Where is the genus *Elysia* in the western Atlantic? Potential distribution, species richness and representation in marine protected areas

Lina Marcela Jiménez[1,2,3], Nuno Simões[4,5,6] and Carlos Yáñez-Arenas [ID][2,4]

[1]*Posgrado de Ciencias Biológicas, Facultad de Ciencias, Universidad Nacional Autónoma de México, Ciudad Universitaria, Delegación Coyoacán, Ciudad de México 04510, Mexico;*
[2]*Laboratorio de Ecología Geográfica, Unidad de Biología de la Conservación, Unidad de Ciencia y Tecnología de Yucatán, Facultad de Ciencias, Universidad Nacional Autónoma de México, Carretera Sierra Papacal Chuburná Puerto Km 5, Sierra Papacal 11800, Yucatán, Mexico;*
[3]*Facultad de Ingenierías, Universidad de San Buenaventura sede Medellín, Carrera 56C Nro. 51–90, Medellín 050010, Colombia;*
[4]*Unidad Multidisciplinaria de Docencia e Investigación Sisal, Facultad de Ciencias, Universidad Nacional Autónoma de México, Puerto de Abrigo, Sisal 97356, Yucatán, Mexico;*
[5]*Laboratorio Nacional de Resiliencia Costera (LANRESC), Puerto de Abrigo, Sisal 97356, Yucatán, Mexico; and*
[6]*International Chair for Coastal and Marine Studies, Harte Research Institute for Gulf of Mexico Studies, Texas A&M University—Corpus Christi, Corpus Christi, TX 78412, USA*

Correspondence: C. Yáñez-Arenas; e-mail: lichoso@gmail.com

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ABSTRACT

The western Atlantic Ocean is one of the areas with the largest species richness of sea slugs in the genus *Elysia* (30 out of the 101 species described have been reported in this region). Nevertheless, the lack of knowledge on many of these species hinders efforts to estimate regional richness and identify the factors affecting their distribution. We used the maximum entropy algorithm Maxent to develop ecological niche models for 14 species of *Elysia* in the western Atlantic Ocean. These models were meant to show the potential distribution of the genus and identify locations with the highest richness. Input data used to build niche models were presence records (obtained from several sources) and bioclimatic and geophysical variables from the Bio-ORACLE and MARSPEC platforms. Species with less than seven records were considered for the calculation of richness, but not for modelling. Results show low habitat suitability for the species modelled here at the mouth of rivers and in hypoxic zones and low-temperature areas. The two variables that best explained species distribution patterns were the distance to shore and the maximum monthly temperature. From the total area with adequate environmental conditions for the genus, only 20.3% is located within marine areas under some protection category.

INTRODUCTION

Elysia Risso, 1818 is a sea slug genus in the order Sacoglossa. Currently, 101 species in this genus have been described (MolluscaBase, 2020), with 30 of them distributed throughout the western Atlantic Ocean (Muniain & Ortea, 1997; Krug, Vendetti & Valdés, 2016). *Elysia* species are herbivores and are ecologically significant because they play an important role in trophic networks and have been observed to control invading algae populations (Coquillard *et al.*, 2000; Thibaut *et al.*, 2001). Some of these species exhibit poecilogony (i.e. presence of two different larval morphotypes), a phenomenon that has only been reported in 12 marine invertebrates (3 of them in the genus *Elysia*). Therefore, these organisms are used as a model for larval development (Vendetti, Trowbridge & Krug, 2012; Krug *et al.*, 2015). *Elysia* species are also relevant for the pharmaceutical industry (Fontana *et al.*, 2001; Suárez *et al.*, 2003) and have been widely studied because they exhibit kleptoplasty. Kleptoplasty is the ability to absorb chloroplasts from algae and keep these organelles

active in the new host's digestive cells, thus making it possible for sea slugs to photosynthesize and survive periods of food scarcity (Christa *et al.*, 2014). This is a unique example of functional photosynthesis in metazoans (Melo-Clavijo *et al.*, 2018).

In the western Atlantic Ocean, research on this genus has focused mainly on taxonomy and isolated faunistic inventories (Ardila, Báez & Valdés, 2007; Zamora-Silva & Naranjo-García, 2008; Ortea *et al.*, 2012; Zamora-Silva & Ortigosa, 2012; Camacho-García *et al.*, 2014; Caballer-Gutierrez *et al.*, 2015; Galvão-Filho *et al.*, 2015; Goodheart *et al.*, 2016), field guides (Valdés *et al.*, 2006; García, Domínguez & Troncoso, 2008) and new distributional records (Padula *et al.*, 2012; Malaquias, 2014; Ferreira *et al.*, 2015; Ortigosa, Lemus-Santana & Simões, 2015). So far, the most in-depth work is a phylogenetic study of *Elysia* species from the Caribbean (Krug *et al.*, 2016). However, not much is known about the ecology of this genus aside from descriptions of its habitat and diet (Jensen & Clark, 1983; Clark, 1994; Krug *et al.*, 2016), and a study by

Sanvicente-Añorve *et al.* (2012) on the influence of habitat type and food availability on the distribution of sea slugs in the Arrecife Alacranes National Park in Mexico, including five *Elysia* species. Regarding geographic patterns of species richness, large-scale data on oceanographic regions (e.g. the Caribbean) are available in biogeographical studies (García, Domínguez & Troncoso, 2007; Jensen, 2007; García & Bertsch, 2009; Camacho-García *et al.*, 2014). However, not much is known about the environmental factors that limit the distribution of individual *Elysia* species, and this is true of both fine-scale geographical patterns of taxonomic diversity and the conservation role of marine protected areas (MPAs).

MPAs are a key management tool employed worldwide to conserve biodiversity (Watson *et al.*, 2014). Although these areas reflect the biotic diversity of the marine ecosystems, the scarcity of biological and ecological information for many taxa has adversely affected conservation planning and management (Cardoso *et al.*, 2011). For instance, some species for which data are lacking or scarce, such as the sea slugs of the genus *Elysia*, have unique biological processes (e.g. kleptoplasty and poecilogony) that are important for maintaining the functioning of ecosystems. Detailed knowledge of a species geographical distribution is one of the most important components in conservation planning. However, obtaining this kind of data for species of the genus *Elysia* exclusively through fieldwork is time-consuming and expensive due to the complexity of marine environments and the cryptic appearance of these organisms. Nonetheless, different modelling techniques are currently used to fill geographical gaps in species distributions (Elith *et al.*, 2006). Ecological niche modelling is one of the most reliable and practical approaches to achieve this, since it can use quite basic information about species. In this approach, the ecological niche of a target species is estimated by statistically associating presence records with environmental conditions. The modelled niche is then projected onto geographical space to predict areas of potential distribution (Peterson *et al.*, 2011). This approach has not been used before to model the niche of species of the order Sacoglossa or to predict the potential distribution of highly host-specialized animals.

In this work, we modelled the ecological niches of *Elysia* species in the western Atlantic Ocean to provide basic information on their ecology and distributional patterns. Niche models were used to estimate the potential distribution and the most important environmental variables for each species. In addition, we estimated the potential taxonomic richness, and evaluated the representativity of richness in the protected marine areas of this region.

MATERIAL AND METHODS

Biological data

In our analysis, we included all *Elysia* species reported by Krug *et al.* (2016) and Muniain & Ortea (1997) for which precise locality records (i.e. with geographical coordinates) are available. We obtained other occurrence records from a range of different sources. These were the Ocean Biogeographic Information System (http://iobis.org), Global Biodiversity Information Facility (https://www.gbif.org/), Naturalista (https://www.naturalista.mx/), National Mollusc Collection of UNAM (CNMO), Mollusc Collection of the Marine Biodiversity Group of Yucatan (BDMY), Smithsonian National Museum of Natural History (https://collections.nmnh.si.edu/search/iz/), Florida Museum of Natural History (http://specifyportal.flmnh.ufl.edu/iz/), Academy of Natural Sciences (http://clade.ansp.org/malacology/collections/), Colombia's Marine and Coastal Research Institute (INVEMAR, http://siam.invemar.org.co/) and scientific literature. We cleaned databases using the taxonomic information presented by Krug *et al.* (2016), and removed duplicate records as well as those with georeferencing errors (e.g. occurrences in the continent or outside the known accessible geographic area of a species). Species

with less than seven presence records were not considered for modelling to avoid mischaracterization of their environmental requirements, but such taxa were included in the estimation of the taxonomic richness. Although previous studies have reported that the minimum number of occurrences needed to build acceptable distribution/niche models might be less than seven (e.g. Loiselle *et al.*, 2003: four; Anderson & Martínez-Meyer, 2004: seven; Pearson *et al.*, 2007: five; van Proosdij *et al.*, 2015: three), this strongly depends on the environmental representativeness of the data. Here, we defined our minimum number of records for modelling through a series of pilot experiments in which overprediction was visually assessed along with the evaluation metrics described below.

Furthermore, since presence records of *Elysia crispata* were clearly clustered in more intensively sampled areas, a thinning procedure was performed using the 'spatially rarefied occurrence data tool' in SDMtoolbox 2.0 (Brown, Bennett & French, 2017) at 10, 20 and 65 km of the buffer. We measured spatial autocorrelation of the four databases, obtained after thinning, using Moran's I statistic in ArcGIS 10.2 (ESRI, 2013). Of the four databases, we selected the one that had the highest number of occurrences but in which spatial autocorrelation was eliminated. This procedure was not applied to the other species since they have a low number of presence records.

Accessible area determination

The hypothetical area of historic accessibility (*M*; *sensu* Soberón & Peterson, 2005) was determined for each species through the superposition of their occurrences with the marine provinces (Spalding *et al.*, 2007). In addition, we expanded *M* based on information of the marine currents (Piola & Matano, 2001; Richardson, 2001; Stramma, 2001). Given that these species belong to the same genus and have similar physical characteristics (i.e. their dispersal capacity is affected by the same physical barriers), the same value of *M* was used for most of them. Since the presence records of *E. chlorotica* encompass a smaller area than those for the other species, a different value of *M* was used for this species. Thus, the southern limits of *E. chlorotica* were placed in the Carolinian ecoregion (Central Florida) under the assumption that the directionality of the Gulf Stream (south–north) is a potential dispersal barrier for this species (Supplementary Material Fig. S1).

Environmental predictors

We downloaded benthic environmental variables from Bio-ORACLE (Tyberghein *et al.*, 2012) and geophysical variables from MARSPEC (Sbrocco & Barber, 2013). Variables were obtained in an ASCII raster format with a 5-arcmin resolution (*c.* 9.2 km^2) and were cropped using *M* as a mask. In this reduction, only the areas available for each species were included. For availability, we considered dispersal capacity and physical barriers. We ensured that the model did not include other areas that had favourable environmental conditions but could not be accessed by these species (Soberón & Peterson, 2005). To prevent overfitting caused by the use of many bioclimatic layers in the models (Peterson & Nakazawa, 2008), a Pearson correlation analysis was carried out on four sets of variables: (1) Bio-ORACLE variables (set 1); (2) MARSPEC variables (set 2); (3) Bio-ORACLE plus MARSPEC variables (set 3); and (4) Bio-Oracle plus two MARSPEC variables (bathymetry and coast distance) (set 4). Only one of the highly correlated pair of variables ($r \geq 0.8$) was kept for each set (the most meaningful in terms of biology). We used the 'remove highly correlated variables' tool from SDMtoolbox (Brown *et al.*, 2017) in ArcGIS for this analysis. The predictor set used to make the final model for each species was chosen by applying an evaluation procedure that is described in the following section. We compared evaluation metrics obtained from this procedure for each predictor set using a Kruskal–Wallis test. We then used a Wilcoxon rank-sum test to asses for differences between pairs of sets.

Potential distribution modelling

We used Maxent v. 3.4 (Phillips *et al.*, 2017) to estimate environmental suitability and potential distribution of species. This algorithm was chosen because it is one of the most precise modelling methods using only presence records, it is less affected by location errors, and its performance is better than other approaches when fewer data are available (Elith *et al.*, 2006; Pearson *et al.*, 2007; Graham *et al.*, 2008; Wisz *et al.*, 2008). The ENMeval package v. 0.3.0 (Muscarella *et al.*, 2014) in R (R Development Core Team, 2017) was used to identify the optimal configuration (balancing complexity and generalization) of Maxent parameters for each species. ENMeval provides an automated method for running Maxent models with different user-specified setting combinations ('regularization multiplier' and 'features'). We tested 48 model candidates per species by using all combinations of feature types (L, LQ, LQH, LQHP and LQHPT) and regularization multipliers from 0.5 to 4. Evaluation records were obtained through a 'block' partition (Shcheglovitova & Anderson, 2013) for species with more than 20 presence records and the '$n − 1$ jackknife' procedure (Pearson *et al.*, 2007) for species with less than 20 records. Among candidate models, we prioritized the combination of parameters that would generate predictions with a lower omission rate (OR; the percentage of test records that are not included in a binary prediction of the model using a specified threshold). Second, we used the area under the curve (AUC) of the receiver operating characteristic curve, since this metric takes into account the capacity of models to discriminate unsuitable areas. Third, we employed the delta Akaike's criterion corrected for sample size (ΔAIC_c) to select models with lower complexity (Muscarella *et al.*, 2014). Once the best features and regularization multipliers were defined, we ran models in Maxent with a 'logistic' output format, its bootstrap functionality (five replicates) and 10,000 background points randomly selected within the area *M*. Likewise, we selected the jackknife analysis and the response curve options to measure and visualize the individual contribution of each predictor to the model. Continuous models of environmental suitability generated with Maxent were transformed into binary maps of potential distribution using a threshold acceptable OR of 5% (Peterson, Papeş & Soberón, 2008; Cooper & Soberón, 2018). This threshold prevents the inclusion of presence records from sink populations, taxonomic misidentifications and other errors that were not identified during the database cleansing phase.

Richness maps

The construction of potential distribution models for species with less than seven records was done by classifying pixels of each environmental predictor as follows: ecoregions coinciding with presence records were selected and environmental layers were cropped with reference to this area. For the species with a single record, a value of 1 was assigned to every pixel that coincided with the value of each predictor in that record and a value of 0 was assigned to each of all the other pixels. For species with two to six records, the value range for each predictor was determined, assigning a value of 1 to each pixel within the range and 0 to each of all the other pixels. Then, we summed the reclassified predictors and assigned a value of 1 to the pixels that had values of 1 for more than five predictors (in terms of overprediction, this value was different for each species). Finally, taxonomic richness was estimated by 'stacking' all the binary models (the ones generated from Maxent as well as those described in this section). The term richness in this study refers to the number of species in a given space (Magurran, 2004). All GIS analysis and processing were done using ArcGIS. In Figure 1, we show the procedure used to obtain the binary models.

Representativity of the genus Elysia in MPAs

We superposed the richness and MPA maps to calculate the number of pixels contained in these areas for each richness category.

The MPA shapefile was downloaded from the database of the World Commission on Protected Areas (UNEP-WCMC & IUCN, 2019), which lists a total of 2,225 MPAs for our study area. Considering that some MPAs overlap because areas with different IUCN categories exist within the same zone, some of them were merged to avoid duplication, obtaining a total of 1,573 MPAs within our study area. The 'zonal statistics as table' tool in the SDMtoolbox was used in ArcGIS to determine richness statistics for the MPAs.

RESULTS

Potential distribution

In this study, we obtained 314 presence records for the genus *Elysia*. These represent 21 of the 30 species that have been reported from the western Atlantic Ocean. Niche models were built for the 14 species with seven or more presence records each (Table 1). The final model for *Elysia crispata* was constructed by applying a 20-km buffer around presence records since Moran's *I* coefficient indicated that there was no spatial autocorrelation ($I = 0.08$, $P > 0.05$) within this dataset (Supplementary Material Table S2).

With regard to the predictors, the Kruskal–Wallis test did not show meaningful differences for the OR ($H = 3.44$, df $= 3$, $P = 0.33$) and the AIC_c ($H = 0.45$, df $= 3$, $P = 0.92$) of the evaluated sets, but there were differences in the AUC ($H = 10.02$, df $= 3$, $P = 0.02$). In the Wilcoxon rank-sum test for AUC values, the only meaningful differences found were between sets 1 and 2 ($P = 0.04$) and between sets 1 and 4 ($P = 0.02$). Set 1 was discarded for not having a good AUC performance. Even if sets 2, 3 and 4 did not show meaningful differences for this parameter, set 4 was selected because it had AUC values greater than 0.93. Out of the 74 environmental variables represented in this set, 21 were selected for the modelling phase (Table 2) once collinearity was assessed (Supplementary Material Table S3). All the evaluated models had a good performance, with AUC vales being greater than 0.9. The predictive capacity was good in general, with ORs of less than 10%, except for *E. subornata*. For half of the species, the least complex models ($\Delta AIC_c = 0$) were also the ones with higher performance (i.e. higher AUC and lower OR). In the remaining species, models with a higher AUC and a lower OR did not have the lowest ΔAIC_c, or it was not possible to calculate ΔAIC_c because there were not enough occurrences (Table 1).

Most of the modelled species presented a potential distribution restricted to the Gulf of Mexico, the Caribbean and Brazil; the only exception was *E. chlorotica* that has a potential distribution in the region between North Carolina (USA) and Newfoundland and Labrador (Canada). According to the models, nearly all the species studied has a potential distribution that extended across the following provinces: Warm Temperate Northwest Atlantic, Tropical Northwestern Atlantic, Tropical Southwestern Atlantic and part of the Warm Temperate Southwestern Atlantic. The exception was *E. chlorotica*, which has a potential distribution in the Cold Temperate Northwest Atlantic and part of the Arctic region. Coastal zones consistently showed a greater suitability for all species. Yet, in general, the mouth of the Amazon River and the northern part of the Gulf of Mexico (specifically, the coastal zone of the states of Texas, Louisiana and Mississippi) represent zones of low environmental suitability for most species, apart from *E. cornigera*, *E. patina*, *E. velutinus* and *E. zuleicae*, which do occur in the northern part of the Gulf of Mexico. The potential distribution map of *E. crispata* was selected as an example (Fig. 2) and the models for the other species are presented in Supplementary Material Figures S4–S16.

According to the jackknife analysis, the environmental predictor that contributed most to the niche models was the distance to shore (13 out of 14 species). Environmental suitability of all species increased as distance to shore decreased. The maximum monthly temperature was the second variable that contributed most to
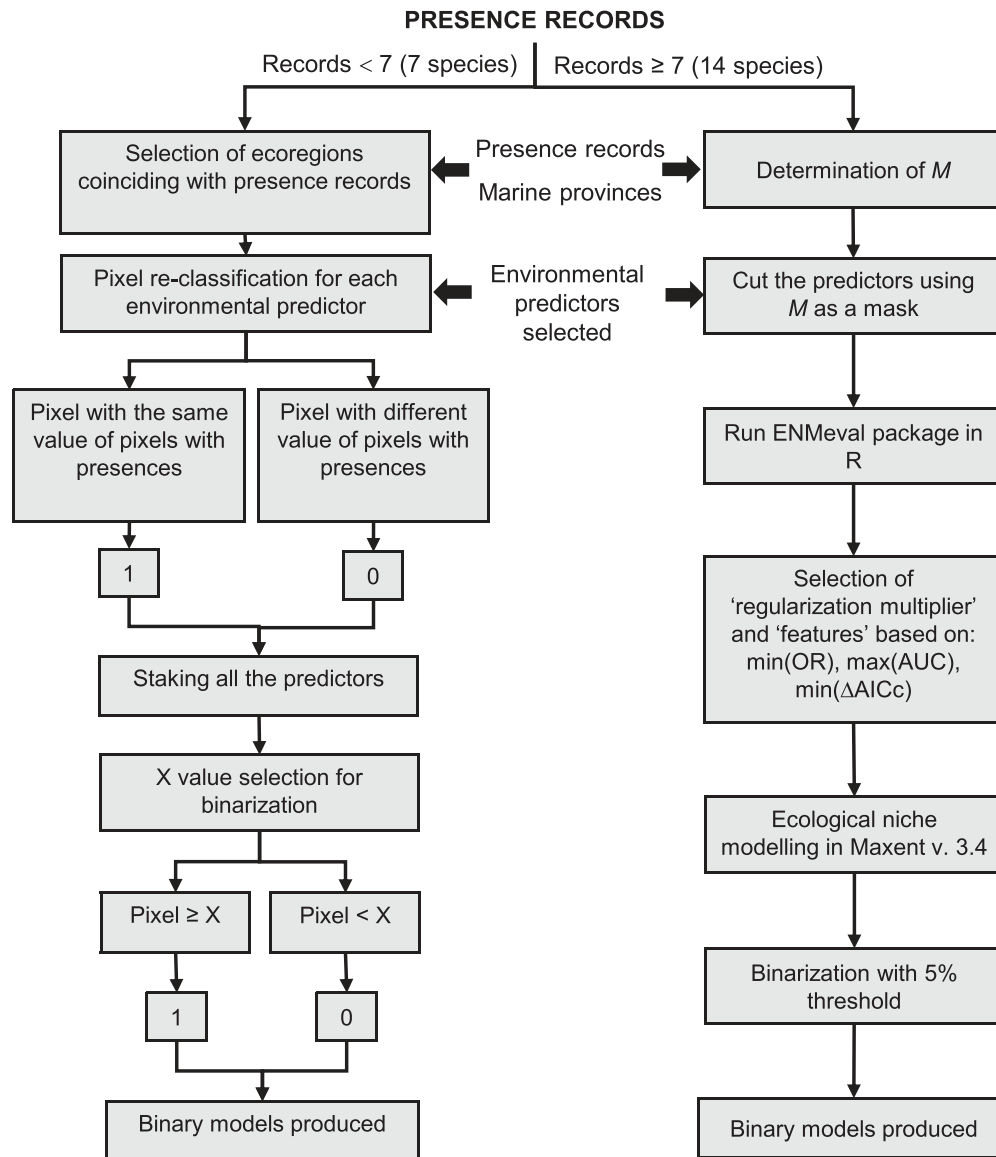
PRESENCE RECORDS

Figure 1. Tests and procedures carried out to obtain binary models. Arrows indicate the stepwise procedure. *X* value selection for binarization is the pixel value under which zones with obvious overprediction were selected.

the models of six species and was the most important variable for *E. canguzua* (Fig. 3). Other variables that had an important contribution in some models were minimum light at bottom (*E. canguzua*), range of phosphate (*E. cornigera*) and range of dissolved oxygen (*E. chlorotica*). Response curves are shown in Supplementary Material Figures S17–S19.

Taxonomic richness

The highest potential richness values were obtained for the Bahamas (between 14 and 17 species), followed by several coastal zones in the southern Gulf of Mexico, Caribbean and Brazil (between Ceara and Belmonte) with richness values between 10 and 13 species. Zones with low potential richness (one species) occurred between Canada and Virginia Beach, Trinidad and Tobago and the Amazon delta, and from Palmares do Sul to the extreme south of South America. The zones with richness equal to zero were the

deltas of the Mississippi, Amazon and La Plata Rivers and, more generally, areas away from the coast (Fig. 4).

Representativity of Elysia in MPAs

From the total area with environmental conditions adequate for at least one species of the genus, 20.3% is included within marine areas under some sort of protection. Two national parks located in the Bahamas (Graham's Harbour and Westside) include 26.5% of the total area of maximum richness modelled. On the other hand, although the largest MPAs are located in the region between Florida and Canada, only one species in the genus (*E. chlorotica*) is represented in them. Although the coastal zones between Cameron County (Texas, USA) and Ciudad del Carmen (Mexico) and between Nicaragua and Colombia show high values of potential richness, MPAs in these regions are scarce and are less extensive than others (Fig. 4).

Table 1. Summary of ecological niche modelling inputs and evaluations.

Species	TO	FO	OR	AUC	ΔAIC$_c$	F	RM
Elysia buonoi Krug, Vendetti & Valdés, 2016	2	2	–	–	–	–	–
E. canguzua Er. Marcus, 1955	16	9	0.06	0.92	NA	L	1.5
E. chlorotica Gould, 1870	48	17	0.01	0.92	8.07	L	3.5
E. christinae Krug, Vendetti & Valdés, 2016	1	1	–	–	–	–	–
E. cornigera Nuttall, 1989	19	14	0.02	0.95	NA	H	4
E. crispata Mörch, 1863	262	57	0.04	0.97	0.00	LQ	2
E. ellenae Ortea, Espinosa & Caballer, 2013	9	6	–	–	–	–	–
E. evelinae Er. Marcus, 1957	16	14	0.02	0.99	0.00	L	3
E. flava Verrill, 1901	5	4	–	–	–	–	–
E. marcusi (Ev. Marcus, 1972)	17	12	0.03	0.94	50.05	LQH	4
E. ornata (Swainson, 1840)	34	21	0.00	0.95	17.20	L	1.5
E. papillosa A. E. Verrill, 1901	19	18	0.01	0.95	0.00	L	2.5
E. patagonica Munian & Ortea, 1997	2	2	–	–	–	–	–
E. patina Ev. Marcus, 1980	16	16	0.01	0.98	395.51	LQHP	4
E. pawliki Krug, Vendetti & Valdés, 2016	2	2	–	–	–	–	–
E. pratensis Ortea & Espinosa, 1996	19	16	0.07	0.98	0.00	L	4
E. serca Er. Marcus, 1955	5	5	-	–	–	–	–
E. subornata A. E. Verrill, 1901	34	26	0.17	0.98	40.81	LQ	1.5
E. taino Krug, Vendetti & Valdés, 2016	11	7	0.06	0.95	0.00	L	4
E. velutinus Pruvot-Fol, 1947	63	42	0.02	0.97	0.00	L	4
E. zuleicae Ortea & Espinosa, 2002	27	23	0.00	0.95	0.00	L	3.5

Only species with data for all columns were modelled. Abbreviations: TO, total occurrences; F, features; FO, filtered occurrences; OR, omission rates; AUC, area under the curve; ΔAIC$_c$, delta Akaike corrected by sample size; RM, regularization multiplier; L, linear; Q, quadratic; P, product; H, hinge; NA, scenarios where the number of parameters is greater than the number of records.

Table 2. Environmental variables used to model ecological niches.

Layer	Units	Source	Abbreviation
Maximum chlorophyll	mg/m^3	Bio-ORACLE	MaxCh
Minimum chlorophyll	mg/m^3	Bio-ORACLE	MinCh
Distance to shore	km	MARSPEC	DShore
Range of phosphate	μmol/m^3	Bio-ORACLE	RangeP
Minimum iron	μmol/m^3	Bio-ORACLE	MinFe
Range of iron	μmol/m^3	Bio-ORACLE	Fe.R
Maximum light at bottom	E/m^2/year	Bio-ORACLE	MaxLB
Minimum light at bottom	E/m^2/year	Bio-ORACLE	MinLB
Range of nitrate	μmol/m^3	Bio-ORACLE	RangeN
Minimum dissolved molecular oxygen	μmol/m^3	Bio-ORACLE	MinDO
Range of dissolved molecular oxygen	μmol/m^3	Bio-ORACLE	RangeDO
Minimum primary productivity	g/m^3/day	Bio-ORACLE	MinPP
Depth of the seafloor	m	MARSPEC	Depth
Maximum salinity	PSS	Bio-ORACLE	MaxSal
Minimum salinity	PSS	Bio-ORACLE	MinSal
Minimum silicate	mol/m^3	Bio-ORACLE	MinSil
Range of silicate	mol/m^3	Bio-ORACLE	RangeSil
Maximum temperature	°C	Bio-ORACLE	MaxTem
Maximum current velocity	m/s	Bio-ORACLE	MaxVel
Minimum current velocity	m/s	Bio-ORACLE	MinVel
Range of current velocity	m/s	Bio-ORACLE	RangeVel

DISCUSSION

This is the first study to model the potential distribution of species in the order Sacoglossa, as well as the first to estimate the potential taxonomic richness of the genus *Elysia* and its representation in MPAs in the western Atlantic Ocean. Only the ecological niche of other heterobranch sea slug, *Bulla occidentalis*, has been modelled prior to the present study (Saupe *et al.*, 2014a,b). Most of the species we studied in the niche models were based on a small number of presence records. However, the implementation of a protocol (through ENMeval) for the selection of the best predictors and parameters in Maxent allowed us to construct reliable models, with a good compromise being reached between performance, predictive capacity and complexity. The parameters that generated the best metrics were different from those established by default in Maxent and varied between species. Our results agree with other research showing that the use of specific settings for individual species increases the robustness of models (Shcheglovitova & Anderson, 2013; Radosavljevic & Anderson, 2014); when presence records are not plentiful, defining fewer parameters than the default set used by Maxent usually results in more generalized models (Anderson & Gonzalez, 2011; Warren & Seifert, 2011; Warren *et al.*, 2014). Despite the good performance of the models, our results must be interpreted with care, with due consideration being given to the possibility that any species misidentification could obscure the conclusions; this issue may be particularly problematic for cryptic species.

The distributional ranges of species at higher latitudes (*E. chlorotica* and *E. patagonica*) were smaller than tropical species, and this agrees with the findings of studies on other marine organisms (Macpherson, 2003; Magris & Déstro, 2010). *Elysia* species from tropical regions occur in the same geographical area, with small variations; this could be explained by phylogenetic niche conservatism, that is the tendency for species to preserve ancestral niche traits (Peterson, Soberón & Sánchez-Cordero, 1999). Furthermore, the potential distributions of *Elysia* species were much wider than their known distributions. The most likely explanation for this is that our models lack detailed information on dispersal processes, microhabitat conditions and biotic interactions. With regard to biotic interactions, since *Elysia* species are host specialized (Jensen, 1993), the presence of the algae could be a limiting factor in their distribution. However, data are lacking on the geographical variation in abundance of algal species associated with *Elysia* species.
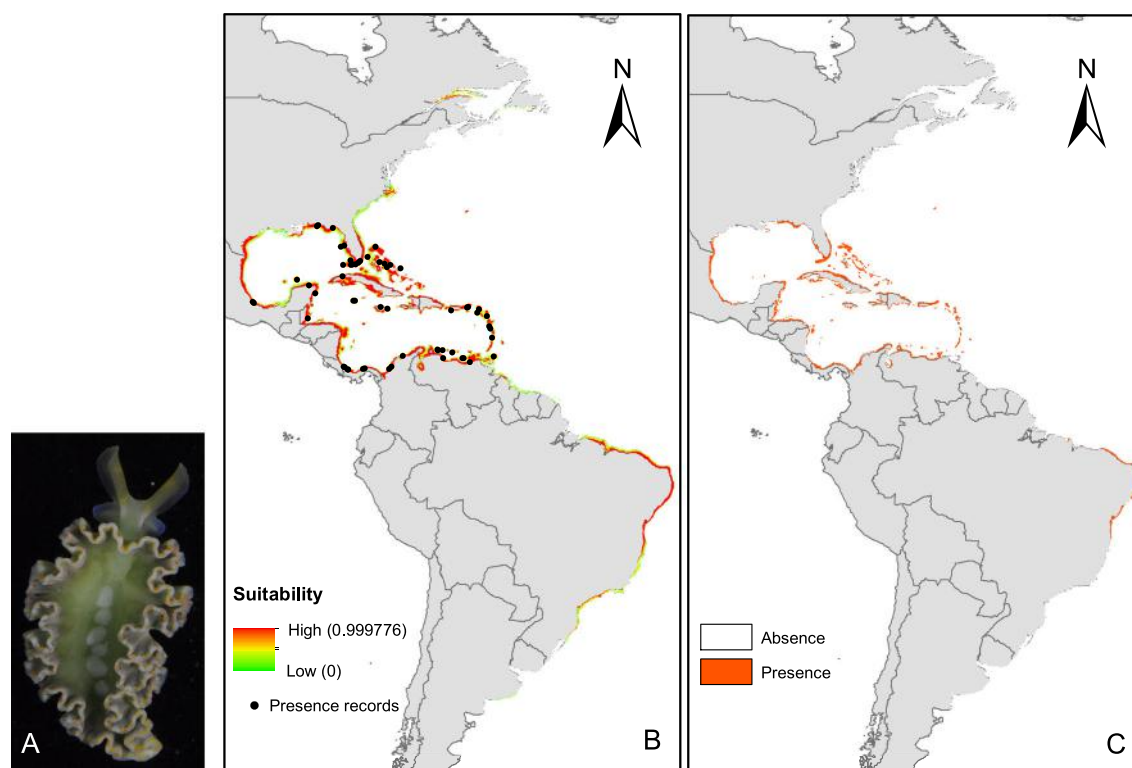
Figure 2. Ecological niche model of *Elysia crispata*. **A.** *Elysia crispata*. **B.** Continuous prediction. **C.** Binary prediction.
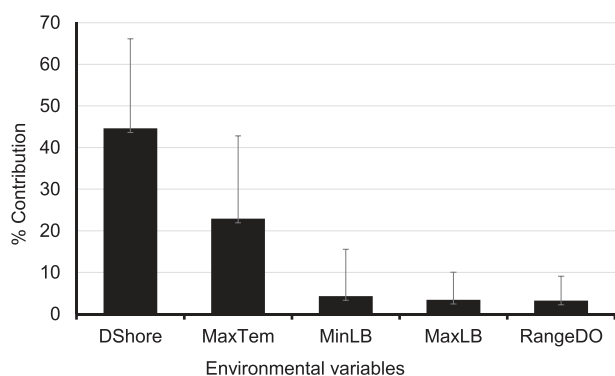

Figure 3. Contribution of the five most important variables to the ecological niche models of the 14 *Elysia* species. Bars indicate the mean contribution of each variable. Data are expressed as the mean and standard deviation. Abbreviations: DShore, distance to shore; MaxTem, maximum temperature; MinLB, minimum light at bottom; MaxLB, maximum light at bottom; RangeDO, range of dissolved molecular oxygen.

Among the environmental predictors used, the largest contribution to niche models was made by distance to shore. This variable does not have a direct effect on the physiology of organisms (it is a distal predictor *sensu* Austin, 2002) and although it is only weakly correlated with the other variables ($r < 0.5$), it is related to other factors that do affect survival. For instance, areas closer to the coast are usually warmer, with higher productivity and availability of light than those further away (Kleypas, McManu & Mene, 1999; Davies *et al.*, 2008; Costa *et al.*, 2015); these are the most suitable conditions for the presence of species in the genus *Elysia* (Krug, 2009; Krug *et al.*, 2016). Published studies on other marine organisms have also shown that distance to shore was the variable that contributed the most in explaining distributional patterns (Lirman *et al.*, 2008; Friedlaender *et al.*, 2011; Gowan & Ortega-Ortiz, 2014; Costa *et al.*, 2015).

Maximum temperature was the variable with the second largest contribution to the explanatory power of the models, and this makes biological sense because it is directly related to the physiology of organisms. Specific negative effects of high temperature on the Heterobranchia have been reported, mostly in relation to the early phases of development; effects include the inhibition of embryonic development (Dehnel & Kong, 1979), death of embryos (Biermann, Schinner & Strathmann, 1992), low oxygen levels in egg masses (Moran & Woods, 2007), reduced duration of intracapsular development, reduced survival of veligers and increased incidence of deformations in veligers (Dionísio *et al.*, 2017). Temperature is also an important factor in photosynthesis, affecting the growth of algae. Also, it has been reported that a temperature range of 20–30 °C is required for kleptoplasty in sea slugs (Singh & Singh, 2015). Waugh & Clark (1986) reported that in *E. velutinus* the optimum temperature for the partitioning of photosynthates in macromolecules was 30 °C. Other variables with a high contribution in the models of some species are directly related to the physiology of organisms and the presence of algae. Dissolved oxygen is one of the limiting factors for physiological metabolism in aquatic environments. Light conditions are an essential source for photosynthetic activity and autotrophic growth (Singh & Singh, 2015). Phosphorus deficiency can alter the response of algae to light and temperature (Sterner *et al.*, 1997).

We found that the greatest richness in western Atlantic *Elysia* species occurs in the Caribbean, and this agrees with the results of Jensen (2007), who suggested this region was a centre of diversification for the genus. The phylogenetic study presented by Krug *et al.* (2016) has revealed that all of the species of the *E. papillosa* complex (this lineage is considered to be the ancestral one) are in the Caribbean, while some species in all the other complexes are distributed only in the Caribbean or in the Caribbean and off Brazil. This pattern suggests that several dispersal events have
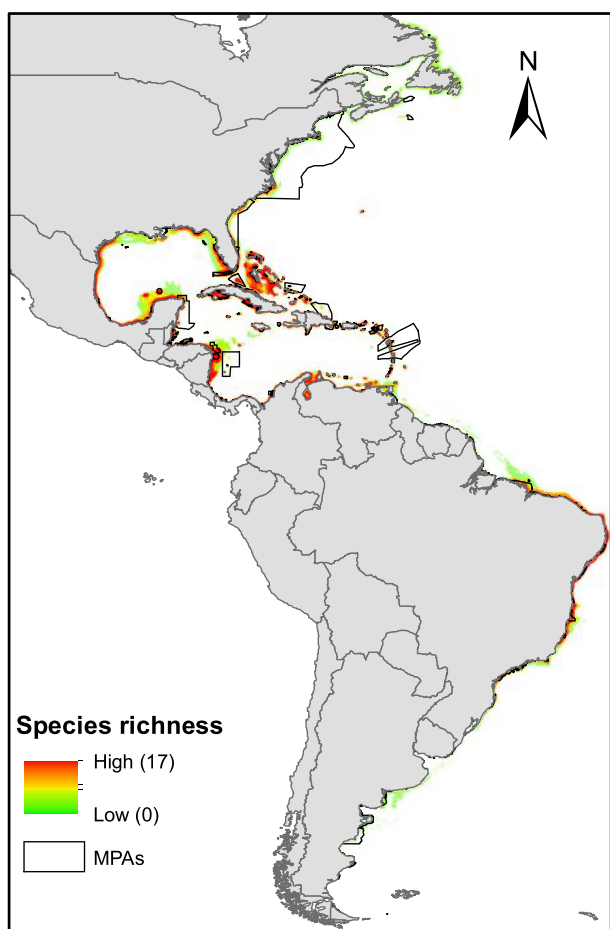
Figure 4. Potential taxonomic richness of the genus *Elysia* in the western Atlantic and its representation in existing MPAs.

taken place. The connectivity of taxa in the Caribbean and off Brazil is hindered by the physical and chemical properties of coastal waters affected by the Amazon–Orinoco plume (AOP). However, despite the AOP being a strong dispersal barrier (Jensen, 2007), six of the species in this study (*E. canguzua*, *E. evelinae*, *E. ornata*, *E. serca*, *E. subornata* and *E. velutinus*) are distributed north and south of it. When sea levels increase, sedimentation diminishes, resulting in normal salinity conditions in the surface layer of the AOP and generating a corridor facilitating larval dispersal between the Caribbean and the Atlantic off Brazil (Rocha, 2003). Since benthic organisms have limited dispersal abilities, the dispersal of *Elysia* occurs during the planktonic larval stage (Krug, 2009). Dispersal distances depends on external factors, such as marine currents, maternal effects (egg size and internal properties of the egg mass) and larval characteristics (larval type, development rate and habitat choice) (Briggs, 1974; Krug, 2009; Luiz *et al.*, 2012; Krug *et al.*, 2015). Depending on the kind of larvae, organisms with planktotrophic larvae may be transported over long distances, since they can feed while they complete their development (Hedgecock, 1986; Krug *et al.*, 2015). In contrast, lecithotrophic larvae depend on the nutritional energy provided by the mother to complete their development (Krug, 1998). In this kind of larvae, an increase in dispersal capacity depends on larval size and the energy invested by the mother (Marshall & Keough, 2003). Of the six species found off Brazil, three have lecithotrophic larvae (*E. evelinae*, *E. subornata* and *E. velutinus*), while the larvae of the other three are planktotrophic (*E. canguzua*, *E. ornata* and *E. serca*). Therefore, the type of larva did not hinder dispersal through the AOP. This finding agrees with the results of Luiz *et al.*'s (2012) study. While Luiz *et al.* (2012) showed

that larval development type was important in explaining the occurrence of distributional patterns that extended across the AOP, no obviously relevant differences between development types were found. The wider geographic range of these species may reflect maternal effects and/or the capacity of these sea slugs to establish a population in a new habitat after dispersal across the AOP; these traits may depend on tolerance to new environmental conditions and, at least in some species, the presence of a metamorphic signal.

In contrast to the Caribbean, the coast between Canada and Florida, the northern Gulf of Mexico, the AOP and the coast between southern Brazil and Argentina have, in general, the lowest levels of taxonomic richness. Conditions at the northern and southern extremes of the range of genus are too cold for most *Elysia* species; the exceptions are *E. chlorotica* and *E. patagonica*, which are adapted to low temperatures (Muniain & Ortea, 1997; Krug *et al.*, 2016). One of the locations with the highest coastal hypoxia in the world is located in the northern Gulf of Mexico (dissolved oxygen levels below 2 mg/l) in the continental platform of Louisiana and Texas (Rabalais, Turner & Wiseman, 2002). Moreover, this area, which covers an area of *c.* 21,000 km^2 is also affected by the discharge of the Mississippi and Atchafalaya Rivers. The AOP includes discharges from two large rivers. These discharges are associated with substantial turbidity, low salinity and excessive levels of sediment, which are poor conditions for sea slugs (Rocha, 2003; Luiz *et al.*, 2012).

The tendency of the stacking method to overestimate local taxonomical richness should be noted (Guisan & Rahbek, 2011; Calabrese *et al.*, 2014). Guisan & Rahbek (2011) proposed the spatially explicit species assembling modelling framework as an attempt to solve overprediction problems. This framework was not used for the determination of richness in this study because of the lack of robust inventories that allowed the richness obtained through stacking to be corrected by a macroecological model. If the potential overestimation of taxonomic richness is taken into account, its representation in the MPAs may be lower than the estimates considered here, stressing the importance of incorporating detailed data on the ecology and conservation status of these species.

Nonetheless, even with limited data, we were able to build reliable models that could potentially form the basis of future ecological studies of these organisms. Our models may also contribute to testing hypotheses on specific spatial patterns of benthic biodiversity and to making predictions on the responses to climate change. Potential distribution maps provide the basis for the inclusion of these species in future efforts to delimit new MPAs and revise the boundaries of existing MPAs. Our richness estimates included species that due to a lack of data would have been excluded from other modelling approaches, thus allowing them to be considered in conservation strategies. In the future, working on independent inventories would allow the richness hypothesis to be tested and the models presented in this study to be validated.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Molluscan Studies* online.

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