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Modelling the Distribution of Key Mediterranean Gorgonians: An Ensemble Approach to Unravel Broad-Scale Patterns and Guide Conservation Efforts

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ABSTRACT

Aim: Determining the species distribution and factors shaping it is a major challenge for conservation planning. Ecological niche models (ENMs) facilitate the comprehension of how environmental factors may influence species occurrence, providing spatially explicit information relevant to conservation. Therefore, our aim was to estimate the potential distribution of key habitat-forming Mediterranean gorgonians, whose conservation would protect many co-occurring species.

Location: Mediterranean Sea.

Methods: We modelled the potential distribution of the Mediterranean gorgonians *Eunicella singularis*, *Eunicella cavolini*, *Paramuricea clavata* and *Corallium rubrum*, using an ensemble ENM that combines nine algorithms. An extensive dataset of presence records (> 4378) collected through scientific surveys and citizen-science was intersected with oceanographic and topographic information within the coralligenous habitat depth range (< 150 m). This approach was used to map the habitat suitability of the study area for each species, assess related uncertainty, identify the most important factors shaping their distribution, and evaluate the overlap with the current network of Marine Protected Areas.

Results: The model identified higher habitat suitability for the occurrence of each gorgonian species in the NW Mediterranean, with roughness and temperature as the main drivers of their distribution. Conversely, the poorly sampled SE Mediterranean showed low habitat suitability, although there is a greater uncertainty associated with this estimate. The combined potential

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distribution of the four species is estimated to cover a quarter of Mediterranean shallow and mesophotic waters, but only 19% was included within protected areas.

Main Conclusions: The habitat suitability and uncertainty maps provide a valuable tool for the conservation and management of Mediterranean gorgonian species by offering spatially explicit information critical for marine spatial planning. The model estimates of habitat suitability showed low uncertainty for most of the study area, with few exceptions in the SE Mediterranean. Further studies, particularly in the SE Mediterranean will contribute to validate these results and will provide new information to improve future modelling efforts.

1 | Introduction

Mediterranean coralligenous temperate reefs represent a highly diverse habitat of particular ecological concern, threatened by local and global stressors including overharvesting, marine pollution, invasive species, recreational activities, and, more recently, warming-driven mass mortality events (Ballesteros 2006; Bevilacqua et al. 2021; Garrabou et al. 2022). Within these systems, gorgonians play a key structural role by creating dense forests that support a wide range of species (Ballesteros 2006). These characteristics make them particularly valuable for marine conservation, and their loss could lead to cascading effects throughout the entire ecosystem (e.g. Ponti et al. 2014, 2016). However, our understanding of the distribution of these Mediterranean coralligenous species at a regional scale is very limited and mainly focused on the NW Mediterranean (see Linares et al. 2020). In this sense, spatial modelling approaches would be key to increase our knowledge about their distribution at large spatial scales.

Ecological niche models (ENMs), also known as species distribution models (SDMs) or habitat suitability models, have become central to understand species distribution and their determinants, generating relevant information for ecology and conservation biology. Notably, the recent rise of global environmental and species occurrence databases (e.g., COPERNICUS, Bio-Oracle, European Marine Observation and Data Network—EMODnet, Global Biodiversity Information Facility—GBIF) together with the development of multiple user-friendly tools (e.g., MAXENT, R packages such as ‘biomod2’, ‘dismo’ etc.; Hijmans, Phillips, and Elith 2023; Phillips and Dudík 2008; Thuiller et al. 2009), are fostering a rapid expansion of their use. This trend is further supported by innovative projects that aim to enhance the current understanding of species distribution, such as enlarging the number of species records through the use of expert-validated citizen science databases (Matutini et al. 2021).

However, ENMs still present some challenges. The proper selection of environmental predictors and the appropriate spatial scale for modelling species ecological niche are crucial aspects often overlooked (see Saupe et al. 2012). Additionally, identifying the optimal ENM method includes a wide range of different techniques and algorithms, from statistical regression methods (e.g., generalised linear models) to machine-learning decision processes (e.g., random forest trees). Advancements in ENMs are leading to the adoption of ensemble—or consensus—techniques aimed at balancing under- and over-estimations of species potential distribution from different individual modelling techniques (Araújo and New 2007; Hao et al. 2019; Thuiller 2003). This approach typically improves model accuracy (Marmion et al. 2009) and predictive performance (Crossman and

Bass 2008) by reducing uncertainty and estimation bias (Buisson et al. 2010; Guo et al. 2015). A further improvement involves reporting model uncertainty alongside the estimate of the species potential distribution to prevent erroneous conclusions (Barry and Elith 2006; Robinson et al. 2017).

The number of publications modelling species distribution in marine systems has increased in the last decades (Melo-Merino, Reyes-Bonilla, and Lira-Noriega 2020; Robinson et al. 2011) along with advances in underwater surveying and habitat mapping technologies (Misiuk and Brown 2024). This trend is noteworthy, as the spatially explicit nature of ENMs output (i.e., distribution maps) is commonly used to guide conservation efforts, for instance by assessing climate change impacts on species distribution or the spread of invasive species (e.g., Adams et al. 2016; Gormley et al. 2015; Srivastava, Lafond, and Griess 2019), among other topics. Marine ENMs have focused mainly on commercial species rather than those forming habitats (Melo-Merino, Reyes-Bonilla, and Lira-Noriega 2020), such as corals, macroalgae and seagrasses. Yet, habitat conservation has proven to be more effective than single-species protection and is gaining prevalence in conservation (Primack 2006). In this sense, marine habitat-forming species should be represented further in habitat suitability models as these species play an important role in highly diverse benthic ecosystems in tropical and temperate seas, providing structural support to associated communities. Furthermore, the adverse effects of global warming may threaten the distribution of marine habitat-forming species and thereby impact numerous coexisting species (Martinez et al. 2018; but see Assis et al. 2022). As such, modelling the distribution of the main habitat-forming species within the coralligenous might be key for its conservation.

To date, few studies have however modelled the distribution of the whole Mediterranean coralligenous habitat (Martin et al. 2014) or single gorgonian species (Boavida et al. 2016; Pulido Mantas et al. 2022), while other studies have focused on limited areas of the well-studied NW Mediterranean (Bellin and Rossi 2023). Outside these areas, the lack of data on the distribution of coralligenous species represents a big challenge for the effective management and conservation of this vulnerable habitat (Giakoumi et al. 2013), highlighting the necessity to expand modelling efforts across the entire Mediterranean basin scale. In this context, we aim to (i) map the regional potential distribution of the four most abundant and representative gorgonian species of shallow and mesophotic depths in the Mediterranean coralligenous assemblages (i.e., *Eunicella singularis*, *Eunicella cavolini*, *Paramuricea clavata* and *Corallium rubrum*) using an ensemble ENM technique; (ii) provide a measure of accuracy about model estimates; (iii) determine the main environmental conditions that better describe the species distribution at the

Mediterranean scale; and (iv) explore the overlap between species' potential distribution and the current network of Marine Protected Areas (MPAs).

Considering the lack of knowledge about the distribution of these species across the entire Mediterranean, this study represents a unique opportunity to enhance the current understanding on the distribution of the modelled species on unexplored regions (i.e., SE Mediterranean) and to estimate their extension at the Mediterranean shallow and mesophotic waters. These insights will enhance our ability to develop comprehensive management and conservation strategies at the Mediterranean scale by prompting spatially explicit information to focus conservation actions and guide the identification of suitable focal areas for further investigations, complementing empirical data on their distribution.

2 | Methods

2.1 | Modelled Species and Presence Data

The four gorgonian species considered in this study are endemic of Mediterranean rocky bottoms. The temperate gorgonian *Eunicella singularis* (Esper, 1791) is a common octocoral in Mediterranean coralligenous and precoralligenous assemblages at depths ranging from 10 to 70 m (Gori et al. 2011; Linares et al. 2008). It is known as the only Mediterranean gorgonian with symbiotic microalgae in their tissue (Carpine and Grasshoff 1975). The yellow octocoral *Eunicella cavolini* (Koch, 1887) establishes distinct facies in the Mediterranean coralligenous assemblages, displaying a broad distribution, albeit with variable abundance. It is known to occur from the western Mediterranean and Tunisian coasts to the Aegean Sea and the Sea of Marmara, extending further eastwards compared to the other modelled species (Sini et al. 2015). The red gorgonian *Paramuricea clavata* (Risso, 1827) is a long-lived species with slow growth and annual recruitment rates, and late reproductive maturity, making it especially vulnerable to disturbances (Linares, Coma, and Zabala 2008; Linares et al. 2007). The red coral *Corallium rubrum* (Linnaeus, 1758) is a precious octocoral endemic of the Mediterranean rocky bottoms and adjacent Atlantic waters. Although it can inhabit depths up to 800 m, its current occurrence has been restricted to areas of difficult access to fishing activities (e.g., caves, vertical walls, isolated rocks) due to decades of overexploitation driven by its very high commercial value (e.g., Montero-Serra et al. 2015).

Presence-only data for the four species were extracted from different scientific and expert-validated citizen science databases. Georeferenced occurrences from scientific data and technical reports were taken from CorMedNet database (<https://cormednet.medrecover.org/>; Linares et al. 2020), while citizen science data were extracted from the *Observadores del Mar* (www.observadoresdelmar.es; Chic and Garrabou 2021) and Reef Check Med (www.reefcheckmed.org; Turicchia et al. 2021) platforms. Additionally, for the red coral, we included validated local ecological knowledge data obtained from SCUBA diving fishermen (Garrabou et al. 2024). Finally, we complemented the remaining information with OBIS data (www.obis.org). We excluded occurrences that fell outside the Mediterranean Sea province as defined by Spalding et al. (2007), those that occurred on land,

and any duplicates. To reduce the spatial clustering of data points (spatial autocorrelation), we thinned our dataset using the 'spThin' package (Aiello-Lammens et al. 2015) of R (R Core Team 2023), which uses a randomization algorithm to maximise the number of presence records within a given thinning distance. A 10-km buffer was established around each presence location to prevent clustering at the spatial resolution of the environmental predictors (0.042°—approximately 4 × 4 km).

2.2 | Environmental Predictors

The selection of the environmental predictors (Table 1) relied on their potential relevance for the ecology of the species and thus, their distribution. Bathymetry has been identified as a determining factor driving the distribution of marine benthic species (e.g., Pulido Mantas et al. 2022; Anakha et al. 2023; Bellin and Rossi 2023; but see Tittensor et al. 2009). In this study, the bathymetric range was restricted to depths ranging from 0 to 150 m, excluding areas devoid of coralligenous habitats (Ballesteros 2006) from the modelled habitat suitability estimation. Temperature, nutrients, current velocity, and light have been highlighted as main factors driving their distribution. Temperature is a key factor for the distribution of the modelling species, with thermal tolerances from 16°C to 20°C in *C. rubrum*, 14°C to 20°C in *E. cavolini*, and 14°C to 22°C in *E. singularis* and *P. clavata* (Previati et al. 2010). Nutrients and current velocity are critical for coral feeding, and may also influence the distribution of these species (Coma et al. 1994; Gori et al. 2015). Light availability is also expected to play an important role shaping the distribution of the zooxanthellae *Eunicella singularis* (Weinberg 1979).

Oceanographic predictors (i.e., temperature, salinity, chlorophyll *a*, nitrates, phosphates, silicates, and current velocity) were extracted from Copernicus Marine Environmental Monitoring services (CMEMS; <https://marine.copernicus.eu/>), using a multiyear annual average (Table 1). Notably, since the four modelled species are sessile, the annual average temperature of seawater at the sea floor (i.e., bottom temperature) was selected, while for the other variables, the values for the sea surface were used. The topographic predictors bathymetry and its derivatives (i.e., bathymetric position index [BPI]; and roughness index elevation [RIE]) were extracted from the European Marine Observation and Data Network (EMODNet; <https://emodnet.ec.europa.eu/>; Table 1) data service, as well as the seabed substrate type. Notably, BPI calculates the difference between the value of a focal cell and the mean of the surrounding cells contained within an annulus shaped window (Lundblad et al. 2006), while RIE quantifies the standard deviation of residual topography in a focal window calculated as the focal pixel minus the focal mean (Cavalli et al. 2008). Since oceanographic data did not fully cover the spatial extent of the presence records, they were interpolated using the analysis tool Nearest Neighbour Analysis for QGIS (QGIS Development Team 2023). The bathymetry derivatives (BPI and RIE) were calculated using an internal radius/cell of 1 and an external radius/cell of 3, 5 and 11 using the R package 'MultiscaleDTM' (Ilich et al. 2023), at the bathymetry native resolution (approx. 0.001°), and then were resampled at the resolution of oceanographic predictors (0.042°). The seabed substrate type information was reclassified into four categories (sand, hard substrate, mixed and others) prior to rasterization for simplicity.

TABLE 1 | Environmental predictors considered for the fitting of the ensemble model. Note that Seabed substrate is a categorical predictor.

Predictor type	Predictor	Min/max (0–150 m depth)	Units	Source	Native resolution	Time interval
Oceanographic	Bottom temperature	14.02/23.25	°C	CMEMS— Mediterranean Sea Physics Reanalysis ^a	0.042°	1/07/1990–1/07/2020
	Salinity	31.293/39.913	psu			1/07/1990–1/07/2020
	Chlorophyll <i>a</i>	0.040/1.917	mg/m ³	CMEMS— Mediterranean Sea Biogeochemistry Reanalysis ^b	0.042°	1/07/2000–1/07/2020
	Nitrate (NO ₃)	0.003/60.175	mg/m ³			1/07/2000–1/07/2020
	Phosphate (PO ₄)	0.004/0.764	mg/m ³			1/07/2000–1/07/2020
	Silicate (SiO ₄)	0.613/17.766	mg/m ³	CMEMS— Mediterranean Sea Biogeochemical Analysis and Forecast ^c	0.042°	1/01/2020–1/02/2023
	Current velocity	0/0.387	m/s	CMEMS— Mediterranean Sea Physics Reanalysis ^a	0.042°	1/07/1990–1/07/2020
Topographic	Bathymetry	–150/0	m	EMODNet Digital Bathymetry ^d	0.001042°	NA
	<i>Bathymetric position index (BPI)</i>					
	3	–13.691/53.612	NA			
	5	–13.299/86.865	NA			
	11	–29.008/198.461	NA			
	<i>Roughness index elevation (RIE)</i>					
	3	0/25.833	NA			
5	0/32.648	NA				
11	0/71.866	NA				
Environmental descriptor	Seabed substrate ^e	NA	NA	EMODNet ^e	NA	NA

^aEscudier et al. (2020).^bTeruzzi et al. (2021).^cFeudale et al. (2022).^dEMODnet Bathymetry Consortium (2016).^eEMODnet (2021).

^fReclassification of the Seabed substrate: The new category ‘Sand’ included the original substrate categories of ‘sand’, ‘sandy mud’, ‘muddy sand’, ‘fine mud or sandy mud or muddy sand’ and ‘fine mud’. The new category ‘Hard substrates’ included the original substrate categories of ‘rock or other hard substrate’ and ‘Coralligenous platforms’. The new category ‘Mixed substrates’ included the original substrate categories of ‘mixed sediment’ and ‘coarse and mixed sediment’. The new category ‘Other substrates’ included the original substrate categories of ‘seabed’, ‘facies with (*Ficopomatus enigmaticus*) of the euryhaline and/or eurythermal biocenosis’, ‘dead mattes of (*Posidonia oceanica*)’ and ‘(*Posidonia oceanica*) meadows’.

The collinearity between predictors were checked with a multicollinearity variance inflation factor (VIF) analysis (Table S1) using the functions ‘vif’, ‘vifcor’ and ‘vifstep’ from the R package ‘usdm’ (Naimi et al. 2014). Additionally, we have also examined the individual correlations with the Spearman’s correlation coefficient, which is suitable for non-linear models, using the ‘corVar’ function from the R package ‘SDMTune’ (Vignali et al. 2020). After the analysis, 11 predictors were retained: bathymetry (m), BPI, chlorophyll *a* (mg/m³), current velocity (m/s), nitrates (mg/m³), phosphates (mg/m³), RIE, salinity (psu), seabed substrate, silicates (mg/m³), and temperature (°C; Figure S1).

2.3 | Ecological Niche Modelling

We modelled the potential distribution of the four species by estimating the Habitat Suitability Index (HSI) computed using an ensemble ENM approach. We used the R package ‘biomod2’

(Thuiller et al. 2009), which supports ensemble modelling and has been extensively used for marine ENM at regional scale (e.g., Chefaoui et al. 2021; Matos, Company, and Cunha 2021; Principe et al. 2021). We employed a combination of nine different modelling algorithms, combining the regression algorithms generalised linear model (GLM) and multiple adaptive regression splines (MARS), the classification schemes algorithms classification tree analyses (CTA) and flexible discriminant analysis (FDA), the distance-based algorithm surface range envelope (SRE) commonly known as BIOCLIM, and the machine-learning algorithms generalised boosting model (GBM) also known as boosted regression trees, random forest (RF), artificial neural network (ANN) and maximum entropy (MAXENT).

For the algorithms ANN, CTA, FDA, GBM, GLM, MARS, RF and SRE, 10 datasets of pseudo-absences (PA) were generated, each containing 1000 data points. The strategy used for generating these PAs was a random selection of points outside the

suitable conditions estimated by a rectilinear surface envelope, following the recommendations of Barbet-Massin et al. (2012). For MAXENT, one run of 10,000 random background points was used (Phillips and Dudík 2008).

The ensemble model only included single algorithm models with the best predictive performance. Algorithms performance was evaluated using the area under the receiver operating characteristic (ROC) curve (Hanley and McNeil 1982), true skill statistic (TSS; Allouche, Tsoar, and Kadmon 2006), and derived sensitivity and specificity metrics. Sensitivity and specificity analyses quantified the predictive accuracy of the model to discriminate between occurrences and PAs locations respectively (Fielding and Bell 1997). Data were split into calibration (70% of the records) and validation (30% of the records) datasets for each iteration and PAs dataset.

In this pre-evaluation process, algorithms with a mean sensitivity < 85 and mean specificity < 80 were excluded from the analyses. For each combination of algorithm and the PA dataset, a total of four evaluation runs were performed.

The performance of each single-algorithm model included in the ensemble model was evaluated using ROC and TSS values calculated for each species and algorithm. According to the ROC value, the models were classified as poor (ROC values < 0.7), reasonable (ROC values between 0.7 and 0.9) and very good (ROC values > 0.9) following the criteria by Araújo and Pearson (2005), while for TSS, models' predictive performance ranged from poor (< 0.4) to good (0.4–0.8) to excellent (> 0.8; Zhang et al. 2015). For each single-algorithm model (i.e., each combination of algorithm and PA dataset) a total of 11 evaluation runs were performed.

The Habitat Suitability Index (HSI) for each species was calculated incorporating the mean of the single algorithm model selected according to the TSS score (≥ 0.8). We chose the TSS score over the ROC value because the ROC can be misleading when evaluating models' predictive performance (Lobo, Jiménez-Valverde, and Real 2007). The coefficient of variation of model estimates provides a measure of uncertainty and was estimated by dividing the standard deviation by the mean of the habitat suitability values. Lower coefficient of variation values indicates higher agreement between model's prediction (i.e., lower uncertainty), while higher values mean higher uncertainty.

To assess the predictors relative importance, we conducted 10 iterations and derived importance scores from 0 (lowest importance) to 100 (highest importance) by using the built-in method provided within the 'biomod2' package. Finally, response curves were generated for the ensemble model of each species and predictor. To reduce the uncertainty in prediction values beyond the range of environmental conditions where the species were reported, response curves were truncated to values within the predictor range.

2.4 | Estimated Distribution of Key Mediterranean Gorgonians

The continuous habitat suitability maps generated by the ensemble model were transformed into the potential habitat distribution (i.e., binary presence-absence maps) using species-specific thresholds. These thresholds were obtained as the cut-off values

that minimised the difference between sensitivity and specificity (Lobo, Jiménez-Valverde, and Real 2007) using the function 'threshold' from the R package 'dismo' (Hijmans, Phillips, and Elith 2023). Considering that 10 PA datasets were used, the species-specific threshold values corresponded to the mean threshold value derived from all datasets used. The potential habitat distribution was mapped for each species and for the four species combined, where the cells occupied by one, two, three, and/or all four species were considered as combined potential habitat suitability. The potential coverage area within the Mediterranean, ranging from 0 to 150 m depth, was computed for both individual species and the assemblage of the four species.

2.5 | Potential Area of Coverage Within MPAs

The binary potential habitat distribution of each species was compared and intersected with areas covered by MPAs to calculate the percentage of potential habitat areas under some type of protection. The MPAs layer was extracted from MAPAMED/MEDPAN (2019, www.mapamed.org), where only the categories 'Marine Natura 2000 site' and 'MPA with a national statute' were defined as MPAs. The intersection was computed both for each species individually and collectively, using the QGIS *Intersection* tool. The percentage was determined by comparing the number of raster cells categorised as 'potential presences' within MPA polygons, divided by the total number of raster cells identified as 'potential presences'.

3 | Results

From the total 7201 initial data points, 4378 occurrences were retained after the data quality check (Figure S2). Of these, 817 were kept after spatial autocorrelation corrections. The occurrences are even distributed among the modelled species (*E. singularis* 182, *E. cavolini* 181, *P. clavata* 187 and *C. rubrum* 267), although unbalanced between Mediterranean ecoregions (Figure 1; Tables S2 and S3).

3.1 | Environmental Conditions at the Location of Species Occurrence

We examined the range of the environmental conditions at the location of species presences (Figure 2). The four species showed a similar pattern for all the predictors. They were predominantly found at temperatures ranging from 14.43°C and 19.77°C, and were more frequent at phosphate concentrations averaging 0.03 mg/m³ (range: 0–0.28), silicate concentrations averaging 1.73 mg/m³ (range: 0.7–4.36), nitrate concentrations averaging 1.05 mg/m³ (range: 0.42–4.44), and chlorophyll *a* concentration averaging 0.15 mg/m³ (range: 0.07–0.46). All presences were exposed to a current velocity ranging from 0 to 0.19 m/s, and salinity ranging from 36.31 to 39.17 psu. Colonies were observed at bathymetries ranging from –2.81 to –150 m, although it seems that *C. rubrum* was found more frequently at deeper areas (mean = –67.21 m) than, for instance, *E. singularis* (mean = –59.64 m). Presences were more frequent at locations with Bathymetric Position Index (BPI) averaging 2.26 (range: –1.83 to 70.77) and RIE averaging 1.68 (range: 0.02–15.33;

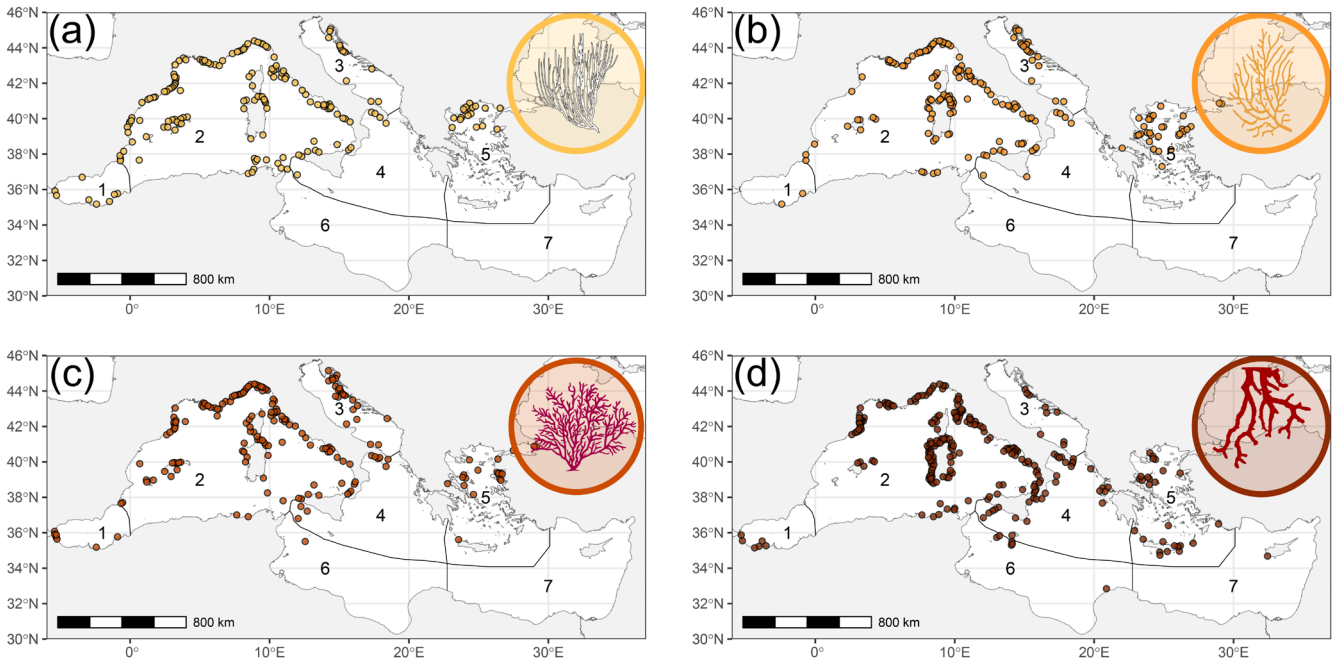


FIGURE 1 | Distribution of the presence records in the Mediterranean Sea by species: (a) *Eunicella singularis*, (b) *Eunicella cavolini*, (c) *Paramuricea clavata* and (d) *Corallium rubrum*. Marine ecoregions according to Spalding et al. (2007) are highlighted using numeric labels: (1) Alboran Sea, (2) Western Mediterranean, (3) Adriatic Sea, (4) Ionian Sea, (5) Aegean Sea, (6) Tunisian Plateau/Gulf of Sidra and (7) Levantine Sea.

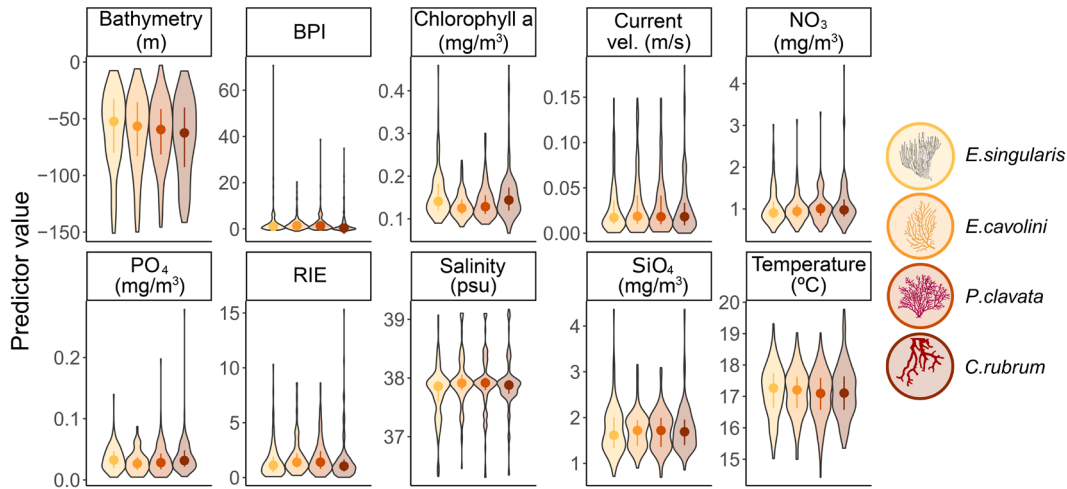


FIGURE 2 | Distribution of species records according to the predictor's gradient. The violin plot represents the density distribution for each modelled species. Median and interquartile range (IQR; 0.25–0.75) are shown for each species. BPI, bathymetric position index, RIE, roughness index elevation.

Figure 2). For the seabed substrate, the majority of presences were consistently found on sand substrate (> 60%), followed by mixed, other types or hard substrates (see Table S4 for details).

3.2 | Modelling Results

3.2.1 | Model Performance

According to the pre-analysis of sensibility and specificity metrics, the SRE algorithm were excluded from the ensemble model for all species. Additionally, the FDA algorithm was also discarded from the ensemble model for *C. rubrum*, and ANN for *C. rubrum* and *E. singularis* (Figure S3; Table S5).

A total of 561 single algorithm models were generated for *C. rubrum* for model fitting, 671 for *E. singularis*, and 781 for both *E. cavolini* and *P. clavata* (see Table S5 for details). All single model algorithms and ensemble models achieved a very good performance on average according to the ROC score (> 0.9). For TSS, the average performance of the ensemble model ranged from 0.82 ± 0.05 to 0.88 ± 0.00 (Figure 3). The single algorithms RFs and GBMs consistently showed the highest performances (Figure 3; TSS > 0.93 ± 0.01). MAXENT and MARS also exhibited the best predictive performances (TSS from 0.82 to 0.88), while the other algorithms (i.e., CTAs, ANNs, GLMs, and FDAs) displayed varying performance (from good to excellent) between species, with some estimates falling below the threshold of 0.8 or displayed a wider range of estimates, indicated higher standard deviation values.

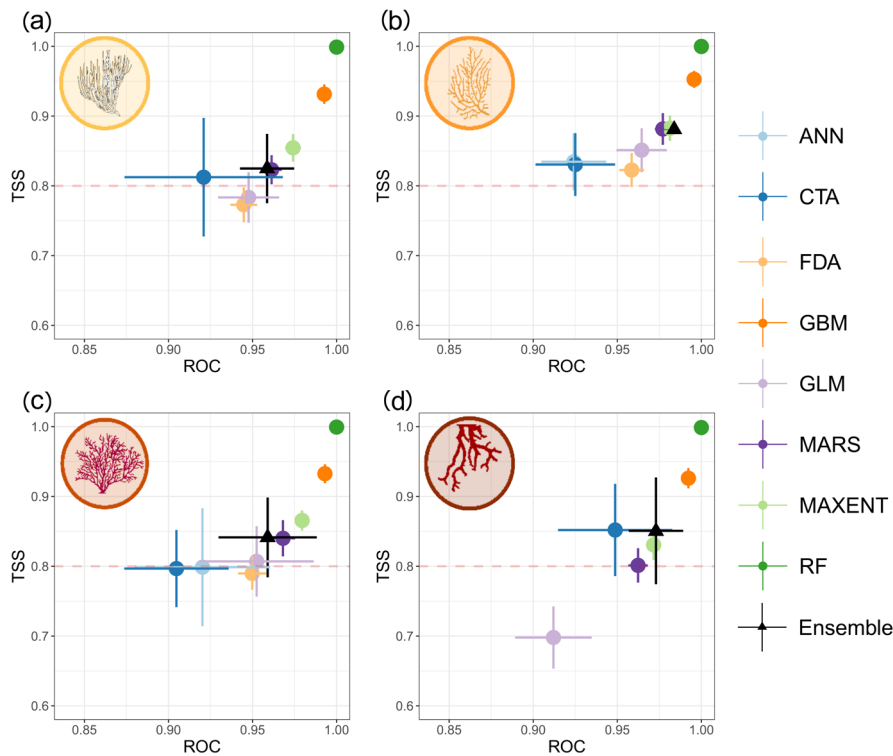


FIGURE 3 | Models predictive performance according to the mean TSS (True Skill Statistic) and ROC (area under the curve of the receiver operator characteristic) by species: (a) *Eunicella singularis*, (b) *Eunicella cavolini*, (c) *Paramuricea clavata* and (d) *Corallium rubrum* and algorithm (horizontal and vertical lines—standard deviation) considering all pseudo-absences and evaluation runs. Dots represent individual model techniques and black triangles the ensemble models. Single algorithm models with performance greater than the TSS threshold (≥ 0.8 pink dashed line) are included in the ensemble model. Only algorithms selected in the species-specific pre-evaluation are considered.

3.2.2 | Contribution of the Environmental Predictors for the Model Estimates

The most important environmental predictors shaping the potential habitat of the four coralligenous species are the RIE (mean contribution = 45%) and mean bottom temperature (mean contribution = 23%; Figure 4). Phosphates, bathymetry, salinity and chlorophyll a are ranked next. Silicates, nitrates, BPI, current velocity and seabed substrate showed small contribution (<8% for all the species; Figure 4) to the prediction of the potential habitat suitability.

3.2.3 | Potential Habitat Suitability and Uncertainty Estimates

The continuous HSI for the four Mediterranean coralligenous species is shown in Figure 5a–d. The highest HSI values estimated (i.e., 80–95) for the four gorgonians was found in the Western Mediterranean ecoregion, particularly in Tyrrhenian and Ligurian Seas, as well as in certain areas of the Balearic Sea. Intermediate to high suitable areas were identified along the Alboran Sea, eastern Adriatic Sea coast, the northern Aegean Sea, and in the Ionian Sea. In contrast, the locations with less suitable environment were found in the SE Mediterranean ecoregions of the Tunisian Plateau/Gulf of Sidra and Levantine Sea.

The habitat suitability estimates from single algorithm models included in the ensemble model were distinct from the

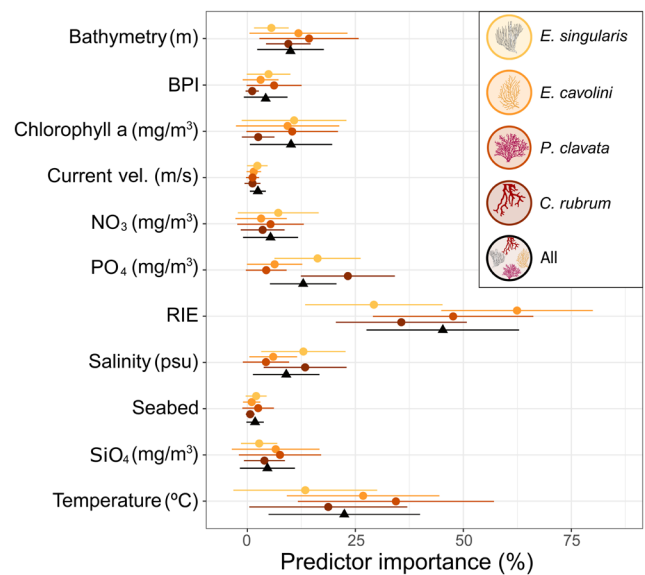


FIGURE 4 | Predictor contributions to the ensemble model prediction by species and all species combined, represented as the mean percentage and standard deviation. BPI, bathymetric position index; RIE, roughness index elevation.

ensemble model projection (see Figure S4 for details). The GBMs algorithms exhibited consistently the small variation. In contrast, the RFs, MAXENTs, MARSs and GLMs tended to underestimate the potential distribution, while FDAs tended

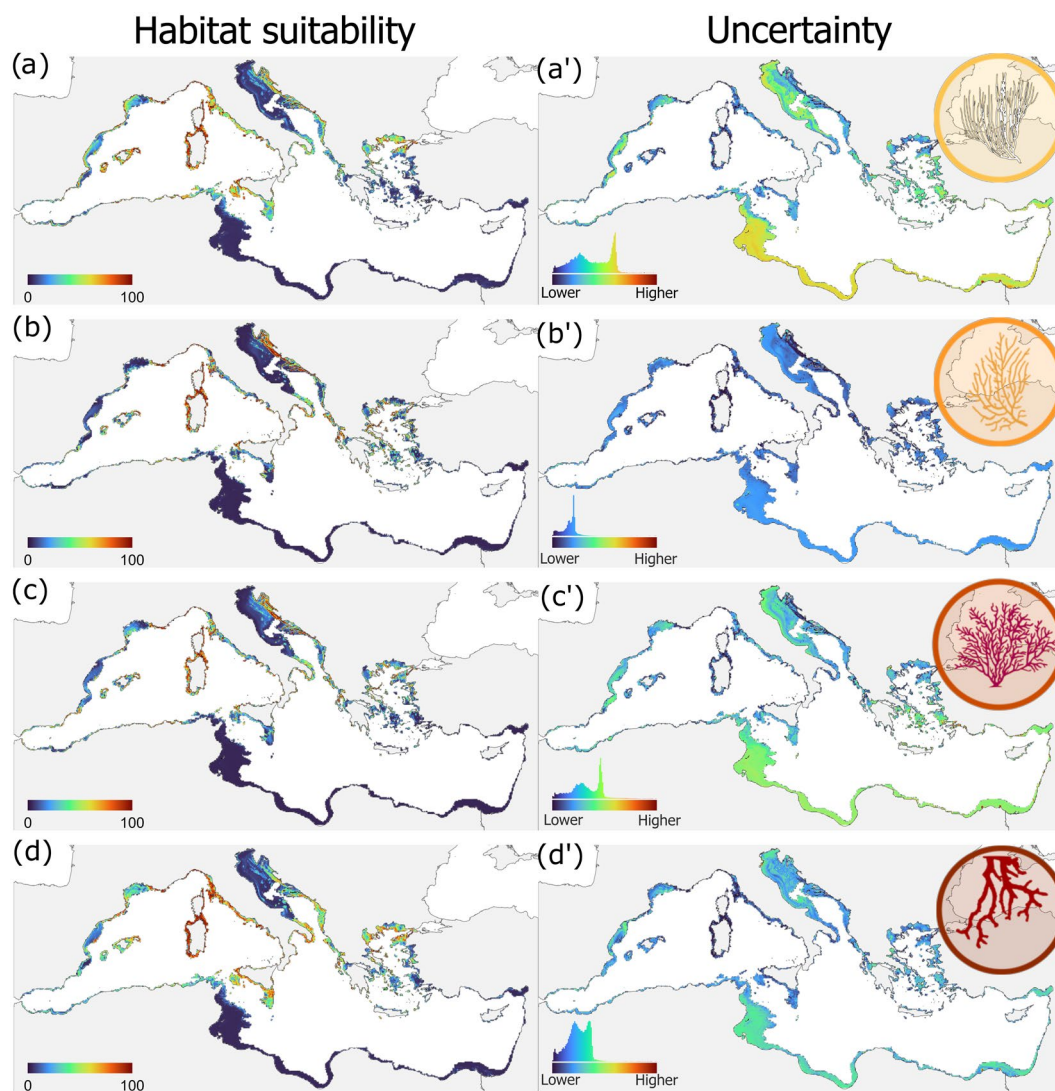


FIGURE 5 | Ensemble model results for each species. Panels on left (a–d) expressed habitat suitability index using a colour scale ranging from blue (less suitable areas; 0) to red (most suitable areas; 100). Panels on right (a'–d') show the model uncertainty estimated by the coefficient of variation (standard deviation/mean of probabilities between algorithms) represented by a colour scale from blue (lower uncertainty) to red (higher uncertainty). The histogram illustrates the frequency distribution of coefficient of variation values for each species. Please note that the uncertainty scale varies across species.

to overestimate it. The difference between the projections of the CTAs and ANNs algorithms with the ensemble varied between species. The MARSS and GLMs algorithms showed the greatest variation compared with the ensemble projection (Figure S4).

The ensemble model coefficient of variation returned overall high uncertainty scores in the SE Mediterranean and NW Adriatic Sea, coinciding with some of the regions where the estimated habitat suitability was lower (Figure 5a'–d'). The uncertainty estimates show a similar pattern for the four modelled species, but with varying levels of uncertainty. The species *E. singularis*, *P. clavata* and *C. rubrum* showed greater variation in uncertainty values, ranging from higher (e.g., SE Mediterranean and NW Adriatic Sea) to lower values (e.g., E Adriatic and Aegean Seas, and overall the Western Mediterranean; Figure 5a',c',d'). The model estimates for *E. cavolini* were less variable, with higher

uncertainty estimates in some specific areas of the Western Mediterranean and Adriatic Sea (Figure 5b').

3.2.4 | Predicted Response Curves

The response curves predicted by the ensemble model (Figure 6) showed contrasting patterns between predictors, in particular with those predictors of greatest importance in the ensemble model for all species (i.e., RIE and temperature). Habitat suitability seems to be higher (HSI > 75 for *E. singularis* and *C. rubrum*, and HSI > 50 for *E. cavolini* and *P. clavata*) in areas where seafloor RIE is higher (> 2). In contrast, the HSI for the modelled species showed a consistent decline with increasing temperature. Most species exhibited high suitability (HSI > 75) in colder waters (15°C–17°C), which then dropped to the lowest values of HSI at higher temperatures (18°C–19°C; HSI < 25 for *E. cavolini*

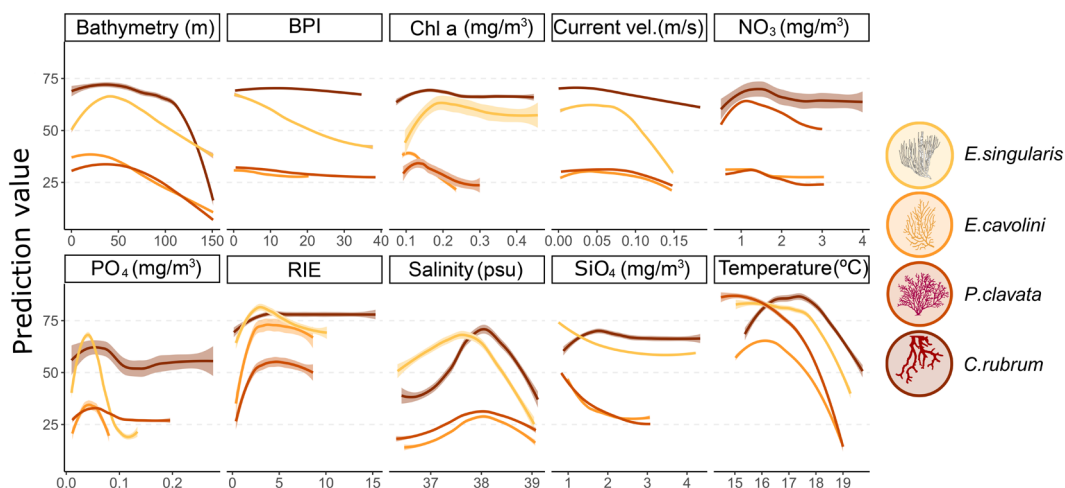


FIGURE 6 | Response curves of the ensemble model for each predictor. The response curves for the species are represented as the mean (solid line) and the 95% confidence intervals (shaded areas) of the ensemble model predictions. The x-axis represents the gradient of the predictor values within the environmental range observed in the presences record. The y-axis represents the predicted habitat suitability values according to the ensemble model. BPI, bathymetric position index; RIE, roughness index elevation.

and *P. clavata*; and $HSI < 50$ for *E. singularis* and *C. rubrum*). For phosphates, the habitat suitability exhibited a peak at concentrations close to 0.05 mg/m^3 , whereas with bathymetry, the environmental suitability consistently decreased from shallow water to higher water depths. The response curves of salinity peaked around 38 psu, while the responses to increasing levels of chlorophyll *a* varied slightly except for *E. singularis*, which showed an increase with increasing concentration of chlorophyll *a* in seawater to values up to 0.2 mg/m^3 . The response curves to the remaining predictors (i.e., nitrates, silicates, BPI, current velocity, and seabed substrate) exhibit minimal variation across the predictor's gradient (Figure 6; see Figure S5 for the complete range of predictor values, and Table S6 for seabed substrate values).

3.3 | Percentage of Areas Potentially Covered by Key Mediterranean Gorgonians and Under Protection

Overall, the combined potential distribution of the four modelled species covers 25.98% of the Mediterranean's shallow and mesophotic areas (Figure 7; Table 2). Notably, *E. singularis* occupies 22.77% of the modelled region, with potential presences determined by cells surpassing a species-specific habitat suitability threshold (minimum difference between sensitivity and specificity: minDSS) of 43.70. *Eunicella cavolini* exhibited a potential occupancy of 14.07%, determined by a minDSS of 57.70, while *P. clavata* can find suitable habitat areas in the 13.58% of the region based on minDSS of 55.49. Finally, *C. rubrum* exhibited an occupancy of 24.01%, based on a minDSS of 44.60 (Figure 7; Table 2).

The percentage of the potential habitat covered by MPAs reached 19.06%. Specifically, *P. clavata* is the modelled species with the highest potential protection coverage by MPAs (18.09%), followed by *E. cavolini* (18.02%). The species *E. singularis* and *C. rubrum* are the species with less area of potential habitat covered by MPAs (11.95% and 10.02%, respectively; Table 2).

4 | Discussion

4.1 | Habitat Suitability and Main Drivers

While ENMs may exhibit a bias towards areas with concentrated presence records (e.g., Western Mediterranean), our models demonstrated the ability to predict relatively higher suitability for locations with intermediate levels (e.g., Aegean, Adriatic, and Ionian Seas) of species occurrence. These ecoregions coincide with well know habitat patches of these species (e.g., Bruckner 2016; Sini et al. 2015; WoRMS 2024). The ensemble model estimated low habitat suitability for all species in the SE Mediterranean (i.e., Tunisian Plateau/Gulf of Sidra and Levantine Sea ecoregions), suggesting poorer environmental conditions for the species occurrence, albeit with higher uncertainty. The paucity of occurrence records in the SE Mediterranean likely influenced these estimates. However, this result may also be attributed to the contrasting temperature gradient between the NW and SE Mediterranean Sea together with a more rugged seascape in the northern Mediterranean compared to the southern regions. Supporting this conclusion is the model's selection of RIE and bottom temperature as the most relevant predictors for estimating habitat suitability. Interestingly, Alboran Sea and the south of the Western Mediterranean ecoregions (i.e., from -5° to 10° longitude), evidenced intermediate to high habitat suitability values with low uncertainty, occasionally surpassing an HSI value of 80 for the *P. clavata* and *E. singularis* species. This suggest that these areas offer greater potential for targeted conservation efforts in the Mediterranean Sea.

Several factors may shape the ecological niche of marine species differently from terrestrial organisms, and this must be considered when applying ENMs. Generally, distribution of mobile marine species relies less on dispersion and more on ontogenetic shifts and feeding conditions. However, coastal benthic species may exhibit greater similarity to their terrestrial counterparts compared to mobile marine species, relying more on dispersion and less on ontogenetic shifts and feeding to find a

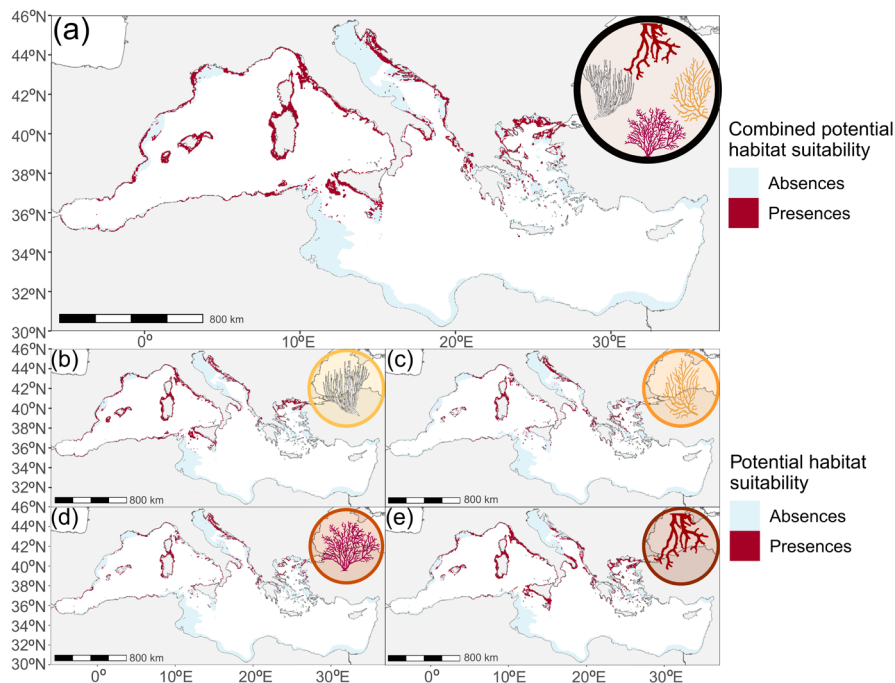


FIGURE 7 | Potential distribution (binary transformation) for the four modelled species combined (a) and species-specific potential distribution: (b) *Eunicella singularis*, (c) *Eunicella cavolini*, (d) *Paramuricea clavata* and (e) *Corallium rubrum*.

TABLE 2 | The percentage of coverage area by potential habitat determined after binary transformation of the continuous estimate from ensemble models for each species and for the four species grouped, as well as the percentage of potential habitat coverage by Marine Protected Areas (MPAs). Binary transformation is based on the minimum difference between sensitivity and specificity (minDSS) threshold.

Species	Coverage area by potential habitat (binary transformation)		Percentage of potential habitat areas covered by MPAs
	minDSS	Percentage of potential habitat	
<i>Eunicella singularis</i>	43.70	22.77	11.95
<i>Eunicella cavolini</i>	57.70	14.07	18.02
<i>Paramuricea clavata</i>	55.49	13.58	18.09
<i>Corallium rubrum</i>	44.60	24.01	10.02
Four species grouped	—	25.98	19.06

suitable habitat to settle and develop (Robinson et al. 2011; but see Hiddink 2003; Manzur, Barahona, and Navarrete 2010). Our study identified (i) roughness—a proxy for rocky habitats—and (ii) mean bottom temperature, as the most important factors determining the distribution of the modelled species. Indeed, the ensemble model prediction for areas classified with higher habitat suitability exhibited low uncertainty, indicating high agreement between single-algorithm models estimate. These areas coincide with steeper slopes, a proxy for rocky habitats, and cooler seawater mean temperatures, which were identified as the most suitable for the species occurrence according to the response curves and predictor contributions.

Roughness index elevation was the most important factor influencing the distribution of Mediterranean gorgonians across the sea basin. Although the importance of the seafloor substrate in marine ENMs is increasingly recognised (Melo-Merino,

Reyes-Bonilla, and Lira-Noriega 2020; Misiuk and Brown 2024), the existing information currently for the Mediterranean scale is only available at a coarser resolution, limiting, for instance, the current representation of areas with hard substrates. Thus, incorporating seabed roughness as a surrogate for seabed substrate has improved the model, enabling to identify highly suitable areas in locations with known rocky bottoms. This type of substrate is preferred settling areas by octocoral larvae (Linares et al. 2008; Zelli et al. 2020). Likewise, the model was able to identify areas with low HSI in environments dominated by sandy substrates. For example, in the Adriatic Sea we observed an estimate of HSI consistent with prior research (Martin et al. 2014; Boavida et al. 2016; but see Bellin and Rossi 2023), with high suitability along the rocky east coast and lower suitability in the sandy west coast. This result ensures our confidence in the model's capability to estimate the distribution in areas with lower sampling effort. Moreover, contrasting to previous findings

estimating the potential distribution of the modelled species for the Spanish and French coasts (Western Mediterranean; Bellin and Rossi 2023; Boavida et al. 2016; Martin et al. 2014), our research also identifies for the first-time higher HSI in rocky regions (i.e., north of the Catalan coast and south of the French coast) and lower HSI in the sandier areas (i.e., south of the Catalan coast). Exceptionally, *E. singularis* displayed higher suitability on the shallower zone of these predominantly sandy regions. This preference for shallower habitats, evidenced by the bathymetry and chlorophyll *a* in the response curves, is explained by the symbiotic relationships with microalgae under light conditions, which only existed in this particular species of gorgonian in the Mediterranean Sea.

Bottom mean temperature was also a critical driver for gorgonian distribution pattern. The high habitat suitability estimated for areas with cooler waters (15°C–17°C) and low suitability for warmer areas (18°C–19°C) is consistent with the thermotolerance range described for these species, which prefer cooler thermal regimes (Gómez-Gras et al. 2022; Cau et al. 2018; Pey et al. 2011; Pivotto et al. 2015; Torrents et al. 2008). These results align with in situ measurements of mean temperatures in those regions and a higher concentration of presence records of the modelled species (e.g., 16.5°C in Le Riou-Marseille; 17°C in Cap de Creus—Western Mediterranean; 17.25°C in Mljet—Adriatic Sea; see www.t-mednet.org). However, the values of bottom temperature used in the ensemble model represent the annual mean for the study area. The Mediterranean Sea is characterised by highly contrasted summer and winter temperatures especially in shallower depths. This seasonal variability, marked by the mixed layer depth variation, can lead to a wider range of temperature conditions. For instance, temperatures can reach a maximum multi-year mean of 22°C in Cap de Creus, a region where the mean annual temperature is 17°C (see www.t-mednet.org for more examples). Previous studies have demonstrated that long duration exposure to temperature > 23°C, such as the observed in marine heatwaves in the Mediterranean, cause the appearance of the first signs of necrosis (Coma et al. 2009; Crisci et al. 2011), driving high mortality rates in these species (Cerrano et al. 2000; Garrabou et al. 2022). In this context, it is important bearing in mind that the higher frequency, intensity, and persistence of thermal anomalies over recent years have led lethal and sublethal effects on these gorgonian populations (Arizmendi-Mejía et al. 2015; Linares et al. 2005; Viladrich, Linares, and Padilla-Gamiño 2022), driving potential range shifts and rendering shallower populations particularly susceptible to the adverse effects of temperature anomalies (Cau et al. 2018; Ezzat et al. 2013).

Contrary to other studies on benthic species (e.g., Anakha et al. 2023; Bellin and Rossi 2023; Pulido Mantas et al. 2022), our results placed less emphasis on bathymetry, even though it ranks as the third most important predictor for *E. cavolini* and *P. clavata*. Despite modelling within the bathymetric range of the coralligenous habitat (up to 150m), a consistently higher predicted probability was observed in shallow waters. This result can probably be attributed to the dim light conditions that favour the development of coralligenous bioconcretions, formed by the growth of calcareous algae (Ballesteros 2006). Notably, *C. rubrum* maintained a consistently high HSI throughout most of the bathymetric range. This result may be due to the

availability of presence records from less accessibility areas as a consequence of overfishing (Tsounis et al. 2007). Nutrients, salinity, chlorophyll *a*, BPI, current velocity, and seabed substrate, displayed lower contribution to the ensemble estimate. Among the nutrients, phosphates exert the strongest influence on the models. This effect probably arise from phosphates playing a limiting role in Mediterranean productivity compared to other nutrients, such as nitrates, exhibiting a clear east–west gradient with higher phosphate concentrations in the Alboran Sea and Western Mediterranean ecoregions (Lazzari et al. 2016). While nutrients may hold less significance for benthic invertebrate feeders (Robinson et al. 2011), they are of greater importance for coral distribution along with current velocity (Thiem et al. 2006). However, at regional scale, grid-based averaging may have failed to capture this finer-scale variations.

The species exhibit distinct responses to environmental factors at different geographical scales (Levin 1992). Coastal benthic species, for instance, are particularly sensitive to fine-scale habitat variations, therefore ENMs may exhibit enhanced predictive accuracy using finer scale environmental information (Guisan and Thuiller 2005; Turner et al. 2019). Consequently, higher roughness—enhanced habitat heterogeneity—emerges as key driver for the modelled species, akin to the influence of slope (e.g., Boavida et al. 2016). Nevertheless, roughness provided a more precise predictor than slope given the preference of these species not only for vertical walls, but also for overhangs and near-horizontal hard substrates. Conversely, predictors such as temperature may assume increased relevance at regional and global scales. Intrinsically linked to the geographical scale, model resolution has a significantly impact on the performance and predictions accuracy of the model (Guisan et al. 2007; Manzoor, Griffiths, and Lukac 2018; Turner et al. 2019). Modelling at smaller scales enable higher resolutions, benefiting from more precise predictors available. However, scaling up demands a delicate trade-off between these factors, as larger grid sizes force species predictions to conform into their broader surroundings, resulting in poor predictions (Guisan and Thuiller 2005). Given that ecological patterns identified at one spatial scale might not be prevalent to another, ecological phenomena and environmental impacts should be studied at multiple scales.

4.2 | Ensemble Ecological Niche Model: Challenges and Opportunities

The accuracy and reliability of ENMs predictions are influenced by the quality and quantity of data, as well as the model settings. Our ensemble model demonstrated a high predictive performance, although estimates for the SE Mediterranean and NW Adriatic Sea exhibited higher uncertainty. Our results may improve by including other variables than abiotic factors, such as biotic determinants (e.g., interspecific interactions) and mechanisms influencing how a species inhabit at a specific location (e.g., dispersal determinants or biogeographical barriers). Although recent advancements in distribution models strive to integrate these multifaceted factors that collectively shape the ecological niche (e.g., joint ENMs approaches or network analysis; Deneu et al. 2021; Ovaskainen and Abrego 2020; Pollock et al. 2014), caution is advised when interpreting ENM results. In our study, the limited presences in the SE Mediterranean may

hinder models from fully capturing the ecological niche of species. The model prediction relies on the best available environmental data available for the entire modelling area and species ecology, but with the inherent limitations at this geographical scale (e.g., lower resolution, varying time scales between predictors, etc.). These limitations, together with model constraints, may restrict accurate predictions in SE Mediterranean, echoing the need of further studies (Hao et al. 2020). Indeed, some evidences, albeit scarce, of the presence of these species in the literature (see for example the evidences of red coral fisheries in the SE Mediterranean, Tsounis et al. 2013) highlight the importance of additional sampling effort directed to this area and to enhance future model attempts. However, it is important to remember that the habitat suitability maps are closely linked with the associated uncertainty maps. In areas with low sampling effort but located in sandy regions, the models were relatively accurate. However, in areas with higher environmental variability than those where the species is present (e.g., SE Mediterranean), the single algorithm estimates were distinct, leading to higher uncertainty. In our study, the combination of the habitat suitability and uncertainty maps about the ensemble models estimates, provide relevant information for future conservation efforts. Nevertheless, it is important to highlight that the projected output represents a model of the potential species distribution, which may not precisely reflect their actual distribution, requiring therefor ground-truthing surveys. The use of the ensemble modelling approaches is however probably the most appropriate approach to achieve balance within under- and over-estimations, and robust predictive performance.

4.3 | Concluding Remarks and Conservation Implications

In light of the dramatic increase of multiple threats affecting coralligenous species, including marine heatwaves driving mass mortality events (Garrabou et al. 2022), coupled with their key ecological role as habitat-forming species, research on their spatial distribution at regional scale and the underlying environmental drivers remain surprisingly limited (but see Bellin and Rossi 2023; Boavida et al. 2016; Pulido Mantas et al. 2022). By combining efforts of both scientific surveys and citizen science, we have gathered a total of 4378 occurrences of the four most relevant Mediterranean species that play key structural roles in coralligenous assemblages. To our best knowledge, this study represents the first attempt to assess the habitat suitability of *E. singularis*, *E. cavolini*, *P. clavata* and *C. rubrum* at the Mediterranean Sea scale, using a multi-algorithm approach and accounting for uncertainty. Implementing a rigorous model approach, we found a clear preference for rocky habitats and an influence of mean bottom temperature shaping their distributional pattern. The NW Mediterranean was the region identified with higher habitat suitability for all species, while the SE Mediterranean region was identified as providing the poorer environmental conditions for the species occurrence, although with higher uncertainty about the model estimates.

The potential extent of coralligenous habitat dominated by key but threatened gorgonian species exceeds a quarter of the Mediterranean bottoms (up to 150m depth). This highlights the importance of this study to guide further investigations to

complement empirical data on their distribution. However, only a fraction (19%) of this potential habitat is currently under protection regimes, underscoring the need for improved conservation and management measures. This estimate is likely optimistic, especially considering the low proportion of highly protected MPAs, the number of MPAs lacking implemented management plans, and the observed lack of enforcement in some MPAs (see Sala et al. 2021). In fact, our results offer spatially explicit information that can guide management strategies, including the expansion of the current MPAs network. Given the potential impact of marine heatwaves on contracting the bathymetrical and geographical distribution of these species, further studies should be focused not only on increasing sampling efforts to validate our estimates but also incorporating projections of species distribution under various climate change scenarios. Yet, current data availability might not be enough to produce useful outputs, as model transferability onto distinct conditions can increase uncertainty to non-relevant levels for spatial planning. Therefore, at the moment, our findings are the best effort to guide future conservation strategies for coralligenous habitat dominated by key gorgonian species. Although achieving the effective international coordination needed for their protection may be challenging, these findings can direct attention to suitable focal areas, to explore with higher resolution models at the local scale. Finally, these outcomes underly the need to redirect management efforts in the face of existing inadequate measures (e.g., sites without protection measures such as Natura 2000 sites) in addressing local stressors that may synergize with global impacts (e.g., climate change and diving frequentation; Zentner et al. 2023). Targeted habitat protection is essential for an effective management that strives to mitigate the current escalating local and global threats.

Author Contributions

C.L. and J.G. conceived the idea and provided funding for the study. L.F.-F. and D.A. prepared the environmental predictors for the model. L.F.-F. and F.L.M. performed and validated the statistical analyses. L.F.-F., Y.Z., D.A., F.L.M., J.G., and C.L. interpreted the results and prepared the visualizations. L.F.-F. and C.L. wrote the first version of the manuscript, with contributions from all co-authors. All authors approved the final version of the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in “CORA. Repositori de Dades de Recerca” at <https://doi.org/10.34810/data1831>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.