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Use of topographic predictors for macrobenthic community mapping in the Marine Reserve of La Palma (Canary Islands, Spain)

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ABSTRACT

Evaluations of the coastal and marine conservation require detailed maps of types of communities that occur in the zone. This paper describes how distribution models are used to develop benthic distribution maps with biological data collected from surveys, and environmental variables derived from a Digital Elevation Model (DEM), including different indices of terrain complexity. We compared the success of two algorithms, Maxent and ENFA, commonly used in the marine environment to identify best suited methods to modelling the distributions of six benthic communities identified in the marine protected area of La Palma (Canary Islands, Spain). The environmental variables depth, slope, type of substrate, Bathymetric Position Index (BPI) and Vector Ruggedness Measure (VRM) were the variables with higher influence on the distribution of communities. The distribution models of both techniques were coincident and congruent, although Maxent produced more constrained predictions than ENFA, highlighting the significantly better performance of the Maxent models for communities with fewer presences, in this study, black coral and brown garden eels. The resulting distribution maps were evaluated and reclassified and they were represented in a unique map that summarises all of the individual maps. Given that the distribution models were made on the same study area and based on presences data collected at the same time, it was possible to make a preliminary analyse of the interactions between the studied communities. In conclusion, distribution models of benthic communities are suitable tools to design reliable and full coverage distribution maps of benthic communities and they provide new information about the behaviour of communities on the range of environmental conditions studied and useful information for management of marine and coastal areas.

1. Introduction

Marine coastal areas play an important role in the socio-economic development of many territories, such as the Canary Islands, where a significant proportion of the economic activities and human population inhabit coastal areas. Therefore, the relevance and recognition of research on ecological studies related to the management of marine and coastal areas has increased, and distribution maps of species and communities are a fundamental tool in this field. In this context, Geographic Information Systems (GIS) have facilitated important advances in marine mapping at different scales (Dolan et al., 2008; Kostylev et al., 2001).

There is a wide variety of GIS methods and techniques used for the creation of distribution maps, in both the data collection and the processing. The selection of the best methods depends on the project objectives, scale, seabed characteristics and the spatial resolution of the resulting map (Diaz et al., 2004; Kenny et al., 2003; Solan et al., 2003). For the collection of data, direct submarine observations, such as diving or video surveys, have been utilised mostly in small-scale areas, and littoral and sublittoral regions (Earll, 1992; Jordan et al., 2005; Norris et al., 1997). The application of remote sensing techniques, such as aerial photographs and satellite images, have enabled the large-scale mapping (Urbanski and Szymelfenig, 2003) but in general these techniques are directed to geophysical exploration (Diaz et al., 2004; Sinclair et al., 1999;

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Vrbanich et al., 2001) or to study communities of shallow water and clear waters with optimum conditions of wind, clarity and sun position (Marchanda and Cazoulat, 2003; West and Williams, 2008). The different strategies in the design of distribution maps from the collected information can be classified in (1) the interpretation of the data by the author (mainly in reports), (2) spatial interpolation (e.g. Jerosch et al., 2006) and (3) the development of predictive distribution models (Guisan and Zimmermann, 2000). The latter technique has been described and applied for species distributions in terrestrial environment (Guisan and Zimmermann, 2000; Hernández et al., 2008b; Segurado and Araújo, 2004), and it has also been applied in marine species in the last years (Degraer et al., 2008; Dolan et al., 2008; Galparsoro et al., 2009; Guinan et al., 2009; Hermosilla et al., 2011; Jones et al., 2012; Leverette and Metaxas, 2005; Skov et al., 2008). These techniques are aimed at distribution of species, but they also have been used in studies on the distribution of benthic communities of certain areas in which the entities or groups of species to modelling are well defined and classified (Degraer et al., 2008; Maggini et al., 2006) or, as an alternative, the dominant species are selected to classify their superimposed distributions, in order to generate simulated community maps (Bandelj et al., 2009; Guisan and Zimmermann, 2000; Ierodiaconou et al., 2011).

Currently, there are numerous methods for modelling the distribution of species. These models have been developed to respond to different ecological and statistical aspects of the distribution (Elith et al., 2006; Guisan and Zimmermann, 2000). The application of different techniques may provide different results, which must be studied and compared to determine the best choice considering that the selection of an appropriate method should not depend solely on statistical considerations. One of these prediction approaches is Ecological Niche Factor Analysis (ENFA), developed by Hirzel et al. (2004). Until now, ENFA has been applied mainly on a regional and global scale to model benthic species distribution (Bryan and Metaxas, 2007; Clark et al., 2006; Galparsoro et al., 2009; Leverette and Metaxas, 2005; Wilson et al., 2007), even in regional studies of cetacean distribution (Compton, 2004; Mandleberg, 2004), although ENFA can be useful for local analyses of marine species (Dolan et al., 2008). The Maximum Entropy Model (Maxent) is a technique developed by Phillips et al. (2006) that is one of the most commonly used tools for modelling the distribution of terrestrial (Elith et al., 2006; Rupprecht et al., 2011) and marine species (Anderson and González, 2011; Hermosilla et al., 2011; Howell et al., 2011; Jones et al., 2012; Ready et al., 2010). The Maxent software package was designed to assess the geographic distribution of species in relation to environmental variables with limited presence-only data (Pearson et al., 2007; Phillips et al., 2006; Phillips and Dudík, 2008), and various studies have proved that Maxent tends to present the best results when ranked against other methods (Elith et al., 2006; Hermosilla et al., 2011; Hernández et al., 2008b; Jones et al., 2012; Rupprecht et al., 2011).

Whatever the modelling technique used in species and communities, topographic variables created from DEMs are the main information used in both terrestrial and marine habitat (Guisan and Zimmermann, 2000). Despite of the numerous and demonstrated applications of DEM and derived parameters in terrestrial habitats, until recently, no detailed terrain data were available for the marine environment. Marine studies focus on ecology, biodiversity and biogeography, only used a basic knowledge of seafloor bathymetry without precise position information for biological samples, and any explicit link to the seabed terrain (Wilson et al., 2007). With the advent of multibeam technology and geospatial technology (GIS, GPS) mapping of marine benthic habitats entered a new era (Kenny et al., 2003). Multibeam surveys provided spectacular detail of sea terrain revealing numerous previously unrecognised features and the detailed bathymetry data necessary for the production of submarine DEMs and terrain analysis (Wilson et al., 2007). The strong relationship between topographic data and the presence of benthic communities and species have proven their value for habitat mapping (Kostylev et al., 2001; Parnum et al., 2004; Wilson et al., 2007) and studies of the distribution of benthic flora and fauna (Galparsoro et al., 2009; Kostylev et al., 2003; Wilson et al., 2007). DEMs represent the most accurate information available about marine environments and in most cases they determine the spatial resolution of the resulting model. Thus, a DEM and its basic derivatives have become the main environmental information used for marine spatial modelling of benthic entities.

Infralittoral benthic flora and fauna of the Canaries are well known and have been amply studied (Afonso-Carrillo and Sansón, 1999; Barquín-Diez et al., 2005; Bianchi et al., 2000; Brito et al., 1984; Brito and Ocaña, 2004; Espino et al., 2006; Haroun et al., 2003). Over the last ten years, the Spanish Ministry of Environment and local government has financed individual projects for each island of the Canary Archipelago to create a database on geophysical data and distribution maps of the main benthic assemblages and habitats from a depth of 0 to 50 m. Although the objective of every project of each island was the same, the projects were developed by different private companies using different methods and in different periods from 2000 to 2006. Consequently, the habitat and community charts and distributions greatly different, reflecting the lack of unified criteria in the methodology. Due to the absence of updated data, the inaccessibility of information and the many mistakes found in the distribution of habitats and communities, these maps lead to erroneous and harmful decision-making for marine management.

The aim of this paper is to establish distribution maps of the main macrobenthic communities of La Palma marine protected area by means of two presence-only analyses, Maxent and ENFA. Only the topographic information derived from the DEM is used as an environmental predictor, and direct observations from underwater video surveys are used for registering the presence of benthic communities. The same training and evaluation datasets were used to compare the accuracies of these two techniques. We examined the relationship of different environmental variables to the benthic communities in the study area, and we determined which ruggedness indices are more relevant. Moreover, this analysis defines the seafloor feature conditions that determine the presence of the different communities and the capacity of bottoms to accommodate different entities.

2. Materials and methods

2.1. Study area

La Palma is a volcanic island located at the northwest of the Canaries, a subtropical archipelago situate in the north of the Eastern Central Atlantic Ocean. The seafloor of the Island is characterised by high slopes of rocky and sandy bottoms that can reach high depths at only a few metres from the coast line. The Marine Reserve of La Palma is located at the western margin of the Island (Fig. 1), and it was established in 2001 to protect fish stocks, highly depleted due to high levels of exploitation. This side of the island also has the status of Special Area of Conservation (SAC) by the Habitats Directive 92/43/EEC to conserve the marine mammals *Tursiops truncatus*, the turtle *Caretta caretta* and *the submerged or partially submerged sea caves* habitat. The marine reserve is about 3455 ha extension and reaches to 1000 m depth but the study area is a water depth from 0 to 50 m, and we included in the analysis adjacent zones to the marine reserve, therefore, the final study extension is about 1574 ha, 597 ha inside the marine reserve and 977 ha outside. This protected study zone is only 18.7% of the marine reserve, but

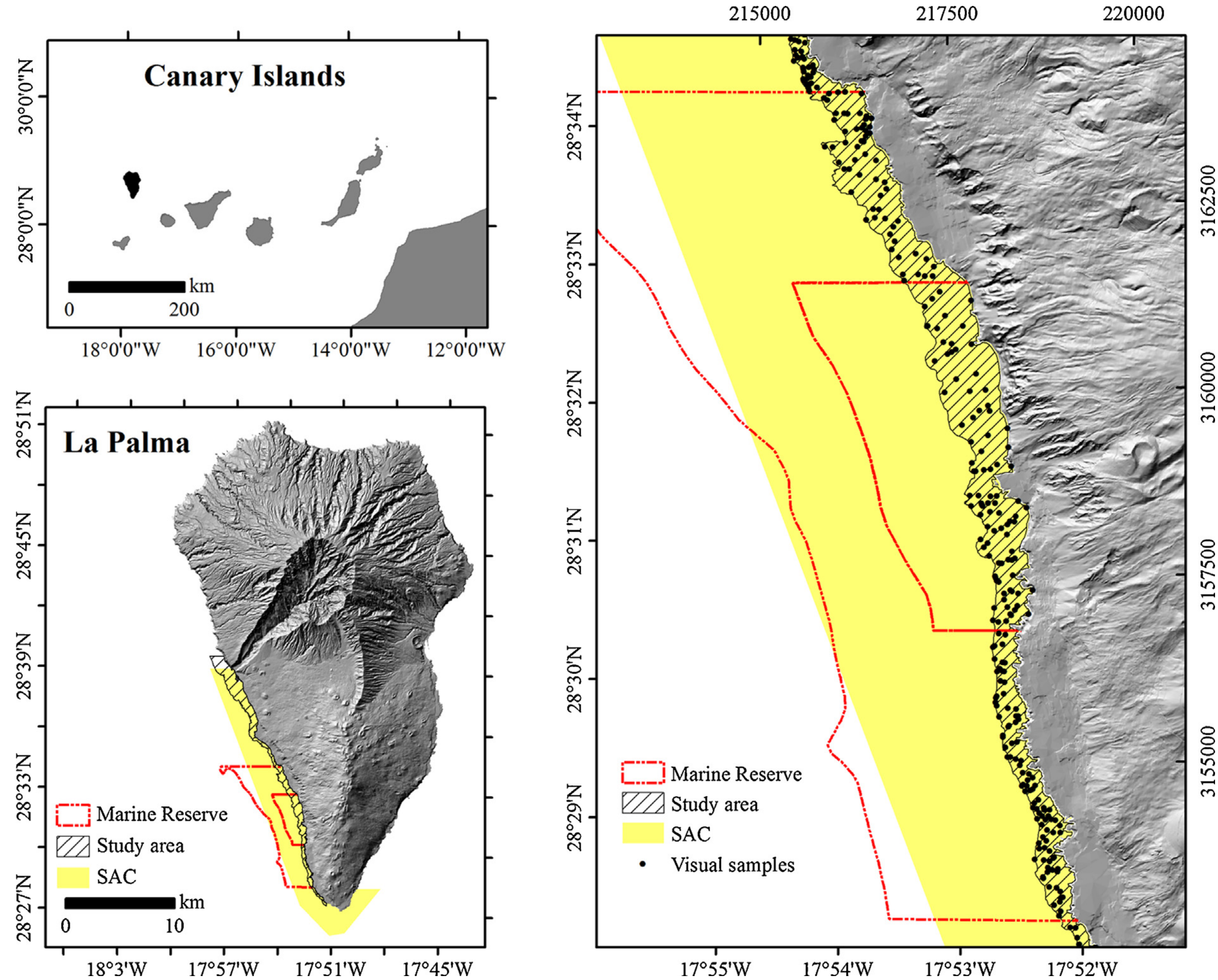

Fig. 1. Location of the study area in relation to the Marine Reserve of La Palma and the spatial area of conservation (SAC).

the most sensitive and expose to the human activities and impacts. Besides, the topography of the area is highly variable and complex and high macrobenthic diversity is expected.

2.2. Environmental data

The DEM used in this study to obtain the quantitative topographic descriptors (Table 1) was acquired from the Eco-cartographic Project developed in 2003, which used multibeam echosounders to obtain bathymetric information at a 5 m resolution at the coasts of La Palma at a depth of 0 to 50 m. Surfer V. 8 (Golden Software) was used to integrate the dataset and produce a DEM using the “Nearest Neighbour” algorithm interpolation method and projected coordinate UTM, Zone 28N (WGS84). This DEM was exported into an ESRI grid format and integrated into a GIS. All GIS analyses of depth, slope and orientation were performed within the ArcGIS 9.3 environment (ESRI). Slope was calculated in degrees, and aspect (orientation) was calculated as the direction of the cell’s slope and was measured relative to North (northness) and East (eastness). All the variables have a resolution of 5 m. Further details of the computation methods are provided by Wilson et al. (2007).

A variety of methods exist in the literature for measuring terrain irregularity in the benthic environment to aid in the identification of areas with high biodiversity. We selected four of these methods (Table 1). The BPI was calculated using the ArcGIS extension Benthic Terrain Modeller (BTM) Version 1.0 (Wright et al., 2005). BPI can be calculated at a variety of user-defined scales to capture local- and broad-scale variations in bathymetric position. Two typical scales of the BPI were calculated from the DEM: one with a factor of 200 (broad scale) and one with a factor of 35 (fine scale). Topographic roughness (TR) was calculated using the Surface Areas and Elevation Grids extension (Jenness, 2002) for Arc View 3.2. This index has been used in numerous studies of marine habitats (Dolan et al., 2008; Guinan et al., 2009; Iampietro et al., 2004; Lundblad et al., 2006). By this method, flat areas will have values near 1, while high relief areas will exhibit higher values of roughness. This extension is also included in the BTM module. The fragmentation index (FI; Idrisi 32.11 2000; Monmonier, 1974) is generally used to describe changes in thematic layers as land cover (deVente et al., 2009) or land use (Boix-Fayos et al., 2008) patterns. In this case, however, the FI was chosen to describe changes in bathymetry. Finally, the Vector Ruggedness Measure (VRM), based on Hobson’s technique (1972), is a method developed for measuring surface roughness in geomorphology and was created for use in GIS. The VRM can provide a better picture of the heterogeneity of terrain than indices based only on slope or elevation (Sappington et al., 2007). The layers of VRM and FI values were calculated using ArcView scripts (available online from ESRI ArcScript website www.esri.com/arcscripts).

By means of the interpretation of the topographic information, it is also possible to classify seafloor types in hard bottoms (rock, cobble and boulder) and soft bottoms (mud, sand and gravel). The

Table 1
Description of the topographic variables obtain from the DEM and include into the distribution models.

Parameter	Description	Software	Reference
Bathymetry (B)	Raster grid of the bathymetric DEM with a resolution of 5 m.	Surfer 8 ArcGIS 9.3	Wilson et al. (2007)
Slope (S)	It is the maximum rate of change between each cell or pixel and its neighbours and was calculated in degrees (°).	ArcGIS 9.3	Wilson et al. (2007)
Aspect (A)	Orientation of the slopes measure by Indices of northness (N) and eastness (E) provide continuous measures (−1 to +1).	ArcGIS 9.3	Wilson et al. (2007)
Bathymetric Position Index (BPI)	A quantitative characterisation of bathymetric features in their local/regional context based on a Digital Elevation Model. Two scales of the BPI are calculated from the DEM, broad scale BPI, with scale factors 200; and fine scale BPI, with scale factors of 35.	BTM tool	Weiss (2001) and Wright et al. (2005)
Topographic roughness (TR)	Measure of terrain complexity that represents the ratio of surface area to planar area.	BTM tool Arcview 3.2	Jenness (2002)
Fragmentation index (FI)	Relative variation of level values of an information layer, over the total number of cells in a window of a given size.	Arcview 3.2	Monmonier (1974) and Idrisi 32.11 (2000)
Vector Ruggedness Measure (VRM)	Terrain complexity grid which combines variation in slope and aspect into a single measure.	ArcView 3.2	Hobson (1972) and Sappington et al. (2007)
Type of substrate (TS)	Presence of rock, cobbles and boulders (hard substrata) or mud, sand and gravel substrata (soft substrata).	ArcGIS 9.3	Verfaillie et al. (2009)
Distance to soft substrate (DSS)	Distance map calculated by minimal distance from point to soft substrata.	DISTAN module of Biomapper 4.0	Hirzel et al. (2004)

minimum distance from hard to soft substrate was calculated for the entire study area, like a measure of sedimentation, using the DISTAN module in BioMapper V. 4.0.

2.3. Sampling of biological data

Sampling surveys were undertaken between 18 and 22 May 2009. These surveys consisted of going through the entire study area with a small boat and a submarine video camera system, consistent with the method described by Barquín-Diez et al. (2003) for data collection. During the cruise, we acquired visual samples or video camera images regarding the presence of the communities and substrate types, and documented the precise position of the samples by means of an on-board GPS. A stratified random sampling approach was conducted for the different environmental conditions (e.g. bathymetry, slope, ruggedness) and for previous information available, such as aerial photographs. Communities were identified in the field according to the occurrence of character species and indicator species. The information was inputted on-board using GPS mapping software Ozi Explorer. These data points only register the presence of the main communities and substrate types, which are listed in order from highest to lowest coverage. Despite being a systematic sampling, the method is based on video data; therefore, absent data are unreliable and presence–absence prediction analyses are not available. In total, 597 samples were taken from the studied area, with an average distance of 98 m between them. The information was identified and mapped as sample points, and the video data were associated and georeferenced with the sample points by applying the ArcGIS 9.3 software. We extracted the values of the available variables for every sample point using the Spatial Analyst tool of ArcGIS 9.3, and we described, prior to ENFA analysis, the environmental preferences of the communities observed. Data points were classified according to the observed communities and 40% of each group of presence records of each community was randomly selected to be used separately as evaluation data to test models.

2.4. Modelling methods

2.4.1. Ecological niche factor analysis (ENFA)

ENFA is a procedure similar to the Principal Component Analysis (PCA) that transforms a set of correlated variables, called eco-geographical variables (EGVs), into the same number of uncorrelated factors, which define the space where the environmental envelope will be delineated. Suitability functions are computed by comparing the observation sites in the EGV space with those of the whole set of cells in the study area (Hirzel and Arlettaz, 2003; Hirzel et al., 2004). The most important feature of ENFA is that its factors have ecological relevance. The first factor accounts for all marginality, and the other factors account for successive degrees of specialisation. Marginality (M) expresses the difference of the species mean (in our case, communities) from the global mean (the mean of the variables in the study area). A large value of marginality (close to 1) means the communities live in a highly particular habitat relative to the reference set. Overall specialisation (S) and tolerance (T, inverse of specialisation) values were also calculated. A high specialisation value indicates that the focal community has a particular requirement for certain EGVs. A high tolerance value indicates that within a given study area, the community occupies a relatively wide niche. The tolerance varies between 0 (very specialised) and 1 (ubiquitous). Further details of ENFA theory are provided by Hirzel et al. (2004). For our ENFA analysis, we used the freely available software BioMapper V. 4.0 (Hirzel et al., 2004), which was applied independently to each community in the study area. The final selection of the number of factors to create the model is based on MacArthur's broken stick distribution (Hirzel et al., 2004). Distribution maps were calculated using the medians algorithm.

2.4.2. Maximum entropy algorithm (Maxent)

Maxent (Elith et al., 2011; Phillips et al., 2006) is a general-purpose method for making predictions or inferences from incomplete information. Maxent estimates a target probability distribution using presence-only data by finding the probability distribution of maximum entropy (the most uniform) subject to a set of available features or variables that represent our incomplete information about the target distribution. Detailed descriptions of the Maxent's methods can be found in Phillips et al. (2006) and Phillips and Dudík (2008). Continuous and categorical predictors can be used in Maxent to define linear, quadratic, product, hinge and threshold terms. The regularisation parameter of Maxent (in this study, the default setting was maintained) ensures that the average values of a given predictor in the estimated distribution match its empirical average. Maxent models were

Table 2
Main information about ENFA and Maxent results and model accuracy for every community: number of presence points that was separated in training data to compute models and evaluation data for test models, percentage of variance explained in Maxent analysis, values for marginality (M), specialisation (S) and tolerance (T) in ENFA analysis.

Community	No. presence data	No. training data	No. evaluation data	MAXENT	ENFA				
				AUC	% variance explained	M	S	T (1/S)	Boyce Index continuous
Black coral	33	20	13	0.988	81.2	2.991	1.971	0.507	0.01 ± 0.43
Barren ground	95	57	38	0.843	67.4	1.199	1.515	0.66	0.63 ± 0.34
Brown garden eel	73	44	29	0.914	93	0.687	6.021	0.166	0.63 ± 0.37
Filamentous red seaweed	90	54	36	0.921	82.3	0.917	3.096	0.323	0.50 ± 0.44
Lobophora	118	71	47	0.903	76.2	0.938	1.664	0.601	0.76 ± 0.37
Mixed algal	142	85	57	0.878	83.6	0.435	2.404	0.416	0.42 ± 0.11

created from the presence-only data of the benthic communities and the set of predictors listed in Table 1 and using version 3.3.3e (http://www.cs.princeton.edu/~schapire/maxent/). Habitat suitability is provided by the cumulative output format, which represents as a percentage the probability value for the current analysis pixel and all other pixels with equal or lower probability values. A value of probability of species occurrence, ranging from 0 to 100, is assigned to each pixel in the study area. The importance of each environmental variable in the model was evaluated by means of response curves and jackknife tests that reflect the dependence of the predicted probability on the selected predictor. The evaluation analysis was executed by initially running the model by excluding one variable in each run, then running the model with only one variable and, finally, including all in the model.

2.5. Evaluation and representation of predictions generated by ENFA and Maxent

Both ENFA and Maxent present independent applications to measure model accuracy. ENFA uses a cross validation procedure based on the method of Boyce et al. (2002), which is implemented in BioMapper. The cross validation applied partitions of the presence data to make cross-validation reproducible and comparable. This approach produces the Boyce Index, which varies from −1 to 1. Positive values indicate a model whose predictions are consistent with the presence distribution in the evaluation dataset, where values close to zero mean that the model is not different from a chance model and negative values indicate an incorrect model that predicts poor-quality areas where presences are more frequent (Hirzel et al., 2006).

Maxent offers a threshold-independent receiver operating characteristic (ROC) approach and calculates the area under the ROC curve (AUC) to measure and compare model performance (Fielding and Bell, 1997), and it is widely used to evaluate distribution models (Elith et al., 2011). Species absences are replaced by background data (by default, 10,000 pixels drawn randomly from the study area). The AUC value then corresponds to the probability that a randomly chosen presence site is ranked above a random background site (Phillips and Dudík, 2008).

To compare the accuracy models of each applications, ENFA and Maxent, and each community we applied a variation of the AUC method described by Benito et al. (2009). This method needs presence data, absence data and a number of iterations (10,000) to compute AUC values. For each community and algorithm, we used the evaluation data (not the training dataset used to compute the models; Table 2) as presences and data of the background as absences, sometimes also referred to as "pseudo-absences" (Elith et al., 2006). The presences and an equal number of absences are selected at each iteration to calculate the AUC value. For a given model and community, the mean of the 10,000 AUC values (AUCm) expresses the probability that the suitability value of the presence record will be higher than the suitability value of the random plot. The AUC ranges from 0 to 1, where a score of 1 indicates perfect discrimination, a score of 0.5 implies predictive discrimination that is no better than a random guess, and values ≤0.5 indicate performance worse than random (Elith et al., 2006). To detect significant differences in the model performance between algorithms, the AUC values were normalised using arcsine transformation to apply a repeated measures ANOVA test using the algorithm as a factor (Benito et al., 2009; Segurado and Araújo, 2004). Models with higher AUCm were selected as the most accurate.

Although the continuous gradient of suitability conveys more information than presence/absence map, it allows a simpler visualisation of the resulting distribution maps and could be more convenient for management support (Hirzel et al., 2006). The resulting Maxent and ENFA maps of every community were

Table 3
Classification of the benthic communities observed in the study area according to the occupied habitat, the key species and the main references that describe each community.

	Habitat	Type of community	Communities of the study area	Character species and indicator species	References
Marine habitats	Infralittoral rock and other hard substrate	Frondose algal communities	Mixed algae	Articulate and crust corallinaceae, *Dictyota* spp., *Lobophora variegata*, *Padina pavonica*, *Asparagopsis taxiformis* and filamentous red seaweeds.	Sangil (2011)
			Lobophora	*Lobophora variegata*	Sangil (2011)
		Coralline crusts communities	Barren ground	*Diadema* aff. *antillarum*	Tuya et al. (2004)
	Circalittoral rock and other hard substrate	Circalittoral communities in caves and overhangs	Black coral	*Antipathella wollastoni*	Brito and Ocaña (2004)
	Sublittoral sediments	Faunal communities in fine sand	Brown garden eel	*Heteroconger longissimus*	González-Lorenzo et al. (1995)
		Seaweed communities	Filamentous red seaweed	*Lophocladia trichoclados*, *Cotoniella filamentosa*	Sangil (2011)

Table 4
Mean and standard deviation (SD) of the environmental variables calculated for occurrence cells of each community and for the whole study area calculated with ArcGIS 9.3. Abbreviations for topographic variables are consistent with Table 1.

Topographic predictors	Barren ground		Black coral		Brown garden eel		Filamentous red seaweeds		*Lobophora*		Mixed algal		Study area	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
B	34.59	12.28	45.88	12.61	37.15	9.80	34.01	10.72	16.17	7.21	18.82	11.04	23.34	14.55
S	16.28	10.46	29.68	12.36	7.77	5.86	14.80	5.59	8.79	8.34	7.16	7.09	7.22	8.54
N	−0.38	0.48	−0.38	0.45	−0.40	0.37	−0.29	0.43	−0.23	0.62	−0.31	0.54	−0.26	0.52
E	−0.70	0.38	−0.62	0.50	−0.78	0.32	−0.85	0.17	−0.33	0.68	−0.53	0.59	−0.63	0.51
BPI 200	6.41	8.05	12.38	11.18	0.66	3.11	9.90	5.19	7.86	9.35	2.25	4.39	2.36	5.68
BPI 35	0.48	1.47	1.03	2.49	0.06	0.47	0.67	0.48	0.48	1.28	0.22	0.74	0.19	1.10
TS	0.92	0.28	0.97	0.18	0.07	0.26	0.38	0.50	0.97	0.18	0.89	0.31	0.53	0.50
FI	0.403	0.233	0.598	0.259	0.222	0.173	0.417	0.191	0.237	0.182	0.186	0.191	0.19	0.20
VRM	0.0023	0.0032	0.0025	0.0044	0.0003	0.0008	0.0005	0.0004	0.0017	0.0032	0.0009	0.0019	0.0017	0.0072
TR	1.066	0.085	1.165	0.256	1.015	0.021	1.040	0.032	1.027	0.068	1.018	0.047	1.024	0.074
DSS	135.95	229.33	244.53	382.34	0.41	1.53	69.53	177.44	258.36	328.57	88.70	146.12	99.75	211.01

reclassified into three discrete categories: unsuitable (with values of probability between 0 and 33%), marginal (33–66%) and optimum (>66%) habitats. Reclassified maps were used only to improve the illustration and compare model performance of the resulting predictive models, thus the boundaries of the categories were the same for both Maxent and ENFA and all the communities. Optimum habitats were used to represent the distribution area of every community in the same distribution map for each modelling application.

3. Results

3.1. Benthic communities

Six main benthic communities were identified from the study area: mixed algae, *Lobophora*, barren ground, black coral, brown garden eel and filamentous red seaweed (Table 3). The total number of records for each community is presented in Table 2. The mean and standard deviation of each predictor or environmental variable was calculated for each grid cell with the occurrence of every benthic community and for the whole study area calculated with ArcGIS 9.3, as shown in Table 4. Descriptively, the communities seem to have differences in habitat preferences for some variables taken into account in this study. All communities, except brown garden eel, were found on hard substrates. These communities also show predilections for certain depth ranges, as algal and *Lobophora* communities were observed in shallow waters (10–20 m depth) and black coral in deep waters (from 45 m depth). Black coral was the community with greatest differences in habitat, not only in depth but also slope and terrain complexity, with high values for both variables (Table 4).

3.2. Environmental variables in the prediction models

The ENFA analysis reduced the EGVs to three specialisation axes in almost all communities, except filamentous red seaweed, which needed only two factors in the analysis to account for the main part of the variance explained (Table 5). All the ENFA models explained a high percentage of variance, especially brown garden eel, which reached a value of 93% of the variance from the original variables (Table 3) even though the model was performed with a low number of presences in comparison with other communities. The ENFA analysis indicated that mixed algae presented the lowest value of marginality and that black coral had the highest marginality. Therefore, the mixed algae mean was very similar to the global mean, and black coral had a habitat differing from the mean environmental conditions over the study area. The specialisation values exceeded unity, and the tolerance was low for all communities, so all of them had a certain level of specialisation. Brown garden eel, with a maximum value of specialisation and a minimum value of tolerance, was quite restrictive in the range of the conditions it occupies (Tables 3 and 4) in relation to the other entities. In this study, marginalities, specialisations and tolerances could be compared between the different communities because the models were built with the same group of variables and for the same study area. Table 5 indicates the relative contribution to each factor by the variables that give details about the relevance of the variables in the distribution of the communities. Parameters making the largest absolute contributions to the factors with the highest percentage of variation were the key drivers for every suitable community habitat. Although the variables affected each community differently, the most important variables identified by ENFA in the distribution of the communities were VRM, bathymetry and type of substrate. The indices derived from aspect, northness, eastness and BPI 35 were the variables that contributed least to the models.

The results of Maxent showed differences with ENFA regarding the contributions of the variables in the models (Table 5) and the prediction maps. According to the heuristic estimations of Maxent, the variables that contribute most to the different models were bathymetry (with the highest percentage of contribution of all the communities), slope (especially in barren ground, *Lobophora* and mixed algae) and BPI 200 (on brown garden eels, filamentous red seaweeds, *Lobophora* and mixed algae). BPI 35, the Fragmentation Index, northness and eastness, and type of substrate showed very little or null gain in the models. Regarding terrain complexity descriptors, Maxent indicated that TR and VRM were important in the distribution of some communities. However, when we applied the jackknife test (data not shown), the information provided by TR was explained by the rest of the topographic descriptors, so it could be removed without influencing the quality of the resulting map. In contrast, the information provided by VRM was not presented in the other variables, and the gain of the model decreased when it was omitted.

3.3. Model accuracy and prediction success

The maps generated by Maxent and ENFA showed the areas with the best-predicted conditions for the benthic communities in the study area, and they were congruent with the samples taken and their known distributions (Figs. 2 and 3). On the whole, the methods used to measure prediction success indicated good quality for most of the models, although we found some differences between them (Table 3). The evaluation measures for ENFA and the Boyce Index confirmed that, in general, the design of our models was adequate according to the requirements described by Hirzel et al. (2006), except for black coral, with a low Boyce index

Table 5
Relative contribution of the environmental variables to the Maxent and ENFA models. The ENFA analysis reduced the eco-geographical variables to three axes or factors in almost all communities, except filamentous red seaweed, which needed only two factors. The first factor explains always 100% of the marginality and some part of specialisation, whereas the other factors (S1 and S2) account for successive amounts of specialisation. Data in bold indicate the highest values of each parameter. Abbreviations: M, marginality; S, specialisation; %, percent contribution. Abbreviations for topographic variables are consistent with Table 1.

Topographic predictors	Barren ground				Black coral				Brown garden eel				Filamentous red seaweeds			*Lobophora*				Mixed algae			
	ENFA			Maxent	ENFA			Maxent	ENFA			Maxent	ENFA		Maxent	ENFA			Maxent	ENFA			Maxent
	M	S1	S2	%	M	S1	S2	%	M	S1	S2	%	M	S1	%	M	S1	S2	%	M	S1	S2	%
B	−0.3	0.1	**−0.5**	**34.9**	−0.3	**0.6**	−0.3	**24.9**	**−0.6**	0.0	−0.1	**20.9**	0.0	0.0	**14.1**	0.3	**0.7**	**−0.6**	**26.7**	0.4	0.1	0.0	**22.5**
BPI200	0.3	0.0	0.2	1.9	0.4	0.1	0.2	3.6	−0.3	−0.1	0.0	**11.7**	**0.7**	0.1	**30.0**	**0.6**	0.0	−0.1	**13.5**	0.2	0.1	0.0	**11.5**
BPI35	0.1	−0.1	0.0	0.0	0.2	−0.2	−0.2	0.6	−0.2	0.1	0.0	0.2	0.2	−0.2	0.3	0.1	0.0	−0.1	0.2	0.1	−0.3	0.1	0.6
DSS	0.1	0.0	−0.2	5.9	0.1	0.0	0.0	2.1	0.2	0.0	0.0	**48.8**	**0.5**	0.0	0.3	0.4	0.0	0.0	4.6	0.2	0.0	0.0	**21.3**
TS	0.4	0.2	**−0.5**	2.6	−0.2	**0.6**	0.3	0.9	**−0.6**	−0.1	0.0	1.0	0.2	0.0	0.9	0.5	−0.2	0.4	9.9	**0.8**	0.1	0.1	7.6
E	−0.1	−0.2	−0.3	1.7	0.0	0.0	−0.2	0.0	−0.2	−0.1	0.0	1.5	0.0	0.1	2.0	0.3	−0.1	0.0	3.7	0.3	0.0	0.0	4.3
FI	**0.5**	−0.1	0.0	0.4	**0.4**	0.1	0.1	0.1	0.1	0.0	−0.1	0.2	0.3	0.2	1.3	0.2	−0.2	0.0	0.5	0.1	0.1	0.0	2.7
N	0.0	−0.1	−0.2	0.1	0.0	0.4	0.0	3.6	−0.2	0.0	−0.1	0.2	0.0	0.1	0.1	0.1	0.0	0.0	0.1	−0.1	0.0	0.0	1.3
S	**0.5**	−0.3	−0.2	**30.5**	**0.5**	0.5	**−0.5**	1.8	0.0	−0.2	−0.3	0.5	0.2	−0.1	5.2	0.1	0.0	0.0	**39.1**	0.0	−0.2	−0.4	**21.9**
TR	0.3	0.4	0.1	6.9	0.5	−0.2	0.2	**58.4**	−0.1	0.1	**0.9**	**10.7**	0.1	−0.2	8.8	0.0	0.2	−0.2	0.0	−0.1	0.0	**0.9**	0.9
VRM	0.1	**0.8**	0.4	**14.9**	0.0	0.4	**0.7**	4.2	−0.1	**0.9**	−0.3	4.3	−0.1	**0.9**	**37.1**	0.0	**0.6**	**0.6**	1.6	−0.1	**0.9**	−0.2	5.3

value of 0.01 ± 0.43 (Table 2). The AUCs for the training data in the Maxent models were all higher than 0.8, meaning the model predictions were also better than randomness (AUC = 0.5), with black coral having the highest AUC value. A comparable accuracy analysis with the evaluation data (Fig. 4) and the ANOVA tests confirmed differences between the algorithms in terms of the AUC values (mixed algae: f = 2103.858, $P \leq 0.0001$; barren ground: f = 9.635, $P \leq 0.0001$; black coral: f = 5733.184, $P \leq 0.0001$; brown garden eel: f = 2047.231, $P \leq 0.0001$; filamentous red seaweeds: f = 80.445, $P \leq 0.0001$; *Lobophora*: f = 2047.213, $P \leq 0.0001$). These results show that Maxent was the best algorithm for modelling the distribution of all benthic communities, highlighting the significantly better performance of the Maxent models corresponding to black coral and brown garden eels.

3.4. Benthic habitat mapping

After reclassification process, the optimum habitat with probability greater than 66% of each community were used to represent the distribution area of benthic communities in the study area (Figs. 2 and 3). The optimal distribution areas for each community were coincident in space between Maxent and ENFA, but they were narrower and more restricted in Maxent, indicating that the overall optimum area for the communities represented only 32% of the study area. However, ENFA showed that 81% of the study area was optimal for some communities. Although some communities presented clear differences in habitat preferences, others shared the optimal ranges and even overlapped, especially in case of mixed algae, *Lobophora* and barren grounds communities. This circumstance is consistent with the experience in the field, so barren grounds are the results of the grazing activity of the sea urchin *Diadema* aff. *antillarum* on the algal cover. The overlap is not total because the bottoms of shallow waters to 10 m depth are not optimal areas for the sea urchin and thus, these shallow bottoms remain dominated by the algal communities. These results are indicative of the good fit of the models to the actual distribution of the communities.

4. Discussion

4.1. Data collection

Generally, in the collection of samples for benthic mapping management, a large number of samples are collected through different sampling techniques and about different species, communities or habitats. The methodology described by Barquín-Diez et al. (2003) in data collection and used in this study is an efficient and effective way to create distribution models because the occurrences of species and communities is collected immediately with a high-accuracy location as a point of video observations. Other methods based on video transects allow a rapid survey of large areas that have few environmental and community changes (Kendall et al., 2005), but the narrow platforms and the variety of habitats and communities present in the bottoms of the Canaries makes the method based on the point of video observation more appropriate than the video transect method for the Canary Islands and similar environments in other territories. In any case, sampling is performed evenly in the study area, and the sampling density is high according to the scale and the characteristics of the bottoms. Therefore, the sample size in both methods is normally sufficient to obtain reliable distribution models on each observed entity, species or community and to explain how the environmental variables affect them. However, simple interpolation techniques or interpretation of data are commonly used for the creation of these maps, and the abundant initial information is filtered to show only a layer of

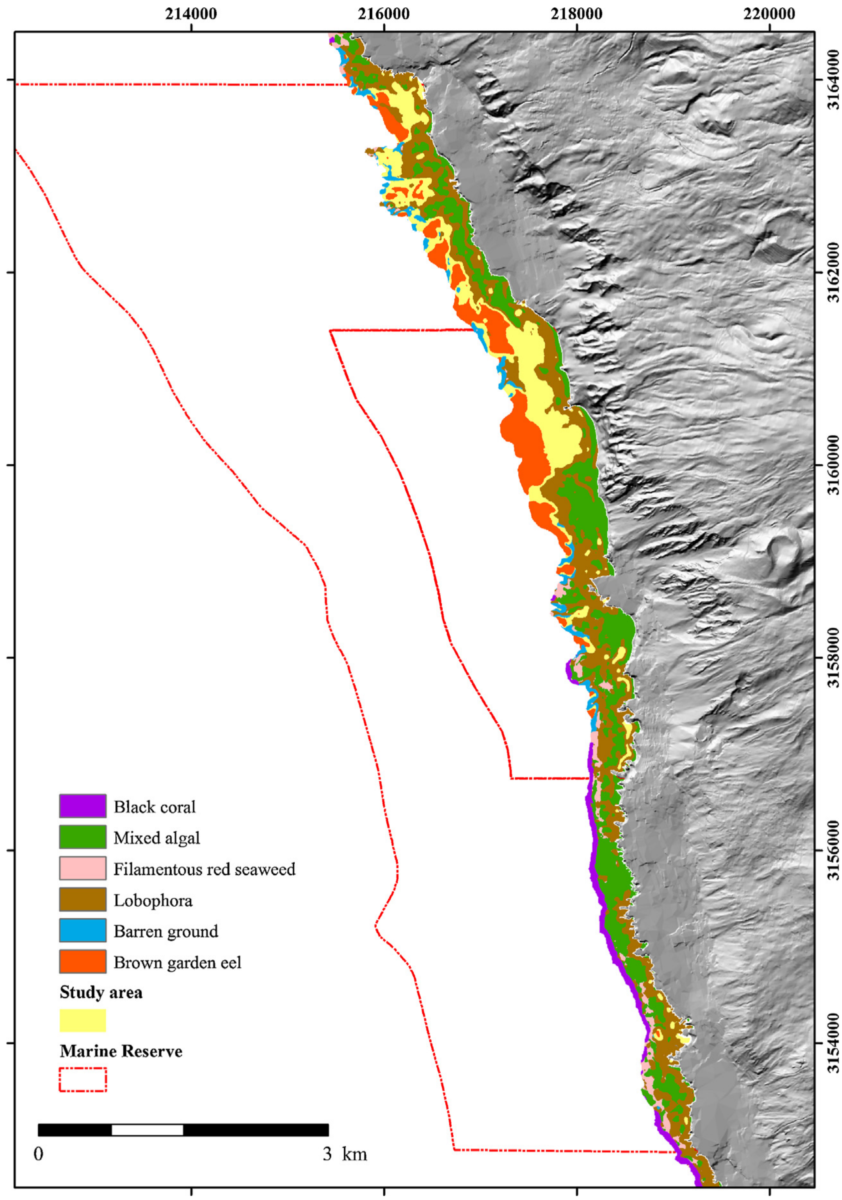

Fig. 2. Distribution maps of benthic communities in the study area created from the combination of the optimum or most suitable habitat overlapped of ENFA predicted maps for every community.

dominant communities as a final result (Ierodiaconou et al., 2011; Jordan et al., 2005). In this study, the distribution models allowed us to obtain continuous habitat suitability maps that were interpreted as the potential of a site to accommodate each community. These maps were reclassified as potential community distribution maps to facilitate the interpretation of data.

4.2. Distribution of benthic communities

The distribution patterns of each benthic community in relation to environmental variables are consistent with the literature and observations in the field. Some communities have similar habitats: hard substrates of shallow water with high ruggedness represent an optimal habitat for *Diadema* barrens, mixed algae, *Lobophora* or filamentous red seaweed communities, producing an overlap between their optimal distributions, although they show some differences, mainly in bathymetry. Barren grounds are generated by the intense grazing activity of *Diadema*, which removes the algal cover (Aguilera et al., 1994; Brito et al., 2004; Hernández et al., 2008a; Tuya et al., 2004). This community has the highest values of tolerance (Table 3), and the models indicated the distribution area is a rocky bottom from 25 m depth (Figs. 2 and 3). The dominance or prevalence of barren grounds over algal communities in these habitats has been linked with the conservation status or protection level (Hernández et al., 2008a; Tuya et al., 2004). However, previous studies on the implementation of the marine reserve in 1999 performed by some authors of this article showed extensive algal beds with a high percentage of *Lobophora variegata* in a rocky benthic habitat, despite the intense fishing activity in the area. Actually, the *Lobophora* community is the most extensive in the hard bottoms of the marine reserve. This community also shows a high tolerance and is even present in surrounding non-protected areas. Therefore, further studies are necessary to understand the biotic interactions and human influence that explain the predominance of these communities in this environment. In the case of the filamentous red seaweed community, although it shares the distribution area,

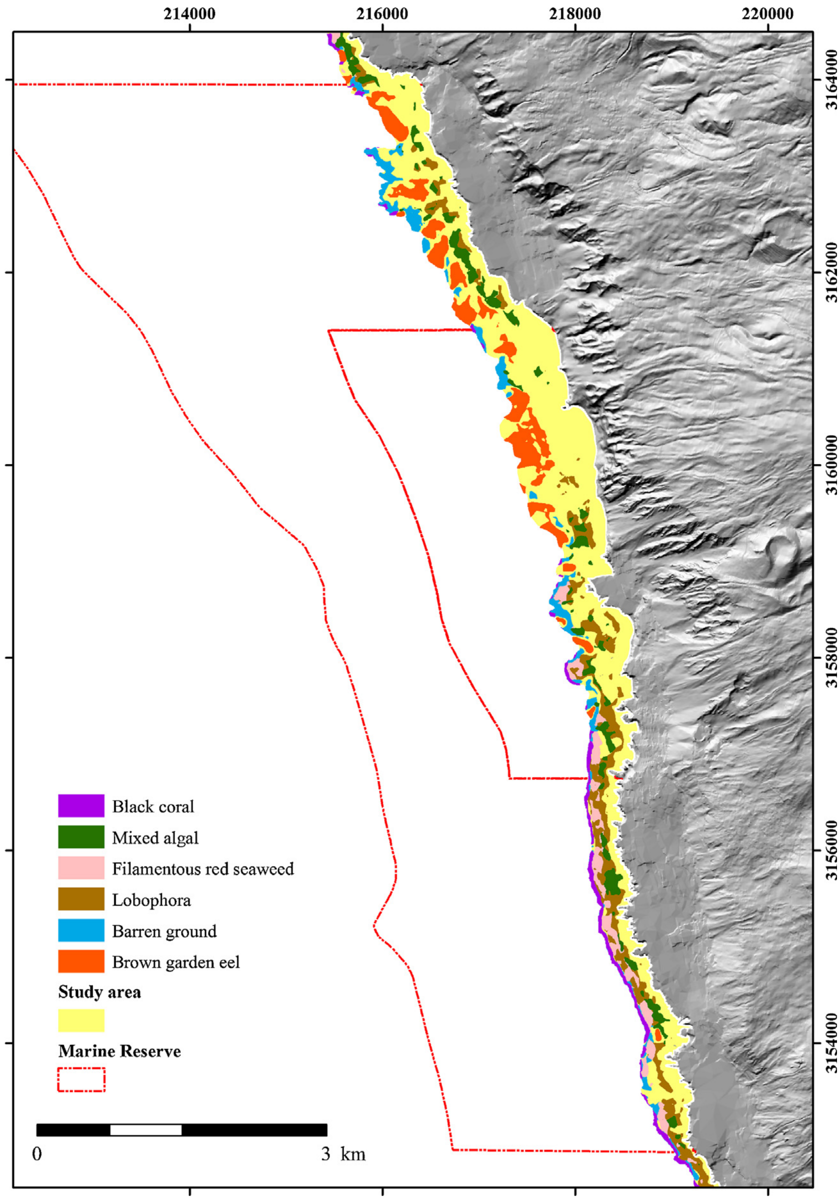

Fig. 3. Distribution maps of benthic communities in the study area created from the combination of the optimum or most suitable habitat overlapped of Maxent predicted maps for every community.

especially with mixed algae and *Lobophora*, it is a dominant community in the interface between sandy and rocky bottoms. For this reason, this community presents low values of VRM and a low range of distance to soft substrate (Table 4) in addition to showing a marginal distribution in the areas with these conditions in the distribution models (Figs. 2 and 3). This result is interesting because, although it has been observed in experimental studies in the Canary Islands (Sangil, 2011), it shows the level of precision these modelling techniques have regarding the marginal distribution of the community. However, black corals were found in extreme conditions where this community presents its optimum distribution area in deep, hard substrate with high values of slope and complex terrain. In some regions black corals also share the optimum distribution with barren grounds. In this case, the presence of barren ground does not seem to hinder the development of black coral and in the field it is possible find both communities sharing the habitat. Finally, brown garden eel (*Heteroconger longissimus*) is one of the most common communities in the sandy bottoms of the Canary archipelago (Barquín-Diez et al., 2005) but is one of the least studied due to its non-existent economic and commercial interest. In our study area, this was the only community present in the soft substrate flats, so any other community competes with this one for habitat. Even the non-optimal areas for brown garden eel did not present any other macroscopic community in either the models or video samples. The distribution of this community is limited by the type of substrate, bathymetry, terrain complexity and BPI 200, so the most suitable habitat is found on sandy flat bottoms from a 30 m depth.

4.3. Model generation and predictor variables

Prediction techniques can help us exploit the information gathered by visual surveys in studies of marine management and can allow us to recognise how the environmental variables influence species or communities and to determine the accuracy of the maps. The limitations in the methodology will be determined by the available information about environmental variables. In our study case, the topographic variables used were sufficient to create reliable

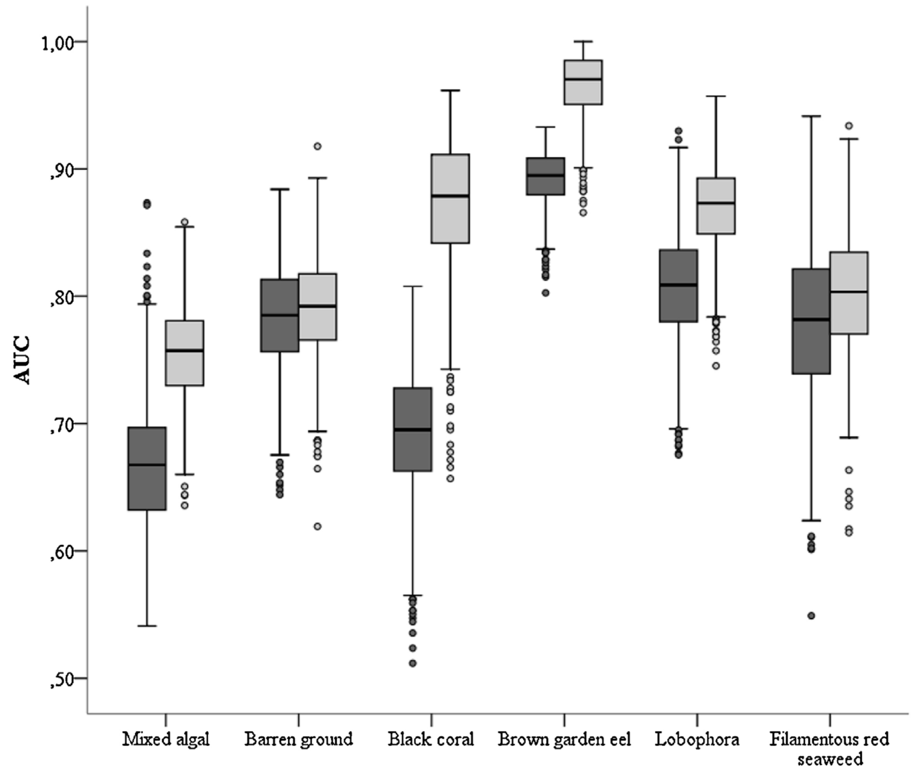

Fig. 4. Results of model evaluation. The boxplot represents the mean (centre lines), standard error (knots), standard deviation (box), range (dot lines) and outliers (circles) of the 10,000 AUC values computed for each model. In dark grey ENFA models; in light grey Maxent models.

distribution models for all the communities, highlighting bathymetry as the main variable contributing to the models. For terrain complexity variables, other descriptors such as curvature or fractal dimension have been included in other studies (Dolan et al., 2008; Galparsoro et al., 2009; Guinan et al., 2009; Wilson et al., 2007), but they were not considered here because of their great similarity to the complex terrain variables used, as they actually represent different methods for calculating the same parameters. Even the two complexity parameters used, topographic roughness and fragmentation index, did not have enough information by themselves to be considered in the final distribution models in most cases. The indices derived from the aspect, northness and eastness, which may be evidence for relation to the wave exposition, had very little or null gain in the models, most likely because of the scale and location of the study area. Multi-scale analysis of the topographic variables (Wilson et al., 2007) has been identified as providing better results than one-scale analysis (Dolan et al., 2008; Galparsoro et al., 2009; Wilson et al., 2007). Nevertheless, the most relevant spatial scales will vary depending on the study area, bathymetric data and biological aspects considered (Wilson et al., 2007). A previous analysis for the present study indicated that the topographic variables exhibited similar behaviour at different scales and that it was necessary to remove broader scales to avoid redundancy of data, with the exceptions of BPI, in which two different resolutions were utilised, reflecting that the study area is too small to show differences in broader resolutions of the variables. Subsequently, BPI 200 showed a greater influence on the characterisation of the ecological niche in ENFA and a higher contribution percentage in Maxent than BPI 35. This case may be explained by BPI presenting a wider range of values with a broad scale. Oceanographic variables (e.g. wave and current exposition, superficial temperature, productivity or water mass properties) were not available at the scale of study area, but they could also be used in tandem with terrain variables to improve the precision of future models and are even essential for explaining the distribution of certain communities working on broader scales.

4.4. Model evaluation and accuracy

The high number of samples was enough to create reliable distribution models in both ENFA and Maxent, which provided very similar distribution maps between the two techniques. However, Maxent was more robust than ENFA: both training and test AUC analysis confirmed that Maxent presented a better performance (Fig. 4). It has also been suggested that complex models such as Maxent are likely to be more accurate at finer resolutions, but would generalise poorly in predicting potential distributions at a large spatial scale, whereas simpler models will offer useful solutions at a broader scale (Jones et al., 2012). The differences in their assessment indicate conceptual differences involving in each of the methods, and a clear distinction of the differences between potential and realised distributions is required (Soberón and Nakamura, 2009). Simple modelling techniques such as ENFA that are based on environmental envelopes generally provide distributions close to the potential, indicating the places where a species could live. Nevertheless, other techniques are able to establish more complex relationships between dependent and independent variables, describing a results model close to the realised distribution, that is, places where a species actually lives, and may over-fit the occurrence data (Jiménez-Valverde et al., 2008; Jones et al., 2012). This situation agrees with the tendency, observed here, of Maxent to produce more constrained predictions than ENFA. Therefore, if these methods are evaluated using presence and absence or pseudo-absence data (data on the realised distributions), the result would be the erroneous conclusion that the complex techniques are more reliable than simpler (Jiménez-Valverde et al., 2008). The differences between the accuracy models are accentuated in communities with fewer presences of black coral and brown garden eels, which presented much lower quality results in the ENFA analysis than those obtained by Maxent. This result confirms the findings of other studies according to which Maxent performs best among different modelling methods and remains effective despite small sample sizes (Elith et al., 2006; Guisan et al., 2007; Hermosilla et al., 2011; Hernández et al., 2008b; Rupprecht et al., 2011). These communities are also the most specific in their environmental requirements, and they had the highest AUC values for Maxent. This result is common for species with restricted environmental tolerances that can be modelled with higher accuracy than those of more generalist species (Tsoar et al., 2007), but this result can be an artefact caused by the comparison of model performances for different species within the same extent, provided that rare/specialist and common/generalist gradients are extent-dependent concepts (Jiménez-Valverde et al., 2008). Given these considerations, both methods are valid although complex techniques as Maxent are more suited for species or communities with few presence data and for studies that need restricted distributions or close to the realised, for example, in the case of endangered species. Studies on broader scale, with sufficient presence data available, ENFA offer less restricted and more general distributions near the potential distribution.

4.5. Distribution models in marine and coastal management

Predictive modelling of species and communities constitutes an important technique with applications in conservation and reserve planning, ecology, evolution, epidemiology, invasive-species management and other fields (Phillips et al., 2006). Knowledge of the geographic distributions and of relations of species with environment is essential for decision-making in the management and conservation of natural resources, offering a means to project the function, composition and structure of sustainable systems over space and time (Richardson and Berish, 2003). Therefore, they can be configured as management tools that have been recognised as local and regional scale. The ability to create reliable distribution models from few georeferenced occurrence data provide many opportunities, such as distribution modelling with historical data and analysis of trends in the distribution of communities. The methodology applied to the rest of the islands of the Canary Archipelago would offer a common analytical framework, and allows the use of important variables on a broader scale. The results of this work provide a methodology and the basis to be followed in future research, enabling to track the changes in the distribution of species and communities.

5. Conclusions

The ENFA and Maxent models provide consistent distribution maps of the main benthic communities identified in the Marine Reserve area of La Palma from the optimum habitat of the model distributions. Prediction techniques allow important information to be obtained from the visual surveys in studies of marine management, namely, the high potential of an area to accommodate different communities, to recognise how environmental variables influence species or communities and to determine the accuracy of the maps. The topographic variables derived from the DEM used in this study were sufficient to create reliable distribution models for all the communities studied and affected the communities in different ways. Bathymetry, type of substrate and VRM are the variables with the highest influence on the distribution of communities in ENFA, and bathymetry, slope and BPI 200 have the greatest influence in Maxent, highlighting VMR as the main terrain complexity variable. The values of the main environmental variables related to the communities are congruent with previous ecological studies. In addition, the results provide new information about the tolerance of communities to the values of topographic variables. This information about habitat characteristics can explain some relationships between different communities that share similar habitats. The distribution models of both techniques were coincident and congruent, although Maxent produced more constrained predictions than ENFA by overfitting the occurrence data. As a result, Maxent presented a better performance than ENFA according to the AUC analysis.

Knowledge of the distribution of benthic communities is essential for good management of marine resources in the Canaries, and these techniques based on distribution models should be considered in subsequent management studies. These tools are useful for continued exploration of the seabed beyond 50 m depth, where the difficulty of sampling increases, provided that sufficient environmental information is available. In the future, these models can be applied at island scale to check whether the patterns of the distributions of benthic communities are preserved or not outside protected areas. These steps will allow the possible effects of human activity to be analysed by adding to the model analysis anthropogenic variables such as fishing, the oversupply of nutrients by sewage discharge or agricultural runoff. Similar studies that include oceanographic variables could even detect possible changes in the distribution of benthic communities due to climate change.

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