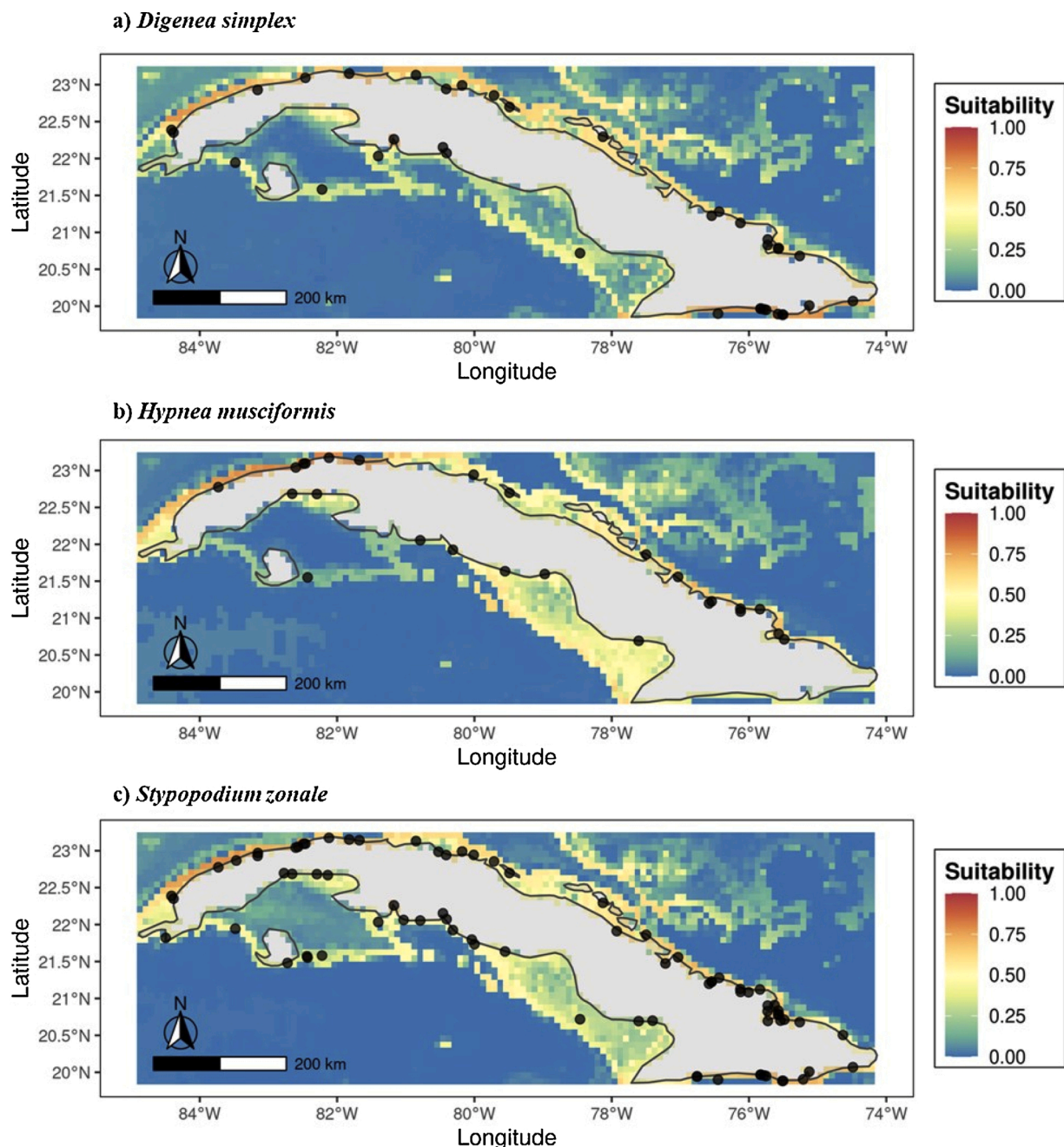


Fig. 2. Potential distribution of habitat suitability above 0.5 of the hosts macroalgae in Cuban marine shelf. Black points indicate occurrences used to train and test the models.

In AV models, the areas of the Cuban shelf with the highest potential species richness of epiphytic macroalgae (8–10 species) are located in the regions where the three host macroalgae species coexisted (Fig. 3B). Areas with a potential abundance of two host species coincide with areas with a potential abundance of between five and eight epiphytic species. In the Gulf of Batabanó the lowest values of potential epiphytic macroalgae richness are recorded. However, in the models BV + AV (Fig. 3C), the areas with the greatest potential wealth of epiphytic macroalgae are shrinking, while the areas with the least wealth of epiphytic macroalgae are increasing, especially on the southern coast of the archipelago.

Finally, Kendall correlation analysis confirmed that the potential richness of host macroalgae in the AV models (Kendall's correlation, $r^2 = 0.899$) and in the AV + BV models (Kendall correlation, $r^2 = 0.869$) is positively related to the potential richness of epiphytic macroalgae in

the Cuban marine shelf. Furthermore, the habitat suitability values of *Stypopodium zonale* also showed a positive relationship with the potential richness of epiphytic macroalgae, while *Hypnea musciformis* was the least related. These relationships presented the same behavior in AV models and AV + BV models (Table 3).

3.3. Environmental tolerance range, breadth and niche overlap

All epiphytes and hosts had a tolerance range between 35.5–36 UPS for the annual average maximum salinity values (Table 4). The annual average maximum values of both flow velocity and light in the lower range showed the highest variability of the tolerance range. The tolerance of flow velocity was $0.1 \text{ m}\cdot\text{s}^{-1}$ in the models of the macroalgal host *Hypnea musciformis* and the epiphytes *Jania adhaerens*, *Herposiphonia secunda* and *Canistrocarpus cervicornis*. The lower light intensity showed

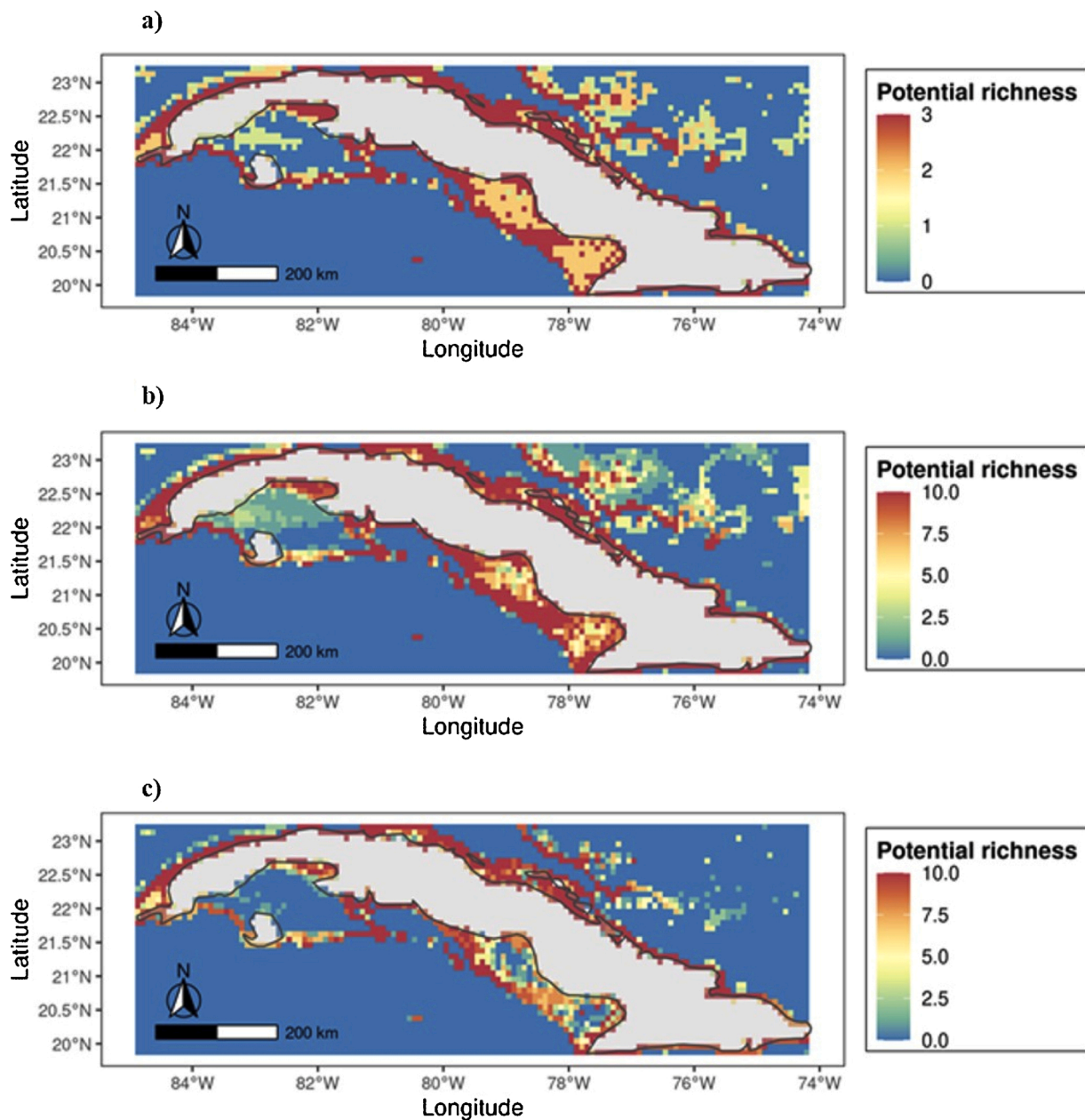


Fig. 3. Potential Species Richness (PSR) of the hosts (A) and epiphytes using abiotic variables (B) and biotic variables (C).

Table 3

Epiphytic macroalgae potential richness correlations (Kendall r_k) between the habitat suitability values of the host macroalgae and the host potential richness in the Cuban marine shelf.

Macroalgal Hosts	Epiphytic macroalgae potential richness	
	Abiotic variables model (AV)	Abiotic + biotic variables model (AV + BV)
<i>Hypnea musciformis</i>	0.679	0.616
<i>Digenea simplex</i>	0.777	0.787
<i>Styopodium zonale</i>	0.886	0.885
Hosts macroalgae potential richness	0.899	0.869

tolerance values of more than $10 \text{ E}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ for *J. adhaerens*, *H. secunda* and *Caulerpa sertularioides*. For the other models the current velocity was between $0.1\text{--}0.8 \text{ m}\cdot\text{s}^{-1}$ and the light values at the bottom were between

$10\text{--}60 \text{ E}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$.

Distribution models of macroalgal epiphytes and hosts showed niche amplitude values of more than 0.8 (Table 5). The niche amplitude values were lower in the models that included biotic variables. *Hydrolython farinosum* showed the smallest niche amplitude values both in the AV model (0.82) and in the AV + BV models (0.76). Macroalgal hosts and epiphytes showed a high overlap of their potential distribution models ($D \geq 0.82$ and $I \geq 0.52$) (Table 6). In the models AV + BV the overlap values were lower. The low overlap was found for *H. farinosum* and its macroalgal host *Hypnea musciformis*, *Digenea simplex*, *Styopodium zonale*.

Scatter plots of habitat suitability values between macroalgal hosts and their epiphytes confirm the general character of epiphyticism in the CMS. All models show a positive interaction for the hosts *Hypnea musciformis* (Fig. 4), *Digenea simplex* (Fig. 5) and *Styopodium zonale* (Fig. 6). In these figures it can be seen that in the AV models (pink line and dots) there was a greater dependence between the suitability habitat values of macroalgal hosts and epiphytes. However, in the AV + BV models (green

Table 4

Tolerance range of the environmental variables that most contribute to the ecological niche models of the epiphytic and host macroalgae in the Cuban marine shelf.

Macroalgae	Range of environmental tolerances in potential distribution models							
	Current (m·s ⁻¹)	D.O. (mol·m ⁻³)	Light (E·m ⁻² ·yr ⁻¹)	NO ₃ (mol·m ⁻³)	Salinity	Hmusc	Dsimp	Szona
Epiphytes								
<i>Amphiroa fragilissima</i>	0.1–1	160–190			35.5–36		0.3–0.7	0.6–0.8
<i>Hydrolythion farinosum</i>	0.1–1		10–60	–	35.5–36			0.5–0.8
<i>Jania adhaerens</i>	≥0.1		≤10	0–0.5	35.5–36		0.3–0.7	0.5–0.8
<i>Gelidium pusillum</i>	0.2–1		40–60	0–1	35.5–36			0.1–0.7
<i>Herposiphonia secunda</i>	≥0.1	160–210	≤10		35.5–36		0.2–0.7	0.6–0.8
<i>Laurencia caraibica</i>			20–60		35.5–36			≥0.1
<i>Canistrocarpus cervicornis</i>	≥0.1				35.5–36	≥0.1		≥0.1
<i>Caulerpa cupressoides</i>	0.1–1			0–0.5	35.5–36			0.2–0.7
<i>Caulerpa sertularioides</i>	0.1–0.4		≤10		35.5–36	≥0.3		0.2–0.7
<i>Anadyomene stellata</i>	0.1–0.7	160–200	20–60		35.5–36		0.1–0.2	0.1–0.7
Hosts								
<i>Hypnea musciformis</i>	≥0.1				35.5–36			
<i>Digenea simplex</i>		160–200	≤10		35.5–36			
<i>Styopodium zonale</i>	0.1–0.8	160–240	20–60		35.5–36			

Hmusc = habitat suitability values of the distribution of *Hypnea musciformis*, Dsimp = habitat suitability values of the distribution of *Digenea simplex*, Szona = habitat suitability values of the distribution of *Styopodium zonale*.

Table 5

Niche breadth, based on Levins (1968), of the epiphytic and host macroalgae in the Cuban marine shelf.

Macroalgae	Niche breadth	
	Abiotic variables model (AV)	Abiotic + biotic variables model (AV + BV)
Epiphytes		
<i>Amphiroa fragilissima</i>	0.90	0.85
<i>Hydrolythion farinosum</i>	0.82	0.76
<i>Jania adhaerens</i>	0.86	0.81
<i>Gelidium pusillum</i>	0.88	0.84
<i>Herposiphonia secunda</i>	0.87	0.82
<i>Laurencia caraibica</i>	0.88	0.83
<i>Canistrocarpus cervicornis</i>	0.87	0.82
<i>Caulerpa cupressoides</i>	0.88	0.83
<i>Caulerpa sertularioides</i>	0.86	0.82
<i>Anadyomene stellata</i>	0.88	0.83
Hosts		
<i>Hypnea musciformis</i>	0.87	–
<i>Digenea simplex</i>	0.89	–
<i>Styopodium zonale</i>	0.88	–

line and dots) a non-linear relationship was found between the suitability values of macroalgal hosts and epiphytes. In the scatter plot, values between 0.4 and 0.6 of the habitat suitability of macroalgae hosts are associated with the habitat suitability of epiphytic macroalgae.

Of the three macroalgal hosts, *Styopodium zonale* had the highest number of regression models with good adaptation (Table S2). In the models of potential distribution with abiotic variables, regression models with the best adaptation were established for *S. zonale* with the epiphytes *Amphiroa fragilissima*, *Herposiphonia secunda*, *Laurencia caraibica* and *Anadyomene stellata* (Fig. 6). However, in the models AV + BV for the potential distribution the best agreement was found with the epiphytes *A. fragilissima*, *Jania adhaerens*, *L. caraibica*, *Canistrocarpus cervicornis*, *Caulerpa cupressoides* and *C. sertularioides*.

The second host with the highest number of regression models with good adaptation was *Digenea simplex*, and the host with the lowest number was *Hypnea musciformis* (Table S2). In the models of potential distribution with abiotic variables, the regression models with better adaptations were found for *D. simplex* with the epiphytes *Amphiroa fragilissima*, *Jania adhaerens*, *Herposiphonia secunda* and *Anadyomene stellata* (Fig. 5). The best agreement in distribution models with the AV + BV models for *D. simplex* was found with the epiphytes *A.*

Table 6

Niche overlap for the epiphytic and host macroalgae, where I = distance from Hellinger and D = overlap from the Schoener D niche.

Hosts	Macroalgae	Abiotic variables model (AV)		Abiotic + biotic variables model (AV + BV)	
		I	D	I	D
<i>Hypnea musciformis</i>	<i>Amphiroa fragilissima</i>	0.94	0.79	0.91	0.75
	<i>Hydrolythion farinosum</i>	0.89	0.65	0.82	0.52
	<i>Jania adhaerens</i>	0.95	0.82	0.91	0.68
	<i>Gelidium pusillum</i>	0.96	0.84	0.94	0.78
	<i>Herposiphonia secunda</i>	0.97	0.85	0.90	0.70
	<i>Laurencia caraibica</i>	0.96	0.79	0.91	0.74
	<i>Canistrocarpus cervicornis</i>	0.99	0.92	0.94	0.75
	<i>Caulerpa cupressoides</i>	0.95	0.80	0.91	0.71
	<i>Caulerpa sertularioides</i>	0.98	0.89	0.94	0.74
	<i>Anadyomene stellata</i>	0.96	0.84	0.90	0.72
	<i>Amphiroa fragilissima</i>	0.97	0.84	0.96	0.82
	<i>Hydrolythion farinosum</i>	0.90	0.64	0.82	0.55
	<i>Jania adhaerens</i>	0.94	0.77	0.92	0.72
	<i>Gelidium pusillum</i>	0.93	0.86	0.93	0.77
<i>Digenea simplex</i>	<i>Herposiphonia secunda</i>	0.98	0.85	0.93	0.75
	<i>Laurencia caraibica</i>	0.93	0.88	0.92	0.75
	<i>Canistrocarpus cervicornis</i>	0.92	0.74	0.91	0.70
	<i>Caulerpa cupressoides</i>	0.93	0.80	0.92	0.74
	<i>Caulerpa sertularioides</i>	0.93	0.76	0.91	0.69
	<i>Anadyomene stellata</i>	0.97	0.83	0.93	0.76
	<i>Amphiroa fragilissima</i>	0.98	0.87	0.97	0.85
	<i>Hydrolythion farinosum</i>	0.91	0.68	0.86	0.56
	<i>Jania adhaerens</i>	0.94	0.82	0.92	0.71
	<i>Gelidium pusillum</i>	0.97	0.85	0.97	0.84
<i>Styopodium zonale</i>	<i>Herposiphonia secunda</i>	0.98	0.92	0.94	0.76
	<i>Laurencia caraibica</i>	0.98	0.92	0.95	0.80
	<i>Canistrocarpus cervicornis</i>	0.95	0.81	0.94	0.73
	<i>Caulerpa cupressoides</i>	0.96	0.85	0.96	0.79
	<i>Caulerpa sertularioides</i>	0.96	0.82	0.94	0.74
	<i>Anadyomene stellata</i>	0.99	0.97	0.95	0.80

fragilissima, *Hydrolythion farinosum* and *Gelidium pusillum*. However, for *H. musciformis* (Fig. 4) the regression models with the best agreement have *Canistrocarpus cervicornis* and *Caulerpa sertularioides* for the distribution models with abiotic variables, and with *C. cupressoides* and *A. stellata* for the potential distribution models with the AV + BV models.

4. Discussion

Distribution models for macroalgal epiphytes and hosts provide an approximation on the ecological requirements' habitat of these taxa on

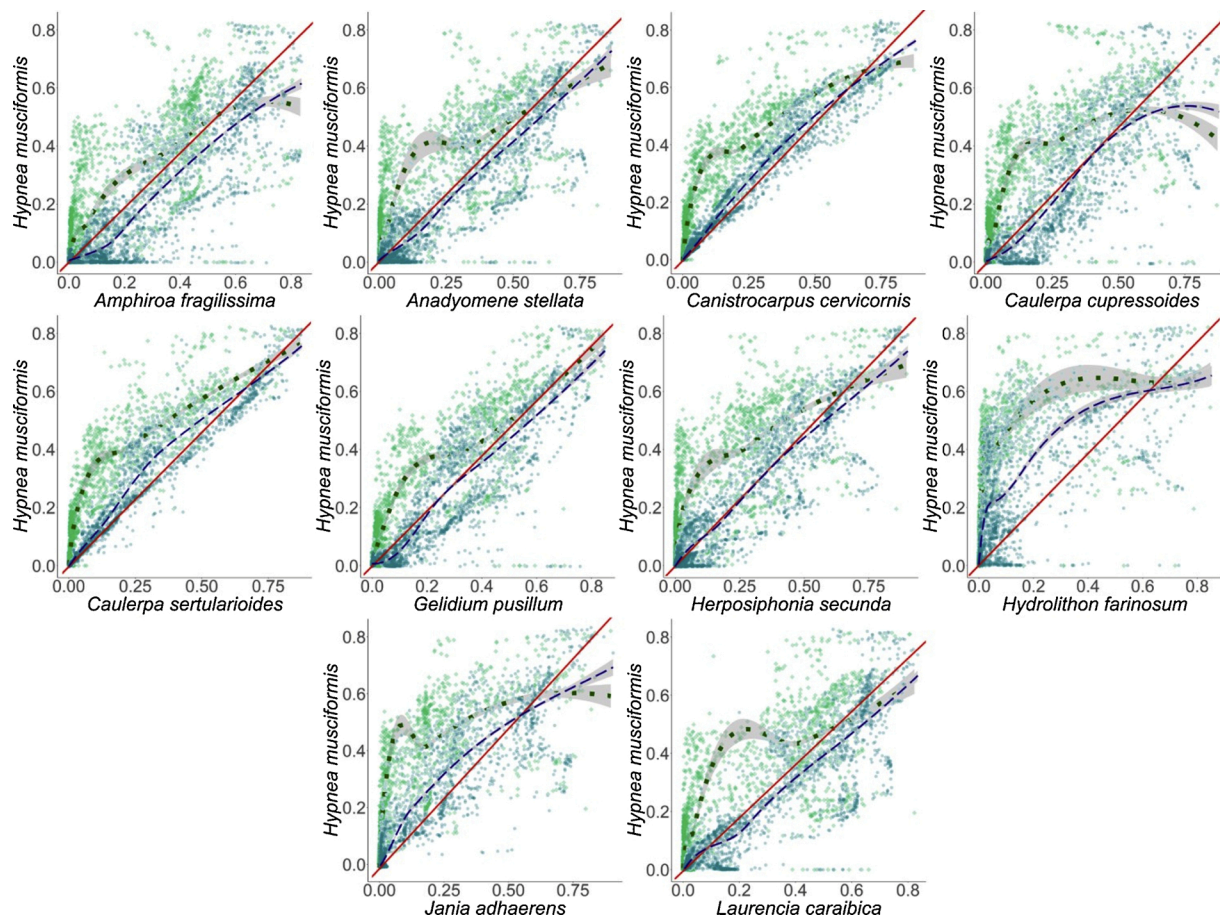


Fig. 4. Scatter plot of distribution modelling of *Hypnea musciformis* versus suitability values of macroalgal epiphytes. In scatter plots, the dotted red line represents the 1:1 relationship, the plain blue line represents the regression line across the cloud of points of the model with abiotic variables, and a simple green line represents the regression line through the point cloud of the model with abiotic + biotic variables (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

the Cuban marine shelf. According to Melo-Merino et al. (2020), throughout these models environmental factors determining the fundamental niche of epiphytic macroalgae in marine ecosystems can be identified for the first time. AUC and TSS values indicate that the models obtained have a good predictive capacity for the species under study (Allouche et al., 2006; Warren et al., 2008; Mateo et al., 2011). In addition, AUC values confirm that the chosen variables can explain the distribution of epiphytes and host macroalgae.

These results support epiphyticism as a phenomenon of wide distribution in the marine shelf of Cuba (Suárez, 1989; Suárez et al., 2015). Moreover, the areas with the highest percentage of presence probability correspond with areas of the rocky substrata, mangroves, and bottoms with a consolidated substratum that favors the richness of epiphytic macroalgae and hosts. This distribution pattern corresponds to that found in tropical areas (Quan-Young et al., 2006; Fredericq et al., 2009; Ramírez et al., 2011; Lucas and de la Cruz-Francisco, 2018).

The current knowledge of Cuban macroalgal distribution is limited because biotic interactions are not considered, and also because of the “Collector Syndrome” (Suárez et al., 2015). The collector syndrome is defined as the process of collecting data on the presence of species in well-known and/or easily accessible locations (Ballesteros-Barrera et al., 2017). According to these authors, it limits the knowledge of species distribution. These two factors are also overlooked in the potential distribution models (Soberón and Townsend, 2005; Jiménez et al., 2019; Soberón, 2019).

The use of ENMs in Ecology meets two functions: (1) to provide knowledge about the potential distribution of species to allow

estimations of richness and diversity of non-sampled areas; and (2) to use such predictions to choose sites of particular interest as biological conservation areas (Meggs et al., 2004; Chen et al., 2007). The areas of the platform that are little-studied according to Suarez et al. (2015), such as the shallow waters of the northeast, southeast, and south-central coasts, register a high potential richness of host and epiphytic macroalgae. Future prospects in the areas identified with greater or lesser potential richness of epiphytic macroalgae and hosts would validate the results of these models (Soberón and Townsend, 2005). According to these authors, this is possible since ecological niche models allow us to fill gaps in the knowledge of the distribution of species. In addition, important areas for the conservation of Cuban marine biodiversity have high values of the potential richness of epiphytes and hosts, such as those found on the south-central and north-central coast according to Valderrama et al. (2018).

Environmental variables such as salinity, light and nutrients modulate the development of macroalgae in marine ecosystems (Kirst, 1990; Hurd et al., 2014) and can predict the distribution of epiphytes and hosts (Bartsch et al., 2012). The narrow response range for the annual average maximum records of salinity shows the low tolerance of epiphytes and host macroalgae to this driver. Salinity values between 30–40 PSU foster the growth of seagrass epiphytes (Biber et al., 2004), whereas higher values limit the development of epiphytes and their hosts (Harlin et al., 1985). The average salinity for the Gulf of Mexico and the Caribbean Sea ranges between 32–35 PSU (Brenes et al., 2017). In the future, laboratory and field studies would allow us to elucidate whether an increase in these maximum salinity values could trigger changes in the distribution

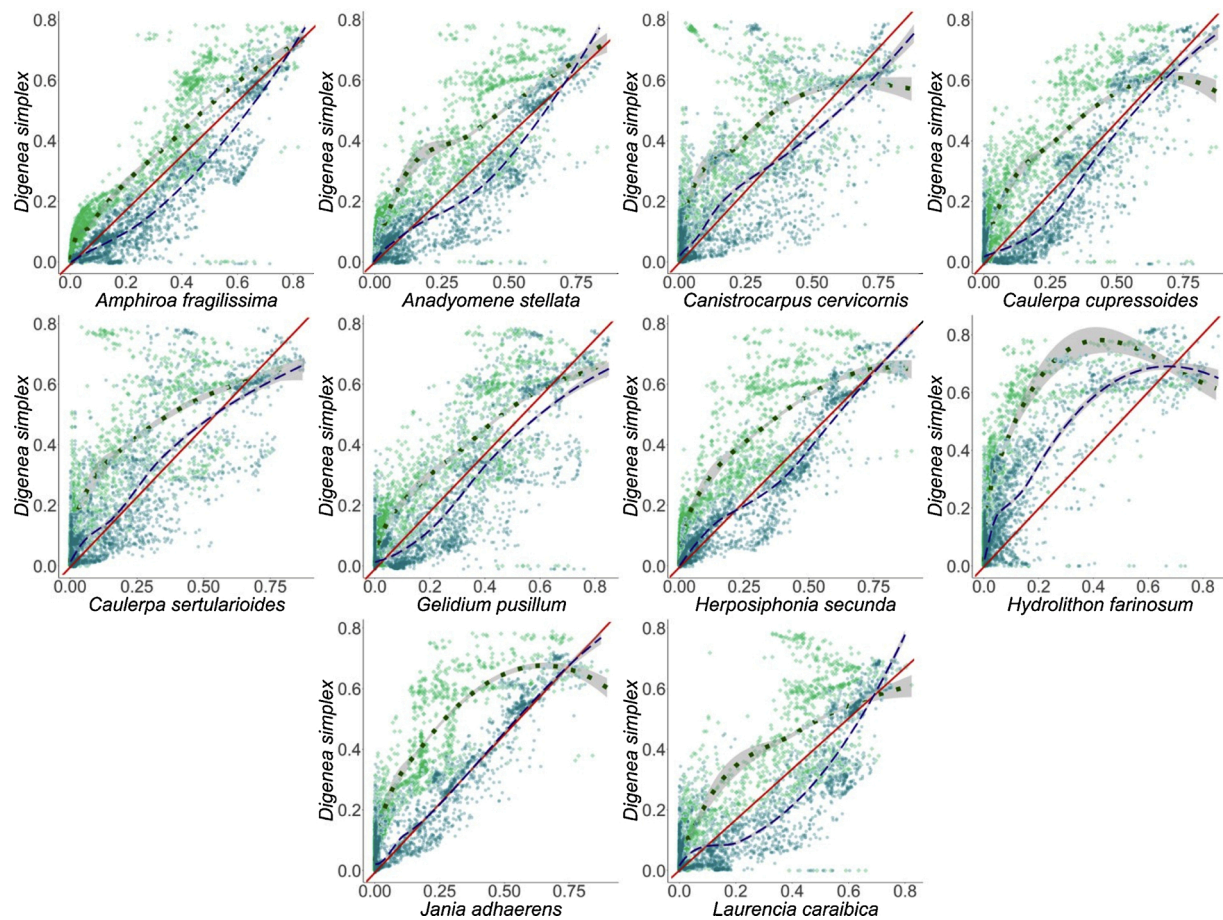


Fig. 5. Scatter plot of distribution modelling of *Digenea simplex* versus suitability values of macroalgal epiphytes. In scatter plots, the dotted red line represents the 1:1 relationship, the plain blue line represents the regression line across the cloud of points of the model with abiotic variables, and a simple green line represents the regression line through the point cloud of the model with abiotic + biotic variables (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

of the host macroalgae and their epiphytes.

Water current affects the growth and morphology of macroalgae (Hurd, 2000; Hurd et al., 2014) as well as nutrient availability and the distribution of dispersal (Bergey et al., 1995; Hawes and Smith, 1995). Both the hydrodynamics and the epibiont load favor the flow of nutrients through the canopy of marine vegetation (Morris et al., 2008; Pujol et al., 2019). It has also been reported that in seagrasses, the top-down flow velocity exerts control over host/epiphyte mesograzers associations (Biber et al., 2004; Jiménez-Ramos et al., 2019).

The positive relationship between the potential richness of host macroalgae and the potential richness of epiphytes could indicate that the more diverse the structure of the host macroalgae association, the greater the richness of epiphyticism. In marine habitats of greater structural complexity, it favors the establishment of host macroalgae and consequently of the epiphytic macroalgae (Otero-Schmitt and Sanjuan, 1992). The three hosts included in the distribution models are frequently found in the Gulf of Mexico and the Caribbean Sea (González-González, 1996; Fredericq et al., 2009; Suárez et al., 2015). *Styopodium zonale* and *Digenea simplex* are among the tropical marine algae with the greatest richness of macroalgal epiphytes (Suárez et al., 1989; Dreckmann and Sentfies, 1994). According to these authors, these two hosts are abundant in the rocky intertidal (including pools) and sublittoral habitats.

Potential distribution models of epiphytic macroalgae showed that *Styopodium zonale* and *Digenea simplex* could function as nurse plants. Nurse plants have a positive net effect on other plant species and on biotic and abiotic conditions through direct or indirect mechanisms

(Stachowicz, 2001). In terrestrial habitats, nurse plants are typically perennial species such as shrubs, trees or cushion plants (Ballesteros-Barrera et al., 2017). According to these authors, the mechanisms that facilitate interactions of macroalgae, such as nurse plants, are 1) improvement of the above-ground microclimate, 2) alteration of soil nutrient fertility, 3) protection from grazing and 4) provision of substratum for the attachment of sedentary organisms.

Kendall's correlation values between the habitat suitability of host macroalgae and the potential richness of epiphytic macroalgae validate *Styopodium zonale* and *Digenea simplex* as important primary basophytes for epiphytic macroalgae (Thomsen et al., 2018). The thallus morphology and aggregation pattern of these host macroalgae are attributes that determine their role as nurse plants (Ortuño-Aguirre and Riosmena-Rodríguez, 2007; Álvarez-Álvarez et al., 2020). The sociable distribution, upright habit, thallus shape (flabellate in *S. zonale* and bushy with branches in *D. simplex*) and crown structure of these two hosts would facilitate the settlement and development of epiphytes by promoting species coexistence (Bulleri, 2009; Bulleri et al., 2016) and improving tolerance to abiotic stress (Scrosati, 2017). These results form the basis for the use of species-niche models in the analysis of algae-algae interactions, with a focus on epibiotic algae.

Niche breadth and overlap values as well as scatter plots of suitable habitats show that the most common macroalgal epiphytes and hosts on the Cuban shelf are generalist species. Analysis of the niche breadth shows that the epiphytes and host macroalgae have similar amplitudes, although they are lines that differ in evolutionary history. The fact that the species of epiphytes and host macroalgae on the CMS are generalist

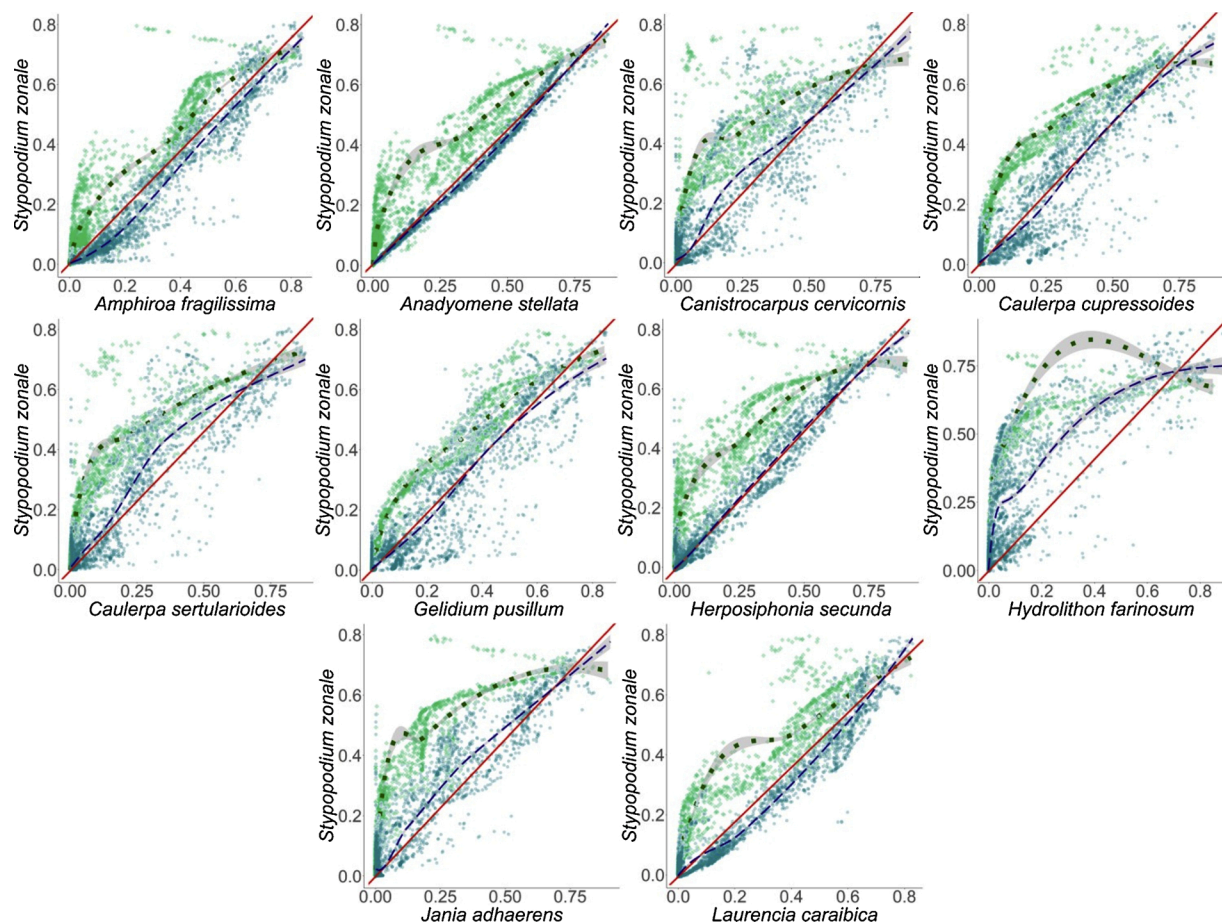


Fig. 6. Scatter plot of distribution modelling of *Stypopodium zonale* versus suitability values of macroalgal epiphytes. In scatter plots, the dotted red line represents the 1:1 relationship, the plain blue line represents the regression line across the cloud of points of the model with abiotic variables, and a simple green line represents the regression line through the point cloud of the model with abiotic + biotic variables (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

favors coexistence and species richness. Simulation studies suggest that the presence of generalist species in assemblages may promote the coexistence of a larger number of species under constant and fluctuating environmental conditions (Richmond et al., 2005).

Previous results and reports for the Gulf of Mexico and Caribbean Sea confirmed the generalist character of macroalgae in their relationship to habitat use (González-González, 1996; Fredericq et al., 2009; Suárez et al., 2015). In the same habitat a species can be registered both as an epiphyte and as a host (Suárez, 1989). Duality in habitat has been recorded for intertidal rocky shores (Diez et al., 2013) and shallow subtidal bottoms (Quan-Young et al., 2006). The specificity of epiphytes and hosts is a rare phenomenon among macroalgae (Pearson and Evans, 1990; Zotz and Schultz, 2008), although it has been recorded for few Cuban species (Suárez, 1989).

The potential range of *Hydrolithon farinosum* has the lowest niche amplitude and the smallest overlap of all recorded epiphytes for the Cuban shelf. This species is the only crust-forming calcareous algae strictly reported as epiphyte in Atlantic Tropical (Fredericq et al., 2009; Suárez et al., 2015; Cabrera et al., 2018). Light intensity, availability of consolidated substratum desiccation and hydrodynamics are factors that limit the spread of encrusting calcareous algae (Steneck, 1986; Vázquez-Elizondo and Enríquez, 2017). Other limiting factors are ocean acidification (Martin and Hall-Spencer, 2017), sedimentation (Fabricius and De'ath, 2001) and eutrophication (Balata et al., 2008). In addition, epiphytic, crust-forming calcareous algae show preferences for the smooth surfaces of the boots of their hosts (Mateo-Cid et al., 2014; Álvarez-Álvarez et al., 2020). The availability of host macroalgae with

these characteristics is a limiting factor for the distribution of these calcareous epiphytes.

In general, potential distribution models of epiphytic macroalgae suggest that host macroalgae represent a resource that facilitates the distribution of epiphytes. Potential distribution models indicated that bottom light intensity, nutrients and flow velocity are the abiotic variables most closely associated with the distribution of epiphytic and host macroalgae of the CMS. In addition, areas of the marine shelf with sandy and muddy-sandy bottoms are less suitable for the development of epiphytic and host macroalgae. The generalist character of epiphytic macroalgae is evident in all potential distribution models. The strongest relationship between potential host distribution and potential epiphyte distribution was found for habitat suitability values between 0.4 and 0.6.

In future research it will be important to analyze the relationship between the potential distribution of main herbivores in addition to other hosts. Aggregation and competition have been identified as critical factors in the distribution of benthic macroalgae (Robinson et al., 2011). Another issue that should be considered is the use of the richness of epiphytic macroalgae and hosts as a response variable in potential distribution models, as presence models tend to overestimate habitat suitability (Reiss et al., 2014).

Despite the biological and methodological limitations of ENMs (Seoane and Bustamante, 2001), the predictions presented provide a basis for understanding epiphyte-host interactions in macroalgae. These potential distribution models provide the theoretical and methodological basis for assessing the effect of host-epiphyte interactions in future

climate change scenarios. These prediction models would also be useful for studies related to anthropogenic activities such as eutrophication, sedimentation and other environmental threats affecting marine biodiversity. Furthermore, these results can be used in the development of early warning systems for invasive species, in the planning of monitoring in different places and time periods scales and in defining long-term strategies for ecosystem management.

Availability of data

Data used are available in the Figshare repository. In this repository, there are available presence record datasets of macroalgae and bibliographic references of the systematic review (Jover et al., 2020a) [dataset]. In addition, there are raster datasets of the ENMs of the epiphytic and host macroalgae (Jover et al., 2020b) [dataset].

CRediT authorship contribution statement

Abdiel Jover: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review & editing. **Asiel Cabrera:** Software, Formal analysis, Investigation, Data curation, Writing - review & editing. **Aliex Ramos:** Methodology, Formal analysis, Investigation, Data curation, Writing - review & editing. **Maurício H. Vancine:** Software, Formal analysis, Writing - review & editing. **Ana M. Suárez:** Resources, Writing - review & editing, Supervision. **John Machell:** Resources, Writing - review & editing. **José Lucas Pérez-Lloréns:** Resources, Writing - review & editing, Supervision.

Declaration of Competing Interest

The authors report no declarations of interest.

Acknowledgements

Special thanks to Rio Claro Campus of the Universidade Estadual Paulista in Brazil for the facilities for performing models. The Doctoral Program of Marine Sciences and Technologies at the Universidad de Cádiz, for the facilities offered in the realization of this work. To Gavin W. Maneveldt, Daniel González Fernández and Dennis Denis Ávila for comments and review of language that substantially improved the manuscript. We also acknowledge the editor's and reviewers' comments that substantially improved the manuscript.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.aquabot.2021.103395>.

References

Allouche, O., Tsoar, A., Kadmon, R., 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *J. Appl. Ecol.* 43, 1223–1232. <https://doi.org/10.1111/j.1365-2664.2006.01214.x>.

Álvarez-Álvarez, J.E., Quiroz-González, N., Rodríguez-Muñoz, D.L., Aguilar-Estrada, L. G., 2020. Epiphytic algae in *Padina durvillei* and *P. crispata* (Dyctiotaceae, phaeophyceae) in the Mexican tropical Pacific. *Acta Bot. Mex.* 2020, 1–16. <https://doi.org/10.21829/abm127.2020.1594>.

Anderson, R.P., Martínez-Meyer, E., 2004. Modeling species' geographic distributions for preliminary conservation assessments: an implementation with the spiny pocket mice (*Heteromys*) of Ecuador. *Biol. Conserv.* 116, 167–179. [https://doi.org/10.1016/S0006-3207\(03\)00187-3](https://doi.org/10.1016/S0006-3207(03)00187-3).

Anderson, R.P., Lew, D., Peterson, A.T., 2003. Evaluating predictive models of species' distributions: criteria for selecting optimal models. *Ecol. Modell.* 162, 211–232. [https://doi.org/10.1016/S0304-3800\(02\)00349-6](https://doi.org/10.1016/S0304-3800(02)00349-6).

Araújo, M.B., New, M., 2007. Ensemble forecasting of species distributions. *Trends Ecol. Evol. (Amst.)* 22, 42–47. <https://doi.org/10.1016/j.tree.2006.09.010>.

Assis, J., Araújo, M.B., Serrão, E.A., 2018a. Projected climate changes threaten ancient refugia of kelp forests in the North Atlantic. *Glob. Chang. Biol.* 24, e55–e66. <https://doi.org/10.1111/gcb.13818>.

Assis, J., Tyberghein, L., Bosch, S., Verbruggen, H., Serrão, E.A., De Clerck, O., 2018b. Bio-ORACLE v2. 0: extending marine data layers for bioclimatic modelling. *Glob. Ecol. Biogeogr.* 27, 277–284. <https://doi.org/10.1111/gcb.12693>.

Balata, D., Bertocci, I., Piazzì, L., Nesti, U., 2008. Comparison between epiphyte assemblages of leaves and rhizomes of the seagrass *Posidonia oceanica* subjected to different levels of anthropogenic eutrophication. *Estuar. Coast. Shelf Sci.* 79, 533–540. <https://doi.org/10.1016/j.ecss.2008.05.009>.

Ballesteros-Barrera, C., Aguilar-Romero, O., Zárate-Hernández, R., Ballesteros-Tapia, L., 2017. Distribución geográfica y conservación de nueve especies del género *Ferocactus* (Cactaceae) en México. *Rev. Fitotec. Mex.* 40, 131–140.

Bartsch, I., Wiencke, C., Laepple, T., 2012. Global seaweed biogeography under a changing climate: the prospected effects of temperature. *Seaweed Biology*. Springer, pp. 383–406. https://doi.org/10.1007/978-3-642-28451-9_18.

Bergey, E.A., Boettiger, C.A., Resh, V.H., 1995. Effects of water velocity on the architecture and epiphytes of *Cladophora glomerata* (Chlorophyta). *J. Phycol.* 31, 264–271. <https://doi.org/10.1111/j.0022-3646.1995.00264.x>.

Biber, P.D., Harwell, M.A., Cropper, W.P., 2004. Modeling the dynamics of three functional groups of macroalgae in tropical seagrass habitats. *Ecol. Modell.* 175, 25–54. <https://doi.org/10.1016/j.ecolmodel.2003.10.003>.

Borowitzka, M., Lavery, P., Van Keulen, M., 2006. Epiphytes of seagrasses. In: Larkum, A., Orta, R., Duarte, C. (Eds.), *Seagrasses: Biology, Ecology and Conservation*. Springer, Dordrecht, pp. 441–461. https://doi.org/10.1007/978-1-4020-2983-7_19.

Brenes, C., Benavides, R., Loza, S., 2017. Descripción de la distribución espacial de la clorofila a, temperatura y salinidad en la plataforma y el talud continentales del Caribe centroamericano. *Rev. Ciencias Mar. y Costeras* 9, 41–59. <https://doi.org/10.15359/revmar.9-1.3>.

Bruno, J.F., Stachowicz, J.J., Bertness, M.D., 2003. Inclusion of facilitation into ecological theory. *Trends Ecol. Evol. (Amst.)* 18, 119–125. [https://doi.org/10.1016/S0169-5347\(02\)00045-9](https://doi.org/10.1016/S0169-5347(02)00045-9).

Bulleri, F., 2009. Facilitation research in marine systems: state of the art, emerging patterns and insights for future developments. *J. Ecol.* 97, 1121–1130. <https://doi.org/10.1111/j.1365-2745.2009.01567.x>.

Bulleri, F., Bruno, J.F., Silliman, B.R., Stachowicz, J.J., 2016. Facilitation and the niche: implications for coexistence, range shifts and ecosystem functioning. *Funct. Ecol.* 30, 70–78. <https://doi.org/10.1111/1365-2435.12528>.

Buonomo, R., Chefaoui, R.M., Lacida, R.B., Engelen, A.H., Serrão, E.A., Airoldi, L., 2018. Predicted extinction of unique genetic diversity in marine forests of *Cystoseira* spp. *Mar. Environ. Res.* 138, 119–128. <https://doi.org/10.1016/j.marenvres.2018.04.013>.

Busby, J.R., 1991. BIOCLIM—A bioclimatic analysis and prediction system. In: Margules, C.R., Austin, M.P. (Eds.), *Nature Conservation: Cost Effective Biological Surveys and Data Analysis*. CSIRO, Canberra, Australia, pp. 64–68.

Cabrera, A., Jover, A., Suárez, A.M., 2018. Algas coralinas (Rhodophyta, Corallinophycidae) de Cuba: estado actual de su conocimiento. *Algas Boletín la Soc. Española Ficológia* 54, 33–42.

Calabrese, J.M., Certain, G., Kraan, C., Dormann, C.F., 2014. Stacking species distribution models and adjusting bias by linking them to macroecological models. *Glob. Ecol. Biogeogr.* 23, 99–112. <https://doi.org/10.1111/gcb.12102>.

Chen, P., Wiley, E.O., Mcnysset, K.M., 2007. Ecological niche modeling as a predictive tool: silver and bighead carps in North America. *Biol. Invasions* 9, 43–51. <https://doi.org/10.1007/s10530-006-9004-x>.

Coudun, C., Gégout, J.-C., Piedallu, C., Rameau, J.-C., 2006. Soil nutritional factors improve models of plant species distribution: an illustration with *Acer campestre* (L.) in France. *J. Biogeogr.* 33, 1750–1763. <https://doi.org/10.1111/j.1365-2699.2005.01443.x>.

Creed, J.C., 2000. Epibiosis on cerith shells in a seagrass bed: correlation of shell occupying with epizoite distribution and abundance. *Mar. Biol.* 137, 775–782. <https://doi.org/10.1007/s002270000429>.

de la Hoz, C.F., Ramos, E., Puente, A., Juanes, J.A., 2019. Climate change induced range shifts in seaweeds distributions in Europe. *Mar. Environ. Res.* 148, 1–11. <https://doi.org/10.1016/j.marenvres.2019.04.012>.

Diez, Y.L., Jover, A., Suárez, A.M., Gómez, L.M., Fujii, M.T., 2013. Distribution of epiphytic macroalgae on the thalli of their hosts in Cuba. *Acta Bot. Brasilica* 27, 815–826. <https://doi.org/10.1590/S0102-33062013000400022>.

Diniz-Filho, J.A.F., Mauricio Bini, L., Fernando Rangel, T., Loyola, R.D., Hof, C., Nogués-Bravo, D., Araújo, M.B., 2009. Partitioning and mapping uncertainties in ensembles of forecasts of species turnover under climate change. *Ecography (Cop.)* 32, 897–906. <https://doi.org/10.1111/j.1600-0587.2009.06196.x>.

Domínguez-Domínguez, O., Martínez-Meyer, E., Zambrano, L., Pérez-Ponce de León, G., 2006. Using ecological-niche modeling as a conservation tool for freshwater species: live-bearing fishes in central Mexico. *Conserv. Biol.* 20, 1730–1739. <https://doi.org/10.1111/j.1523-1739.2006.00588.x>.

Dray, S., Dufour, A.-B., 2007. The ade4 package: implementing the duality diagram for ecologists. *J. Stat. Softw.* 22, 1–22.

Dreckmann, K., Sentés, A., 1994. El alga *Digenea simplex* (Ceramiales: rhodomelaceae) en México: variación biogeográfica. *Rev. Biol. Trop.* 42, 443–453.

Fabricius, K., De'ath, G., 2001. Environmental factors associated with the spatial distribution of crustose coralline algae on the Great Barrier Reef. *Coral Reefs* 19, 303–309. <https://doi.org/10.1007/s003380000120>.

Fredericq, S., Oh, T., Earle, S., Gurgel, C., Mateo-Cid, L., Mendoza-González, A., Norris, J., Suárez, A.M., 2009. Seaweeds of the Gulf of Mexico. In: Felder, D., Camp, D. (Eds.), *Gulf of Mexico Origin, Waters, and Biota: Biodiversity*. Texas A&M University Press, pp. 187–260.

Fricke, A., Titlyanova, T.V., Nugues, M.M., Bischof, K., 2011. Depth-related variation in epiphytic communities growing on the brown alga *Lobophora variegata* in a

- Caribbean coral reef. *Coral Reefs* 30, 967–973. <https://doi.org/10.1007/s00338-011-0772-0>.
- Gauna, M.C., Cáceres, E.J., Parodi, E.R., 2015. Spatial and temporal variability in algal epiphytes on Patagonian *Dictyota dichotoma* (Dictyotales, Phaeophyceae). *Aquat. Bot.* 120, 338–345. <https://doi.org/10.1016/j.aquabot.2014.10.003>.
- Gavish, Y., Marsh, C.J., Kuemmerlen, M., Stoll, S., Haase, P., Kunin, W.E., 2017. Accounting for biotic interactions through alpha-diversity constraints in stacked species distribution models. *Methods Ecol. Evol.* 8, 1092–1102. <https://doi.org/10.1111/2041-210X.12731>.
- González-González, J., 1996. Catálogo onomástico (nomenclátor) y bibliografía indexada de las algas bentónicas marinas de México, Cuadernos Series. Universidad Nacional Autónoma de México.
- Gribben, P.E., Angelini, C., Altieri, A.H., Bishop, M.J., Thomsen, M.S., Bulleri, F., 2019. Facilitation cascades in marine ecosystems: a synthesis and future directions. In: Hawkins, S.J., Allcock, A., Bates, A., Firth, L., Smith, I., Swearer, S., Todd, P. (Eds.), *Oceanography and Marine Biology*. CRC Press, New York, pp. 127–168. <https://doi.org/10.1201/9780429026379-3>.
- Guisan, A., Rahbek, C., 2011. SESAM—a new framework integrating macroecological and species distribution models for predicting spatio-temporal patterns of species assemblages. *J. Biogeogr.* 38, 1433–1444. <https://doi.org/10.1111/j.1365-2699.2011.02550.x>.
- Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. *Ecol. Lett.* 8, 993–1009. <https://doi.org/10.1111/j.1461-0248.2005.00792.x>.
- Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. *Ecol. Modell.* 135, 147–186. [https://doi.org/10.1016/S0304-3800\(00\)00354-9](https://doi.org/10.1016/S0304-3800(00)00354-9).
- Guy-Haim, T., Silverman, J., Wahl, M., Aguirre, J., Noiset, F., Rilov, G., 2020. Epiphytes provide micro-scale refuge from ocean acidification. *Mar. Environ. Res.*, 105093. <https://doi.org/10.1016/j.marenvres.2020.105093>.
- Harder, T., 2014. Marine epibiosis: concepts, ecological consequences and host defence. In: Flemming, H., Murthy, P., Venkatesan, R., Cooksey, K. (Eds.), *Marine and Industrial Biofouling*. Springer, Berlin, Heidelberg, pp. 219–237. https://doi.org/10.1007/978-3-540-69796-1_12.
- Harlin, M.M., Woelkerling, W.J., Walker, D.I., 1985. Effects of a hypersalinity gradient on epiphytic Corallinaceae (Rhodophyta) in Shark Bay, Western Australia. *Phycologia* 24, 389–402. <https://doi.org/10.2216/i0031-8884-24-4-389.1>.
- Harrell, F.E., 2019. Package ‘Hmisc’ [WWW Document]. URL: <https://cran.r-project.org/package=Hmisc%0A%0A>.
- Hawes, I., Smith, R., 1995. Effect of current velocity on the detachment of thalli of *Ulva lactuca* (Chlorophyta) in a New Zealand estuary. *J. Phycol.* 31, 875–880. <https://doi.org/10.1111/j.0022-3646.1995.00875.x>.
- Heiberger, R., 2018. Package ‘HH’ [WWW Document]. URL: <https://cran.r-project.org/web/packages/HH/index.html>.
- Hogarth, P.J., 2015. *The Biology of Mangroves and Seagrasses*, third. ed. Oxford University Press.
- Hurd, C.L., 2000. Water motion, marine macroalgal physiology, and production. *J. Phycol.* 36, 453–472. <https://doi.org/10.1046/j.1529-8817.2000.99139.x>.
- Hurd, C.L., Harrison, P.J., Bischof, K., Lobban, C.S., 2014. *Seaweed Ecology and Physiology*, second. ed. Cambridge University Press, Cambridge. <https://doi.org/10.1017/CBO9781139192637>.
- Hutchinson, G.E., 1978. *An Introduction to Population Ecology*. Yale University Press, New Haven CT, USA.
- Iguchi, K., Matsuura, K., McNyset, K.M., Peterson, A.T., Scachetti-Pereira, R., Powers, K.A., Vieglais, D.A., Wiley, E.O., Yodo, T., 2004. Predicting invasions of North American basses in Japan using native range data and a genetic algorithm. *Trans. Am. Fish. Soc.* 133, 845–854. <https://doi.org/10.1577/T03-172.1>.
- Jackson, S.T., Overpeck, J.T., 2000. Responses of plant populations and communities to environmental changes of the late Quaternary. *Paleobiology* 26, 194–220. [https://doi.org/10.1666/0094-8373\(2000\)26\[194:ROPPAC\]2.0.CO;2](https://doi.org/10.1666/0094-8373(2000)26[194:ROPPAC]2.0.CO;2).
- Jiménez, L., Soberón, J., Christen, J.A., Soto, D., 2019. On the problem of modeling a fundamental niche from occurrence data. *Ecol. Modell.* 397, 74–83. <https://doi.org/10.1016/j.ecolmodel.2019.01.020>.
- Jiménez-Ramos, R., Egea, L.G., Vergara, J.J., Bouma, T.J., Brun, F.G., 2019. The role of flow velocity combined with habitat complexity as a top-down regulator in seagrass meadows. *Oikos* 128, 64–76. <https://doi.org/10.1111/oik.05452>.
- Jover, A., Cabrera, A., Ramos, A., Vancine, M.H., Suárez, A.M., Machell, J., Pérez-Lloréns, J.L., 2020a. List of Presence Records of Macroalgae Epiphytic and Host Frequent in the Cuban Marine Shelf (1900–2019). <https://doi.org/10.6084/m9.figshare.11733735.v1>.
- Jover, A., Cabrera, A., Ramos, A., Vancine, M.H., Suárez, A.M., Pérez-Lloréns, J.L., 2020b. Raster Datasets of Macroalgae Epiphytic and Host Frequent in Cuban Marine Shelf. <https://doi.org/10.6084/m9.figshare.11720655.v1>.
- Jover, A., Ramos, A., Cabrera, A., Suárez, A.M., Machell, J., Pérez-Lloréns, J.L., 2020c. Epiphytic macroalgae and hosts of the marine shelf of Cuba: current status, composition and diversity. *Reg. Stud. Mar. Sci.* 34, 101108. <https://doi.org/10.1016/j.rsma.2020.101108>.
- Jueterbock, A., Smolina, I., Coyer, J.A., Hoarou, G., 2016. The fate of the Arctic seaweed *Fucus distichus* under climate change: an ecological niche modeling approach. *Ecol. Evol.* 6, 1712–1724. <https://doi.org/10.1002/ece3.2001>.
- Kaky, E., Nolan, V., Alatawi, A., Gilbert, F., 2020. A comparison between Ensemble and MaxEnt species distribution modelling approaches for conservation: a case study with Egyptian medicinal plants. *Ecol. Inform.* 60, 101150. <https://doi.org/10.1016/j.ecoinf.2020.101150>.
- Karsten, U., Sawall, T., West, J., Wiencke, C., 2000. Ultraviolet sunscreen compounds in epiphytic red algae from mangroves. *Hydrobiologia* 432, 159–171. <https://doi.org/10.1023/A:1004046909810>.
- Keith, S.A., Kerswell, A.P., Connolly, S.R., 2014. Global diversity of marine macroalgae: environmental conditions explain less variation in the tropics. *Glob. Ecol. Biogeogr.* 23, 517–529. <https://doi.org/10.1111/geb.12132>.
- Kirst, G.O., 1990. Salinity tolerance of eukaryotic marine algae. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 41, 21–53. <https://doi.org/10.1146/annurev.pp.41.060190.000321>.
- la Rosa, P., Suárez, A.M., 1990. Epifitas de *Thalassia*, *Halimeda* y *Laurenciaea* la cayería Bocas de Alonso, Cuba. *Rev. Investig. Mar.* 21, 3–9.
- Lee, Y., Nelder, J.A., Pawitan, Y., 2018. *Generalized Linear Models with Random Effects: Unified Analysis via H-likelihood*. Chapman and Hall/CRC, Boca de Ratón, Florida.
- Leonardi, P.I., Miravalles, A.B., Faugeton, S., Flores, V., Beltrán, J., Correa, J.A., 2006. Diversity, phenomenology and epidemiology of epiphytism in farmed *Gracilaria chilensis* (Rhodophyta) in northern Chile. *Eur. J. Phycol.* 41, 247–257. <https://doi.org/10.1080/09670260600645659>.
- Lessin, G., Artioli, Y., Almroth-Rosell, E., Blackford, J.C., Dale, A.W., Glud, R.N., Middelburg, J.J., Pastres, R., Queirós, A.M., Rabouille, C., et al., 2018. Modelling marine sediment biogeochemistry: current knowledge gaps, challenges, and some methodological advice for advancement. *Front. Mar. Sci.* 5, 19. <https://doi.org/10.3389/fmars.2018.00019>.
- Levins, R., 1968. *Evolution in Changing Environments: Some Theoretical Explorations*. Princeton University Press, Princeton, New Jersey.
- Liu, C., White, M., Newell, G., 2013. Selecting thresholds for the prediction of species occurrence with presence-only data. *J. Biogeogr.* 40, 778–789. <https://doi.org/10.1111/jbi.12058>.
- Liu, C., Newell, G., White, M., 2016. On the selection of thresholds for predicting species occurrence with presence-only data. *Ecol. Evol.* 6, 337–348. <https://doi.org/10.1002/ece3.1878>.
- Lucas, E., de la Cruz-Francisco, V., 2018. Macroflora y macrofauna asociada a las raíces sumergidas de *Rhizophora mangle* (Rhizophoraceae), en la laguna Tampamachoco, Veracruz, México. *Rev. Colomb. Cienc. Anim. Recia* 10, 31–42. <https://doi.org/10.21488/recia.v10.n1.2018.629>.
- Ma, B., Sun, J., 2018. Predicting the distribution of *Stipa purpurea* across the Tibetan Plateau via the MaxEnt model. *BMC Ecol.* 18, 10. <https://doi.org/10.1186/s12898-018-0165-0>.
- Marcelino, V.R., Verbruggen, H., 2015. Ecological niche models of invasive seaweeds. *J. Phycol.* 51, 606–620. <https://doi.org/10.1111/jpy.12322>.
- Marmion, M., Parviainen, M., Luoto, M., Heikkinen, R.K., Thuiller, W., 2009. Evaluation of consensus methods in predictive species distribution modelling. *Divers. Distrib.* 15, 59–69. <https://doi.org/10.1111/j.1472-4642.2008.00491.x>.
- Martin, S., Hall-Spencer, J.M., 2017. *Effects of ocean warming and acidification on rhodolith/maërl beds. Rhodolith/Maërl Beds: A Global Perspective*. Springer, pp. 55–85.
- Martínez, B., Radford, B., Thomsen, M.S., Connell, S.D., Carreño, F., Bradshaw, C.J.A., Fordham, D.A., Russell, B.D., Gurgel, C.F.D., Wernberg, T., 2018. Distribution models predict large contractions of habitat-forming seaweeds in response to ocean warming. *Divers. Distrib.* 24, 1350–1366. <https://doi.org/10.1111/ddi.12767>.
- Mateo, R.G., Felicísimo, A.M., Muñoz, J., 2011. Modelos de distribución de especies: Una revisión sintética. *Rev. Chil. Hist. Nat.* 84, 217–240. <https://doi.org/10.4067/S0716-078X2011000200008>.
- Mateo-Cid, L., Sánchez-Rodríguez, I., Rodríguez-Montecinos, E., 2014. Algas epifitas de *Sargassum sinicola* Setchell y Gardner (Fucales, Phaeophyceae), en las islas Magdalena y Margarita en Baja California Sur, México. *Rev. Investig. Mar.* 34, 31–44.
- Mazzella, L., Alberte, R.S., 1986. Light adaptation and the role of autotrophic epiphytes in primary production of the temperate seagrass, *Zostera marina* L. *J. Exp. Mar. Biol. Ecol.* 100, 165–180. [https://doi.org/10.1016/0022-0981\(86\)90161-9](https://doi.org/10.1016/0022-0981(86)90161-9).
- McNyset, K.M., 2005. Use of ecological niche modelling to predict distributions of freshwater fish species in Kansas. *Ecol. Freshw. Fish* 14, 243–255. <https://doi.org/10.1111/j.1600-0633.2005.00101.x>.
- Meggs, J.M., Munks, S.A., Corkrey, R., Richards, K., 2004. Development and evaluation of predictive habitat models to assist the conservation planning of a threatened lucanid beetle, *Hoplogonus simsoni*, in north-east Tasmania. *Biol. Conserv.* 118, 501–511. <https://doi.org/10.1016/j.biocon.2003.10.001>.
- Melo-Merino, S.M., Reyes-Bonilla, H., Lira-Noriega, A., 2020. Ecological niche models and species distribution models in marine environments: a literature review and spatial analysis of evidence. *Ecol. Modell.* 415, 108837. <https://doi.org/10.1016/j.ecolmodel.2019.108837>.
- Morris, E.P., Peralta, G., Brun, F.G., van Duren, L., Bouma, T.J., Pérez-Lloréns, J.L., 2008. Interaction between hydrodynamics and seagrass canopy structure: spatially explicit effects on ammonium uptake rates. *Limnol. Oceanogr.* 53, 1531–1539. <https://doi.org/10.4319/lo.2008.53.4.1531>.
- Murphy, J.T., Johnson, M.P., Viard, F., 2016. A modelling approach to explore the critical environmental parameters influencing the growth and establishment of the invasive seaweed *Undaria pinnatifida* in Europe. *J. Theor. Biol.* 396, 105–115. <https://doi.org/10.1016/j.jtbi.2016.01.038>.
- Ortuño-Aguirre, C., Riosmena-Rodríguez, R., 2007. Dinámica del epifitismo en *Padina concrescens* (Dictyotales: Phaeophyta) en el suroeste de la Península de Baja California. *Ciencias Mar.*, México.
- Otero-Schmitt, J., Sanjuan, A., 1992. Epibiotic seaweeds of the Cape Verde Islands. *Bot. Mar.* 35, 379–390. <https://doi.org/10.1515/botm.1992.35.5.379>.
- Pearson, G.A., Evans, L.V., 1990. Settlement and survival of *Polysiphonia lanosa* (Ceramiales) spores on *Ascophyllum nodosum* and *Fucus vesiculosus* (Fucales). *J. Phycol.* 26, 597–603. <https://doi.org/10.1111/j.0022-3646.1990.00597.x>.
- Pearson, R.G., Dawson, T.P., Liu, C., 2004. Modelling species distributions in Britain: a hierarchical integration of climate and land-cover data. *Ecography (Cop.)* 27, 285–298. <https://doi.org/10.1111/j.0906-7590.2004.03740.x>.

- Pearson, R.G., Raxworthy, C.J., Nakamura, M., Townsend Peterson, A., 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *J. Biogeogr.* 34, 102–117. <https://doi.org/10.1111/j.1365-2699.2006.01594.x>.
- Penhale, P.A., Smith Jr., W.O., 1977. Excretion of dissolved organic carbon by seagrasses (*Zostera marina*) and its epiphytes. *Limnol. Oceanogr.* 22, 400–407. <https://doi.org/10.4319/lo.1977.22.3.0400>.
- Peterson, A.T., Soberón, J., Pearson, R.G., Anderson, R.P., Martínez-Meyer, E., Nakamura, M., Araújo, M.B., 2011. *Ecological Niches and Geographic Distributions*. Princeton University Press, New Jersey, USA.
- Phillips, S.J., Dudík, M., 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography (Cop.)* 31, 161–175. <https://doi.org/10.1111/j.0906-7590.2008.5203.x>.
- Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. *Ecol. Modell.* 190, 231–259. <https://doi.org/10.1016/j.ecolmodel.2005.03.026>.
- Pujol, D., Abdolhappour, M., Lavery, P.S., McMahon, K., Oldham, C., 2019. Flow velocity and nutrient uptake in marine canopies. *Mar. Ecol. Prog. Ser.* 622, 17–30. <https://doi.org/10.3354/meps12987>.
- Quan-Young, L.I., Díaz-Martín, M.A., Espinoza-Avalos, J., 2006. Algas epifitas de Bajo Pepito, Isla Mujeres, Quintana Roo, México. *Rev. Biol. Trop.* 54, 317–328.
- R Core Team, 2019. *R: A Language and Environment for Statistical Computing*.
- Ramírez, A., Blanco, R., Okolodkov, Y., 2011. Diversidad de especies de algas epifitas marinas. In: Cruz, A. (Ed.), *La Biodiversidad En Veracruz: Estudio de Estado*. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Gobierno del Estado de Veracruz, Universidad Veracruzana, Instituto de Ecología, México, pp. 71–76.
- Reiss, H., Birchenough, S., Borja, A., Buhl-Mortensen, L., Craeymeersch, J., Dannheim, J., Darr, A., Galparsoro, I., Gogina, M., Neumann, H., Populus, J., Rengstorf, A.M., Valle, M., van Hoey, G., Zettler, M.L., Degraer, S., 2014. Benthos distribution modelling and its relevance for marine ecosystem management. *ICES J. Mar. Sci.* 72, 297–315. <https://doi.org/10.1093/icesjms/fsu107>.
- Richmond, C.E., Breitburg, D.L., Rose, K.A., 2005. The role of environmental generalist species in ecosystem function. *Ecol. Modell.* 188, 279–295. <https://doi.org/10.1016/j.ecolmodel.2005.03.002>.
- Robinson, L.M., Elith, J., Hobday, A.J., Pearson, R.G., Kendall, B.E., Possingham, H.P., Richardson, A.J., 2011. Pushing the limits in marine species distribution modelling: lessons from the land present challenges and opportunities. *Glob. Ecol. Biogeogr.* 20, 789–802. <https://doi.org/10.1111/j.1466-8238.2010.00636.x>.
- Robinson, N.M., Nelson, W.A., Costello, M.J., Sutherland, J.E., Lundquist, C.J., 2017. A systematic review of marine-based species distribution models (SDMs) with recommendations for best practice. *Front. Mar. Sci.*
- Roloff, G.J., Haufler, J.B., 2002. Modeling habitat-based viability from organism to population. In: Scott, J.M., Heglund, P.J., Morrison, M.L., Haufler, J.B., Raphael, M. G., Wall, W.A., Samson, F.B. (Eds.), *Predicting Species Occurrences: Issues of Accuracy and Scale*. Island Press, Washington, DC, USA, pp. 673–685.
- Sbrocco, E.J., Barber, P.H., 2013. MARSPEC: ocean climate layers for marine spatial ecology. *ecological Archives E094-086*. *Ecology* 94, 979. <https://doi.org/10.1890/12-1358.1>.
- Schoener, T.W., 1968. The anolis lizards of Bimini: resource partitioning in a complex fauna. *Ecology* 49, 704–726. <https://doi.org/10.2307/1935534>.
- Scrosati, R.A., 2017. Community-level facilitation by macroalgal foundation species peaks at an intermediate level of environmental stress. *Algae* 32, 41–46. <https://doi.org/10.4490/algae.2017.32.2.20>.
- Seoane, J., Bustamante, J., 2001. Modelos predictivos de la distribución de especies: una revisión de sus limitaciones. *Ecología* 15, 21.
- Shmida, A., Wilson, M.V., 1985. Biological determinants of species diversity. *J. Biogeogr.* 12, 1–20. <https://doi.org/10.2307/2845026>.
- Soberón, J., 2019. A grinnellian niche perspective on species-area relationships. *Am. Nat.* 194, 760–775. <https://doi.org/10.1086/705898>.
- Soberón, J., Townsend, A., 2005. Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodivers. Informatics* 2, 1–10. <https://doi.org/10.17161/bi.v2i0.4>.
- Stachowicz, J.J., 2001. Mutualism, Facilitation, and the Structure of Ecological Communities: positive interactions play a critical, but underappreciated, role in ecological communities by reducing physical or biotic stresses in existing habitats and by creating new habitats on. *Bioscience* 51, 235–246. [https://doi.org/10.1641/0006-3568\(2001\)051\[0235:MFATSO\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0235:MFATSO]2.0.CO;2).
- Steneck, R.S., 1986. The ecology of coralline algal crusts: Convergent Patterns and Adaptive Strategies. *Annu. Rev. Ecol. Syst.* 17, 273–303. <https://doi.org/10.1146/annurev.es.17.110186.001421>.
- Suárez, A.M., 1989. Ecología del macrofitobentos de la plataforma de Cuba. *Rev. Investig. Mar.* 10, 187–203.
- Suárez, A.M., Gil, L., Poseck, R., 1989. Variación del epifitismo en *Styopodium zonale* (Lamouroux) Papenfuss a lo largo de un año. *Rev. Investig. Mar.* 10, 3–20.
- Suárez, A.M., Martínez-Daranas, B., Alfonso, Y., 2015. *Macroalgas marinas de Cuba*. Editorial UH, La Habana, Cuba.
- Tax, D.M.J., Duin, R.P.W., 2004. Support vector data description. *Mach. Learn.* 54, 45–66. <https://doi.org/10.1023/B:MACH.000008084.60811.49>.
- Taylor, R.B., 2019. In: Fath, B.B.T.-E. of E (Ed.), *Epiflora and Epifauna*, second ed. Elsevier, Oxford, pp. 375–380. <https://doi.org/10.1016/B978-0-12-409548-9.10922-4>.
- Thomsen, M.S., Altieri, A.H., Angelini, C., Bishop, M.J., Gribben, P.E., Lear, G., He, Q., Schiel, D.R., Silliman, B.R., South, P.M., Watson, D.M., Wernberg, T., Zotz, G., 2018. Secondary foundation species enhance biodiversity. *Nat. Ecol. Evol.* 2, 634–639. <https://doi.org/10.1038/s41559-018-0487-5>.
- Thuiller, W., Brotons, L., Araújo, M.B., Lavorel, S., 2004. Effects of restricting environmental range of data to project current and future species distributions. *Ecography (Cop.)* 27, 165–172. <https://doi.org/10.1111/j.0906-7590.2004.03673.x>.
- Tognelli, M.F., Roig-Junent, S.A., Marvaldi, A.E., Flores, G.E., Lobo, J.M., 2009. An evaluation of methods for modelling distribution of Patagonian insects. *Rev. Chil. Hist. Nat.* 82, 347–360.
- Trotta-Moreu, N., Lobo, J.M., 2010. Deriving the species richness distribution of Geotrupinae (Coleoptera: scarabaeoidea) in Mexico from the overlap of individual model predictions. *Environ. Entomol.* 39, 42–49. <https://doi.org/10.1603/EN08179>.
- Tyberghein, L., Verbruggen, H., Pauly, K., Troupin, C., Mineur, F., De Clerck, O., 2012. Bio-ORACLE: a global environmental dataset for marine species distribution modelling. *Glob. Ecol. Biogeogr.* 21, 272–281. <https://doi.org/10.1111/j.1466-8238.2011.00656.x>.
- Valderrama, S.P., Ávila, A.H., Méndez, J.G., Martínez, O.M., Rojas, D.C., Azcona, H.F., Hernández, E.M., Aragón, H.C., Alcolado, P.M., Amargós, F.P., 2018. Marine protected areas in Cuba. *Bull. Mar. Sci.* 94, 423–442.
- Van der Vaart, A.W., 1998. *Asymptotic Statistics*. Cambridge University Press, Cambridge, UK.
- Vásquez-Elizondo, R.M., Enríquez, S., 2017. Light absorption in coralline algae (Rhodophyta): a morphological and functional approach to understanding species distribution in a coral reef lagoon. *Front. Mar. Sci.* 4, 297. <https://doi.org/10.3389/fmars.2017.00297>.
- Veazey, L., Williams, O., Wade, R., Toonen, R., Spalding, H.L., 2019. Present-day distribution and potential spread of the invasive green alga *Avrainvillea amadelpha* around the main Hawaiian Islands. *Front. Mar. Sci.*
- Verbruggen, H., Tyberghein, L., Pauly, K., Vlaeminck, C., Van Nieuwenhuyse, K., Kooistra, W.H.C.F., Leliaert, F., De Clerck, O., 2009. Macroecology meets macroevolution: evolutionary niche dynamics in the seaweed *Halimeda*. *Glob. Ecol. Biogeogr.* 18, 393–405. <https://doi.org/10.1111/j.1466-8238.2009.00463.x>.
- Warren, D.L., Glor, R.E., Turelli, M., 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution (N. Y.)* 62, 2868–2883. <https://doi.org/10.1111/j.1558-5646.2008.00482.x>.
- Warren, D.L., Glor, R.E., Turelli, M., 2010. ENMTools: a toolbox for comparative studies of environmental niche models. *Ecography (Cop.)* 33, 607–611. <https://doi.org/10.1111/j.1600-0587.2009.06142.x>.
- Wei, T., Simko, V., 2017. R Package “corrplot”: Visualization of a Correlation Matrix.
- Westmeijer, G., Everaert, G., Pirllet, H., De Clerck, O., Vandegheuchte, M.B., 2019. Mechanistic niche modelling to identify favorable growth sites of temperate macroalgae. *Algal Res.* 41, 101529. <https://doi.org/10.1016/j.algal.2019.101529>.
- Wiley, E.O., McNyset, K.M., Peterson, A.T., Robins, C.R., Stewart, A.M., 2003. Niche modeling perspective on geographic range predictions in the marine environment using a machine-learning algorithm. *Oceanography* 16, 120–127.
- Yesson, C., Bush, L.E., Davies, A.J., Maggs, C.A., Brodie, J., 2015. The distribution and environmental requirements of large brown seaweeds in the British Isles. *Mar. Biol. Assoc. United Kingdom. J. Mar. Biol. Assoc. United Kingdom* 95, 669–680. <https://doi.org/10.1017/S0025315414001453>.
- Zheng, X., Huang, L., Lin, R., Du, J., 2015. Roles of epiphytes associated with macroalgae in benthic food web of a eutrophic coastal lagoon. *Cont. Shelf Res.* 110. <https://doi.org/10.1016/j.csr.2015.10.013>.
- Zotz, G., Schultz, S., 2008. The vascular epiphytes of a lowland forest in Panama—species composition and spatial structure. *Plant Ecol.* 195, 131–141. <https://doi.org/10.1007/s11258-007-9310-0>.