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RESEARCH ARTICLE

Improving MaxEnt reliability with multi-criteria analysis and site weighting: A case study on *Caulerpa cylindracea*

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Abstract

1. The rapid spread of invasive alien species (IAS) underlines the urgent need for predictive modelling to accurately forecast future spread under climate change. Correlative ecological niche models (ENMs) serve this purpose, but often struggle with sampling bias, overfitting and uncertainty quantification and rely on a certain degree of subjectivity, which limits their reliability.
2. We have developed an improved ENM framework using MaxEnt that integrates standard and site-weighted performance metrics into a multi-criteria decision process to select models that provide a better balance between explanatory power and transferability. To detect overfitting, we introduced delta metrics that measure the dependence of model performance on the weighting scheme. Furthermore, we performed a sensitivity analysis to quantify the classification uncertainty associated with different probability thresholds. We test this approach on *Caulerpa cylindracea*, one of the most dangerous IAS in the Mediterranean.
3. The selection approach identified an optimal model that showed high and stable performance across all weighting schemes and multiple validation datasets. Both the annual and scenario-based projections show a general shift towards lower habitat suitability, with a statistically significant negative trend in high suitability areas. The decline suggests that the future spread of *C. cylindracea* is likely to be limited to currently invaded areas, assuming no adaptation.
4. The high reliability of the model is supported by the extremely low extrapolation risk (0.21% of the predictions under 'strict extrapolation') and the agreement of the response curves with the known ecophysiology of the species. However, the sensitivity analysis of threshold selection shows a non-uniform pattern of classification uncertainty that appears to be related to invasion stage, with the greatest variability observed in recently invaded regions such as the Northern Adriatic.
5. Practical Implication: This framework provides robust predictions of invasion risk while explicitly quantifying uncertainty. The selection procedure, through delta metrics, explicitly includes model generalisation ability in the ranking process. The annual suitability projections enable temporal prioritisation of control efforts.

Threshold sensitivity analysis identifies areas that require more conservative management approaches, improving the quality and cost-effectiveness of intervention strategies.

KEYWORDS
Caulerpa cylindracea, climate change projections, MaxEnt, model selection, sampling bias, suitability, transferability, uncertainty assessment

1 | INTRODUCTION

Invasive alien species (IAS), an 'alien species whose introduction or spread has been found to threaten or adversely impact upon biodiversity and related ecosystem services' (Regulation (EU) No. 1143/2014, Art 3), pose a significant challenge to the ecological integrity, conservation, and sustainable use of European seas (Coll et al., 2010; Haubrock et al., 2021).

The process of biological invasion consists of several phases—introduction, establishment, spread and persistence—each of which has an impact on long-term management strategies. The latter stages, especially persistence, can have serious ecological consequences, including displacement of native species, habitat modification and disruption of ecosystem services (Boudouresque & Verlaque, 2012).

As climate change can accelerate and alter invasion dynamics (Pyšek et al., 2020), accurately predicting the current and future spread of IAS is crucial for effective control and mitigation measures.

1.1 | Ecological niche modelling and machine learning for IAS predictions

Ecological niche modelling (ENM) is widely used to predict the potential spread of invasive species by estimating the realised niche of an organism under both current and future conditions, thereby supporting risk assessments and management actions (Guisan et al., 2014; Marcelino & Verbruggen, 2015).

Recent advances in the availability of high-resolution data from physical and biogeochemical modelling at global and regional scales (Basher et al., 2018; Cossarini et al., 2017; Fianchini et al., 2024) have improved the resolution and quality of the data used in ENMs. In addition, ensemble approaches that integrate multiple machine learning algorithms have proven to be powerful and help reduce model uncertainties (Thuiller et al., 2009).

Still, ENM applications in IAS studies face several critical challenges. Sparse and spatially biased occurrence data can violate modelling assumptions, inflate performance metrics and compromise results (Yackulic et al., 2013). Climate change further complicates predictions, potentially introducing novel environmental combinations that require models with strong generalisation capabilities to ensure robust predictions (Anderson, 2013). At the same time, 'climate novelty' requires an explicit assessment of extrapolation risk to delineate where and to what extent predictions can be trusted (Fitzpatrick et al., 2018; Owens et al., 2013).

Ensemble methods reduce uncertainty but can obscure ecological signals, which emphasises the need for optimally tuned individual models (Zhu et al., 2021). Overfitting remains difficult to diagnose as standard validation metrics often fail to recognise it, making model selection non-trivial (Merow et al., 2013). Lastly, uncertainty in classification remains a major challenge. Threshold-based suitability assessments can be very sensitive to the choice of parameters, which affects risk interpretation (Liu et al., 2013). Effective quantification and communication of these uncertainties is essential for a transparent and reliable assessment of invasion risk.

Among ENM tools, MaxEnt (Phillips et al., 2006) has proven highly effective for presence-only datasets and is widely used in biological invasion studies (Maruthadurai et al., 2023; Zhu et al., 2014). Extensive research has investigated the theoretical foundations, best practices and the ecological interpretability of the results (Elith et al., 2011; Merow et al., 2013). MaxEnt can be seen as a benchmark for modelling species distribution.

1.2 | Improving the ENM framework

In this study, we present a novel data-driven ENM framework that leverages MaxEnt to improve prediction accuracy while reducing the risk of overfitting. Our approach addresses several long-standing challenges in modelling ecological niches for invasive species by integrating several innovative components. Specifically, our methodology includes:

- A comprehensive exploration of hyperparameter space to optimise the trade-off between model complexity and generalisation.
- Site-weighted performance metrics that account for spatial biases and incorporate complementary data for a more ecologically meaningful assessment;
- A hierarchical multi-criteria decision analysis that uses an objective ranking method to select the best performing model, utilising both cross-validation and independent test datasets.
- Extrapolation risk analysis to assess uncertainty in predictions and a sensitivity analysis to assess the impact of threshold variability on the suitability classification;

- The creation of annual suitability maps that enable dynamic visualisation of projected habitat changes over time.

To demonstrate the effectiveness of this comprehensive framework, we apply it to *Caulerpa cylindracea*, one of the most dangerous IAS in the Mediterranean region. By integrating these novel components, our framework not only improves the reliability of predictions, but also provides managers with additional tools for decision-making. Annual maps provide a detailed overview of forecast trends and interannual variability, while the quantification of uncertainties supports better-informed and risk-aware planning.

1.3 | *C. cylindracea* as a case study

C. cylindracea (Sonder, 1845) is one of the most dangerous clonal invasive algae in the world and has rapidly colonised large areas since its first discovery in the Mediterranean Sea, posing a serious threat to local biodiversity and ecosystem functioning (Klein & Verlaque, 2008).

Due to its easy detectability, identification and well-documented expansion history (Piazzi et al., 2016) *C. cylindracea* represents an ideal model organism for correlative ENM studies.

Its success as an invader is due to its remarkable ecological and physiological characteristics, such as its high growth rate, its highly efficient dispersal mechanism through fragmentation (Uyà et al., 2018) and its ability to rapidly absorb and redistribute nutrients (Gennaro et al., 2015).

Its current distribution and expansion trends show a preference for urbanised coasts and degraded habitats, favoured by the complexity of the substrate and suitable anchorage sites for rhizoids, in synergy with the increasing anthropogenic stress in the Mediterranean (Cantasano et al., 2017; Gennaro & Piazzi, 2011).

A broad spectrum of harmful effects has been documented. *C. cylindracea* competes with canopy-forming macroalgae and seagrasses (Manconi et al., 2020), alters the structure of invaded communities, reduces alpha and beta diversity and prevents the recovery of native populations (Najdek et al., 2020).

2 | MATERIALS AND METHODS

In this section, we detail the data sources, processing steps, modelling framework and evaluation metrics used to develop, select and validate our model. All data manipulations and analyses were performed in R 3.3.0 environment (R Core Team, 2021) and using MaxEnt v3.4.3 (available at https://github.com/mrmaxent/Maxent) through the 'ENMeval2.0' package (Kass et al., 2021).

The study area covers the entire Mediterranean basin (lon.min −5.97, lon.max 36.28, lat.min 30.21, lat.max 45.97; crs = EPSG:4326) with a resolution of 1/24 degree (~16.7 km^2 area). The study period extends from 2000 to 2050 with annual resolution. The future projections are based on the IPCC's Fifth Assessment Report (AR5) using the Representative Concentration Pathway 8.5 (RCP8.5) scenario.

2.1 | Data sources

Data for the period 2000 to 2050 for the Mediterranean Sea were obtained from three different data services: Copernicus Marine Service (CMEMS, https://marine.copernicus.eu/; references of the datasets: Cossarini et al. (2021); Escudier et al., 2021); Centro Euro-Mediterraneo per i Cambiamenti Climatici (CMCC, https://www.cmcc.it/; dataset references: Lovato (2022); Reale et al., 2022); European Marine Observation and Data Network (EMODnet, https://emodnet.ec.europa.eu/; dataset reference: Vasquez et al., 2021). See Table S1 for a detailed description. *C. cylindracea* occurrence records were gathered from European Commission—Joint Research Centre—European Alien Species Information Network (EASIN, https://easin.jrc.ec.europa.eu/; EASIN ID: R18228, verified access 14.02.2024), which harmonises data from a variety of data sources (a list of data sources is available at https://easin.jrc.ec.europa.eu/easin/Partners/Partners). Additional records were obtained from the GBIF service (GBIF.org (2024), dataset DOI: https://doi.org/10.15468/dl.ctg7ht), from Zoheïr (2010), Ould-Ahmed and Meinesz (2007), and from the Reef Check Med (RCMED) Dataset on Key Mediterranean Marine Species monitoring programme (Turicchia, Ponti, Rossi, & Cerrano, 2021); dataset DOI: https://doi.org/10.14284/468, a long-term citizen science project in the Mediterranean Sea consisting of high-quality samples collected by scientifically trained divers (Turicchia, Ponti, Rossi, Milanese, et al., 2021) from 2001 to 2020, including semi-quantitative abundance measurements.

2.2 | Environmental data

Our dataset contains physical, chemical and biological variables as well as two categorical layers, substrate and biozone, for the depth range 0–200 m. For each quantitative variable, the dataset contains five annual statistical descriptors (minimum, maximum, range, mean and coefficient of variance) of the surface and bottom layers. A comprehensive list of the preselected variables can be found in Table S2. See Data S1.1 for a detailed description of the applied methodology.

Categorical rasters were resampled according to the Area Preserving method proposed by Johnson and Clarke (2021), implemented in the 'resample' package (available at https://github.com/mikejohnson51/resample). To focus on biologically relevant regions for *C. cylindracea*, we excluded cells with a bathymetric depth greater than 200 m and considered only the biozone levels (infralittoral, shallow and deep circalittoral) that are ecologically meaningful for the species.

TABLE 1 Layers selected after VIF analysis and used in the modelling process.

Name	Var	Unit	Statistic	Values	VIF score
Temperature	thetao	°C	Max	Surface	1.40
			Min	Surface	1.36
Salinity	so	PSU	Max	Bottom	1.20
Water velocity	KE	m/s	Min	Bottom	1.01
Phosphate	po4	$[\text{mmol}\,\text{m}^{-3}]$	Mean	Bottom	1.69
Net primary production	nppv	$[\text{mg}\,\text{m}^{-2}\,\text{day}^{-1}]$	Mean	Water column sum	1.49
Biozone	-	-	-	Categorical	-
Substrate	-	-	-	Categorical	-

All layers were standardised and projected onto an equal-area, pseudo-cylindrical projection (Eckert IV) to ensure the consistency of the spatial analysis (Renner & Warton, 2013).

A 'present' and a 'future' scenario were created as average values for each bioclimatic variable for the periods 2000–2020 and 2030–2050, respectively.

To identify multicollinearity problems, a stepwise analysis of the variance inflation factor (VIF) was performed using strict threshold values (correlation threshold = 0.5, VIF threshold = 2.5; see Craney & Surles, 2002). From this analysis, we selected a subset of eight variables (Table 1) that were only minimally affected by collinearity issues and that collectively capture important aspects of the species' ecological niche, such as thermal preference, mechanical tolerance, nutrient exploitation and habitat preference.

2.3 | Occurrence and background data

The occurrence dataset was compiled from all available sources for the period 2000–2020, excluding records with incomplete metadata (e.g. missing sampling time or geographic coordinates). We applied a threshold-based labelling method to filter the occurrences. Note that thresholds were chosen as a practical solution to maximise the validity of the dataset while obtaining a sufficient number of observations for robust analyses. A site (i.e. spatial cell) was classified as a presence if it contained at least three unique occurrence records. For RCMED samples that provided abundance values between 0 (species sought but not found) and 6 (very dense meadows), a cell was only classified as absence if it contained at least five records indicating an abundance of zero and no conflicting observations of presence. If multiple records within a cell had different abundance values, the highest value was retained as a precaution.

Background sites were defined as all valid cells within the study area that had a bathymetric depth of less than 200 m to ensure that they were centred on the euphotic zone necessary for photosynthesis and were within 200 km of the presence sites. This conservative definition is consistent with the species' dispersal potential and the documented expansion rate of 1–10 km/year (Iveša et al., 2015; Montefalcone et al., 2015). To preserve spatial independence of the validation set, areas within 20 km of the RCMED sites were excluded from training.

In total, this ecologically informed sampling strategy yielded 449 occurrence sites and 25,740 background sites for model calibration, as well as a curated validation set consisting of 81 presences with abundance and 85 absences. A spatial representation of the occurrences and the study area can be found in Figure 1 (top).

2.4 | MaxEnt framework

The occurrence–background data were partitioned using a 5-fold masked geographically structured approach (Radosavljevic & Anderson, 2014). The identification of an appropriate distance band for data separation was based on the analysis of the semi-variograms of the predictors (*drange*; see Data S1.4 for more details).

To ensure the convergence of the models, the MaxEnt internal maximum number of iterations was increased to 100,000. An extended test of different hyperparameter combinations makes it possible to optimally balance the bias–variance trade-off and ensure robust model selection (Low et al., 2020; von Luxburg & Schölkopf, 2011).

For this reason, we tested all possible combinations of regularisation multipliers (*rm*: from 0.5 to 20, 0.5 each) and MaxEnt feature classes (*fc*: linear, quadratic, products, threshold, hinge), resulting in 1240 models fitted with no clamping (i.e. allowing extrapolation outside the training range; Street, 2020).

The threshold value that maximises the sum of sensitivity (true positive rate), and specificity (true negative rate) (*maxSSS*; following Liu et al., 2016) was used to classify the probability of occurrence into suitability.

2.5 | Model evaluation

We evaluated all fitted models using metrics that capture important aspects of model behaviour: statistical significance (partial ROC), predictive ability (AUC, SEDI, OR10p), transferability (CBI), overfitting (AUCdiff) and complexity (AICc) (see Table 2 for metrics description). Building on previous work by Zhang et al. (2020) and using the package 'enmSdmX' (Smith et al., 2023), we implemented a novel weighting system that mitigates spatial biases in the occurrence data and is more sensitive to the ecological signal. During cross-validation, both occurrences and background test sites were

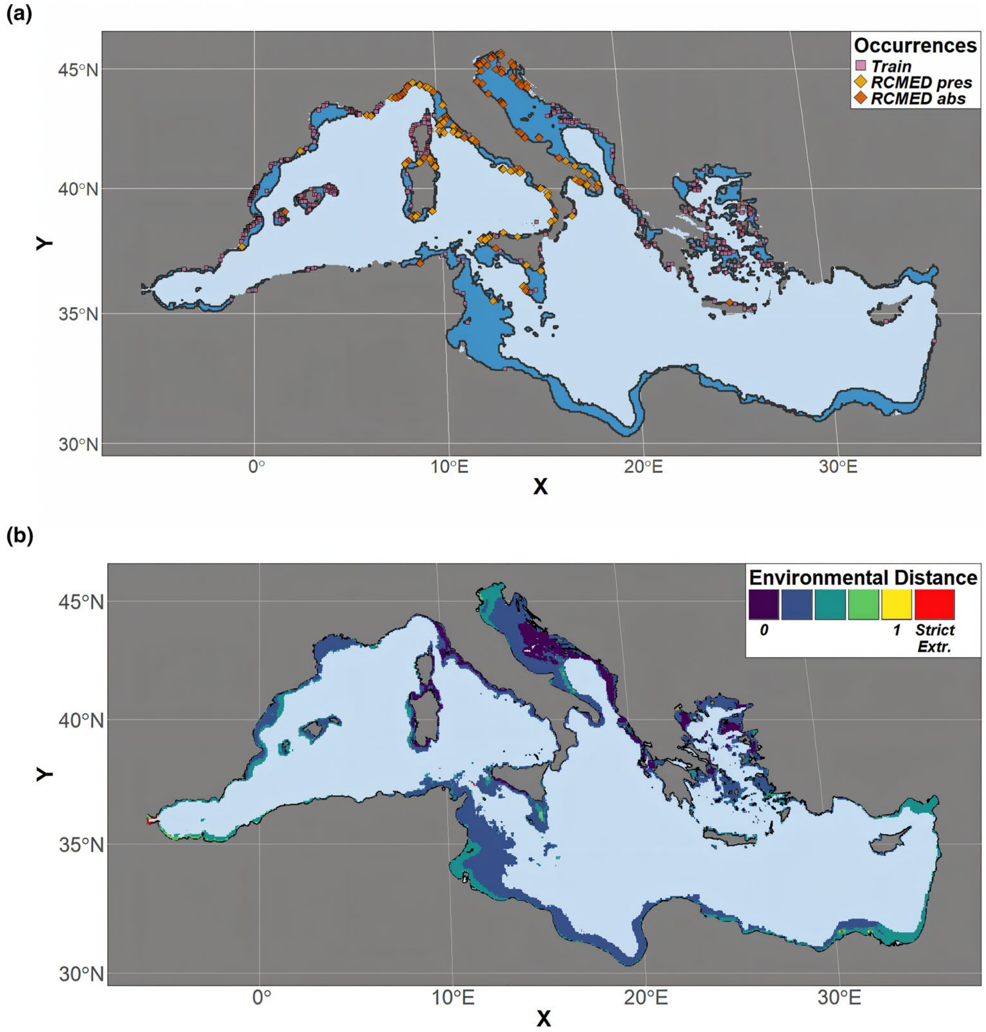


FIGURE 1 Description of the domain. On top, labelled sites and the boundaries of the study area, highlighted in dark blue. Below, mobility oriented parity analysis for the future scenario: The blue to yellow gradient indicates the increasing Euclidean distance between the calibration and the future (2030–2050) environmental space. Red signals areas where future conditions deviate strongly from the environmental combinations used to train the models ('strict extrapolation'). It is noteworthy that there are no visible (significant) 'strict extrapolation' areas, that account for less than 0.21% of the domain surface. This reflects the quality of the training process and the relative lack of 'climate novelties'.

weighted according to their reciprocal distance to reduce spatial autocorrelation effects. For the RCMED dataset, presence sites were additionally weighted by their abundance—reflecting their representativeness for the realised niche—while absence sites were weighted by both reciprocal distance and proximity to presence sites. In practice, this approach ensures that model's extrapolation ability is assessed against ecologically significant observations and is not disproportionately influenced by sample distribution. See Data S1.5 for a technical description of the weighting system.

To detect overfitting, we introduce a complementary set of metrics that measure how much the model's performance changes when weighting is applied, called *delta* metrics. The *delta* metrics are defined as the absolute difference between unweighted and weighted metrics' values. A large *delta* indicates that the performance of the model is distorted by spatial autocorrelation or depends too much on the weights.

Conversely, a small *delta* indicates that the performance of the model remains stable and effectively accounts for the spatial structure and true ecological signal. This stability makes the model more robust against overfitting and therefore more reliable.

2.6 | Model selection

We present a selection procedure that uses the modified Technique of Order Preference by Similarity to the Ideal Solution (TOPSIS; Chakraborty, 2022) to determine the best performing model. TOPSIS is a multi-criteria decision-making tool that ranks alternatives based on their proximity to a positive ideal solution (PIS).

The definition of the PIS is inextricably linked to the purpose of the model (Warren & Seifert, 2011). When modelling the

TABLE 2 Summary of the performance metrics for species distribution models.

Metric	Rationale	Description	References
AUC	Predictive ability	Measures the probability that a randomly selected positive example will be ranked higher than a randomly selected negative one	(Fawcett, 2006)
pROC	Statistical significance	A modified ROC analysis that adjusts the AUC to focus on the proportion of area correctly predicted as present, accounting for model-specific prediction spans and prioritising omission errors.	(Peterson et al., 2008)
SEDI	Predictive ability	Measures the accuracy of deterministic forecasts of rare binary events, robust to low prevalence	(Wunderlich et al., 2019)
OR.10p	Predictive ability	Percentage of test sites where presence was not predicted, using the 10th percentile of training presence values as the threshold	(Muscarella et al., 2014)
AUCdiff	Overfitting	Measures the risk of model overfitting by comparing AUC values between training and test datasets	(Warren & Seifert, 2011)
AICc	Complexity	Relative measure of model fit that considers the number of parameters and penalises overfitting	(Burnham & Anderson, 2003)
CBI	Transferability	Measures the accuracy and the reliability in predicting presence based on the Spearman rank correlation between predicted suitability and observed presence	(Hirzel et al., 2006)
TOPSIS	Transferability	A composite score that measures closeness to an ideal model that maximises all the previous metrics.	

spread of invasive species in the context of climate change, the model must serve a dual purpose: It should maximise its ability to interpolate observed data (explanatory power) while remaining flexible enough to accurately predict unobserved data (transferability). This dual capability is particularly important for invasive species, as overly specialised models may work well with known data but are unable to generalise to new environmental conditions, which poses a significant risk of misleading results in the face of climate change.

The PIS is defined in this study as the ideal model that achieves the highest scores on all performance metrics in both the cross-validation and independent test datasets, while minimising the *delta* metrics.

In the TOPSIS analysis, each criterion (metric) is assigned a weight to determine its influence on the ranking process. To derive these weights objectively, we employ the CRiteria importance through inter-criteria correlation (CRITIC; Krishnan et al., 2021) method. CRITIC assigns weights based on the statistical variance and inter-criteria correlations, ensuring that each criterion's importance is data-driven and avoids subjective bias.

The models are evaluated using cross-validation results, and the candidates are narrowed down to the configurations that maximise each performance metric. In a second step, the shortlisted models are analysed using a hierarchical multi-criteria system. Specifically, we performed separate TOPSIS analyses for the six different metric groups: (1) unweighted cross-validation metrics, (2) weighted cross-validation metrics, (3) cross-validation delta metrics, (4) unweighted test metrics, (5) weighted test metrics, and (6) test *delta* metrics. For each TOPSIS analysis, the criteria weights were determined objectively using the CRITIC method. Each TOPSIS analysis resulted in a sub-score representing the relative closeness of the model to the positive ideal solution (PIS) within that metric group. Finally, these six sub-scores were combined into a new decision matrix and a final CRITIC-TOPSIS procedure was performed to determine the model configuration that showed the best overall performance across all metric groups, that is the model that was closest to our PIS. Further details on this procedure can be found in Data S1.6.

Our multi-criteria approach is explicitly designed to support modelling decisions under high uncertainty. By integrating CRITIC-based weighting, we ensure that no single performance metric (e.g. AUC) dominates the selection process, resulting in a more statistically and ecologically informed ranking of model configurations. This is particularly important for the management of invasive species, where incorrect predictions can lead to costly ecological and economic damage.

2.7 | Projection and classification

The selected model was projected for the entire geographical area according to the 'present' and 'future' scenarios and for each year available in the dataset, assuming that species do not adapt to new conditions. Using the mobility oriented parity (MOP) analysis as defined by Owens et al. (2013) and implemented in the 'mop' package (Cobos et al., 2023), we evaluated the reliability of the model projections under new environmental conditions. Our MOP analysis entails a classification of the Euclidean distance between calibration and projection space, which serves as an index of extrapolation risk. The thresholds for classification were determined using the percentiles of a chi-squared distribution fitted to the degrees of freedom of the environmental variables. In particular, the environmental distances were categorised into quintiles, with all distances exceeding the 90th percentile of the chi-squared distribution being considered as 'strict extrapolation'. The projections in the areas classified as 'strict extrapolation' should be interpreted with caution, as the model attributes probability of occurrence to completely unknown combinations of environmental variables (Elith et al., 2011).

2.7.1 | Suitability classes

From a risk assessment and management perspective, it makes sense to categorise the continuous predicted probability of occurrence (p) into suitability categories rather than presence–absence maps. Based on the *maxSSS* value (th), we have defined four categories: high suitability (HS: $p > \text{th}$), medium suitability (MS: $\frac{2}{3}\text{th} < p \le \text{th}$), low suitability (LS: $\frac{1}{3}\text{th} < p \le \frac{2}{3}\text{th}$) and no suitability (NS: $0 < p \le \frac{1}{3}\text{th}$).

The extreme *maxSSS* values estimated by the fitted models for each partition during cross-validation are used as a measure of classification uncertainty.

2.7.2 | Analysis of annual projections

The analysis of the time series of annual projections integrates the traditional scenario comparison and provides a nuanced visualisation of the predicted evolution of habitat suitability, highlighting both gradual changes and interannual oscillations.

To quantify temporal dynamics, we analysed trends in the spatial extent of each suitability category using the Mann–Kendall trend test (M–K, as implemented in Collaud Coen et al., 2020). See Data S1.7 for an explanation of the test.

3 | RESULTS

In this section, we present the main outcomes of the improved framework applied to *Caulerpa cylindracea*.

TABLE 3 Candidates scores for both cross-validation and RCMED test, ranked by TOPSIS score.

Name	Tune Args	TOPSIS	wAUC (cv)	wAUC (test)	pROC (cv)	pROC (test)	pROC (pval)	wSEDI (cv)	wSEDI (test)	wAUCdiff (cv)	wAUCdiff (test)	OR10.p (cv)	OR10.p (test)	AICc	wCBI (cv)	wCBI (test)
wAUC	fc.H_rm.7	0.88	0.77	0.71	1.40	1.19	0.00	0.52	0.51	0.19	0.10	0.01	0.06	8413.49	0.88	0.76
CBI	fc.HT_rm.6.5	0.85	0.77	0.71	1.40	1.19	0.00	0.52	0.45	0.19	0.10	0.02	0.06	8359.82	0.88	0.76
AUC	fc.T_rm.4.5	0.74	0.76	0.69	1.45	1.19	0.00	0.50	0.46	0.20	0.12	0.03	0.07	8263.02	0.85	0.71
SEDI	fc.T_rm.4	0.73	0.76	0.69	1.46	1.17	0.00	0.53	0.38	0.21	0.12	0.04	0.07	8244.15	0.84	0.69
wSEDI	fc.HT_rm.12.5	0.68	0.77	0.68	1.36	1.16	0.00	0.61	0.44	0.20	0.14	0.01	0.09	8467.64	0.90	0.73
wCBI	fc.H_rm.13.5	0.60	0.77	0.67	1.36	1.15	0.00	0.59	0.44	0.20	0.14	0.01	0.09	8497.15	0.90	0.73
OR10p	fc.T_rm.16	0.41	0.75	0.63	1.22	1.05	0.00	0.56	0.29	0.12	0.10	0.01	0.13	8595.95	0.79	0.42
AICc	fc.QT_rm.1	0.38	0.72	0.63	1.58	1.25	0.00	0.41	0.26	0.37	0.17	0.09	0.09	8114.82	0.61	0.22
wAUCdiff	fc.Q_rm.17	0.38	0.74	0.55	1.23	1.07	0.00	0.47	0.09	0.20	0.14	0.00	0.19	8676.61	0.75	0.22
AUCdiff	fc.Q_rm.20	0.22	0.73	0.52	1.23	1.07	0.00	0.51	0.02	0.18	0.14	0.00	0.22	8701.19	0.74	0.25
pROC	fc.HPT_rm.0.5	0.21	0.71	0.60	1.68	1.25	0.00	0.32	0.15	0.50	0.23	0.19	0.11	8303.27	0.48	0.04

Our final model showed consistently high predictive power in cross-validation and in the independent dataset. Projections for the future environmental scenario indicate that the suitability of the species will decrease in large parts of the Mediterranean region.

Nevertheless, some ‘hotspots’ remain and offer insights into the *C. cylindracea* future distribution. The annual projections emphasise a gradual decline in areas of high suitability and point to long-term ecological pressures that could limit the spread of the species.

3.1 | Model performance and selection

Figure 1 (bottom) shows the results of the mobility oriented parity (MOP) analysis, indicating that only 0.21% of the total cells in the future scenario fall into the ‘strict extrapolation’ category. This result shows that the majority of future environmental conditions are well represented by the training dataset, which increases confidence in the model's projections. The autocorrelation analysis of the environmental variables (see Data S1.4) resulted in a minimum block range of 399106.5 m.

From 1240 fitted MaxEnt models, the multi-criteria decision procedure identified a single configuration that performed best (feature class = hinge, regularisation multiplier = 7.00). This configuration achieved the highest TOPSIS score (0.88) and outperformed the other models in both the weighted and unweighted evaluation metrics. Many alternative configurations showed a significant decrease in predictive accuracy when applied to the independent dataset. However, the selected model maintained consistent performance on both datasets, showed good scores in particular for the weighted metrics and showed low *delta* metrics, suggesting that it robustly captures the relationship between species presence, geography and environment. Details of the candidate metric results can be found in Table 3. A visual comparison of the models' performances can be found in the radar plots in Figure 2 and Figure S4.

3.2 | Projected probability distributions for present and future

The probability density functions (PDFs) of the predicted probabilities of occurrence are shown in Figure 3a (present scenario, 2000–2020) and Figure 3b (future scenario, 2030–2050). A general shift can be observed between the two time periods, with the future projections showing an increase in the lower probabilities of occurrence and a corresponding decrease in the medium to high probabilities. This shift is consistent across all hyperparameter configurations, suggesting a generalised trend towards less suitable habitat conditions for the species in the future.

3.3 | Suitability classification, annual projections and threshold uncertainty

Figure 3c–h illustrates the impact of threshold uncertainty on suitability classification under both current (left column) and future (right column) scenarios.

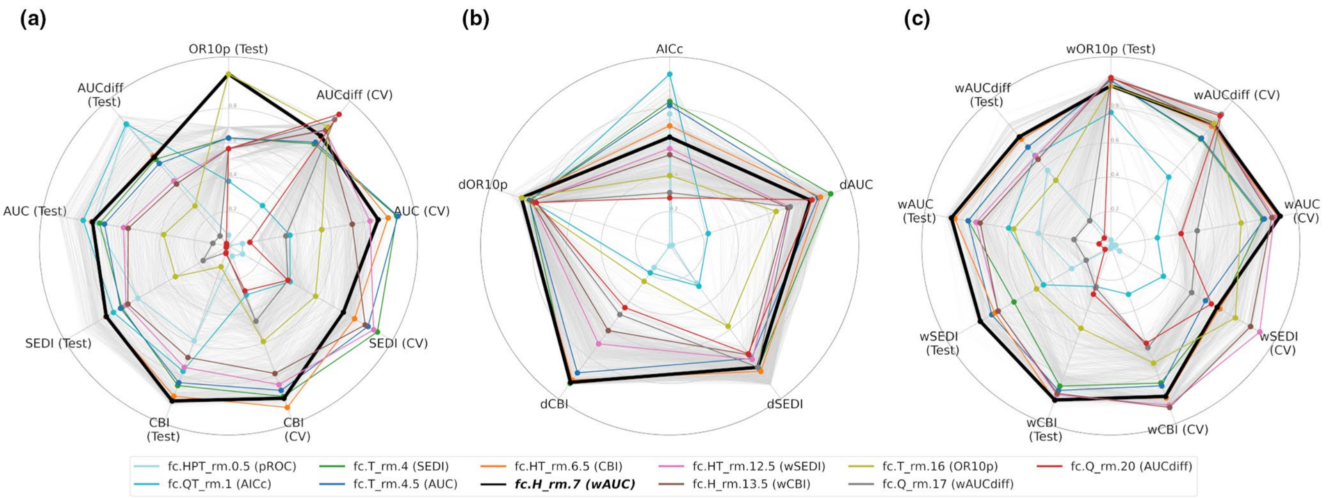
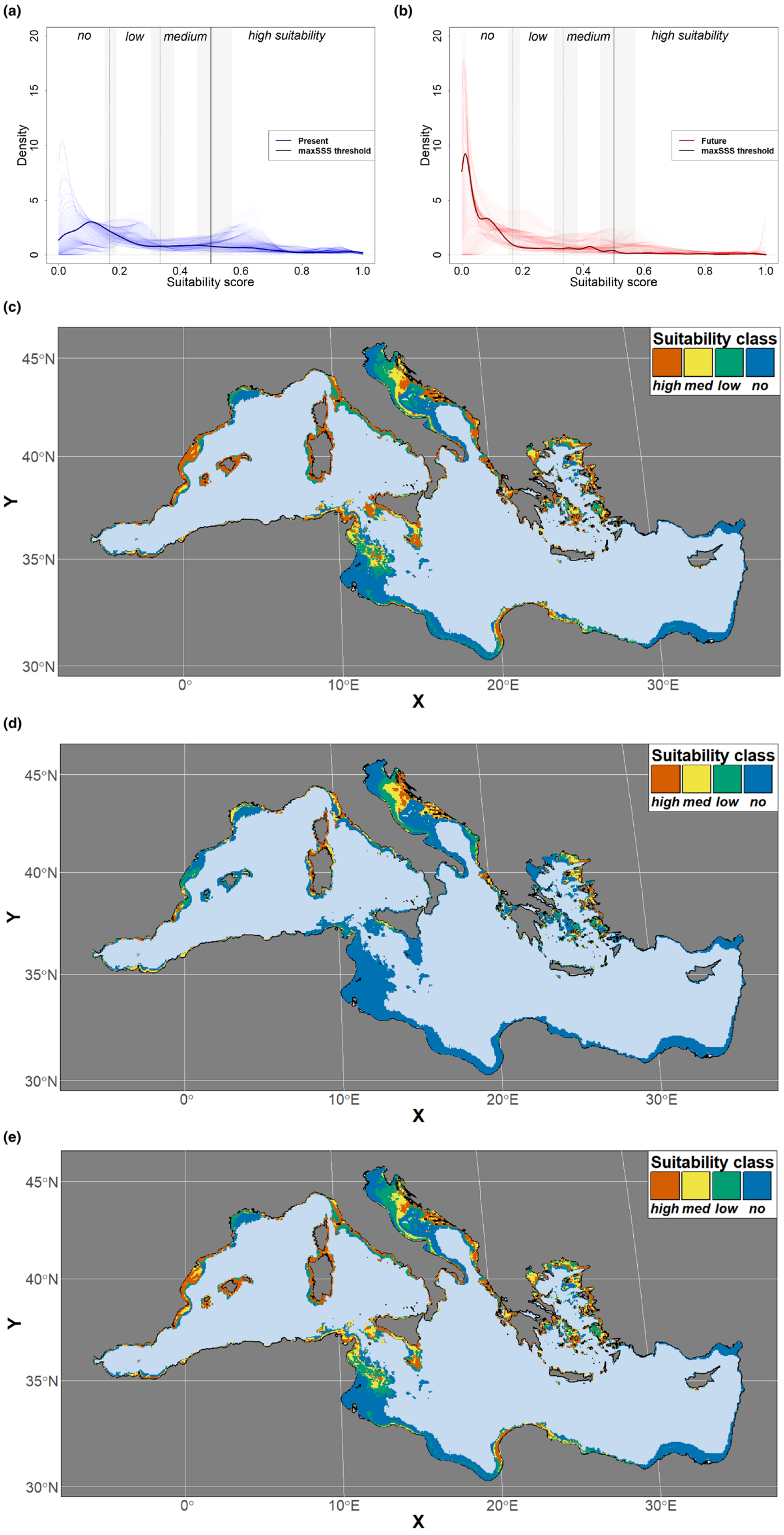


FIGURE 2 Kiviat diagram of model rankings for unweighted (a), weighted (c), AICc and delta (b) metrics. The delta metrics are calculated as follows: $\text{DMETRIC} = |\text{METRIC}_{\text{unw}} - \text{METRIC}_{\text{w}}|$. Coloured lines represent model candidates, while grey lines represent all other model configurations. The model selected by TOPSIS, highlighted in bold, shows the most consistent overall performance.

FIGURE 3 Probability density functions for the predicted probability of occurrence by the 1240 different MaxEnt models for present (a) and future (b) conditions. Thick lines highlight the selected model. Vertical lines represent *maxSSS-based* thresholds used to classify probability of occurrence into suitability. Grey shaded areas indicate threshold range. Suitability maps show how introducing thresholds' uncertainty affects the present (left) and future (right) predictions. ‘worst scenario’ (c, d), using: *maxSSSmin*; ‘normal scenario’ (e, f), using: *MaxSSS*; ‘best scenario’ (g, h), using: *maxSSSmax*.


(a)
no
low
medium
high suitability
Density
0
5
10
15
20
0.0
0.2
0.4
0.6
0.8
1.0
Suitability score
Present
maxSSS threshold
(b)
no
low
medium
high suitability
Density
Suitability score
Future
maxSSS threshold
(c)
Suitability class
high med low no
45°N
40°N
35°N
30°N
0°
10°E
20°E
30°E
Y
X
(d)
Suitability class
high med low no
(e)
Suitability class
high med low no

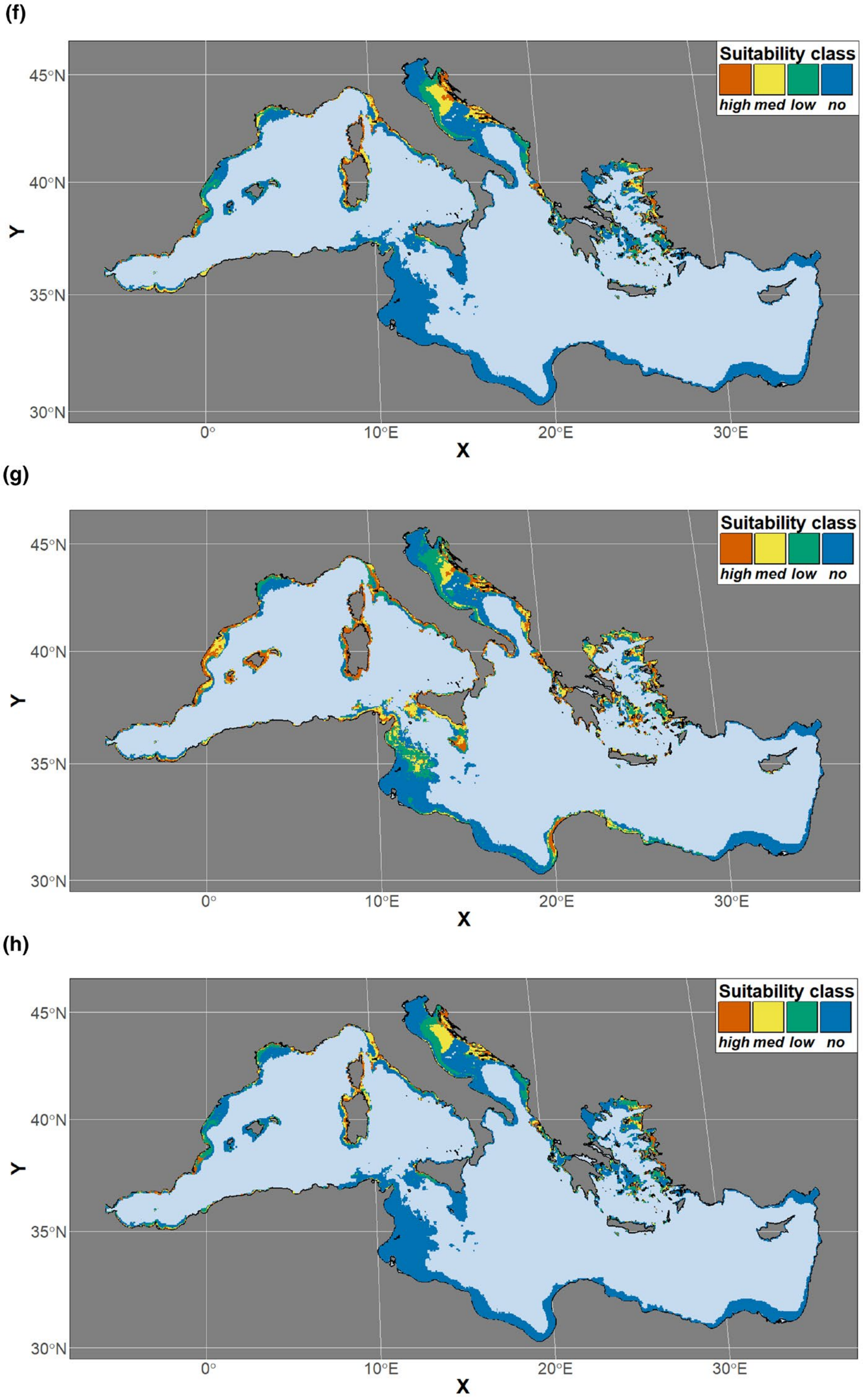


FIGURE 3 (Continued)

The impact of threshold uncertainty varies across the Mediterranean, with the Adriatic Sea showing the highest sensitivity to threshold selection. In this region, suitability classifications vary more between threshold scenarios than in the Western Mediterranean and Aegean. At more conservative thresholds (*max-SSSmax*), large parts of the Adriatic shift from HS to MS or even LS, while the Western Mediterranean and Aegean show a more stable classification pattern.

It is noteworthy that this increased classification uncertainty in the Adriatic aligns with its status as the most recently invaded region. In contrast, the long-established invasion zones in the Western Mediterranean and Aegean show more consistent suitability patterns across all thresholds, indicating a more stable niche occupation.

Regardless of the threshold applied, the spatial extent of HS areas consistently decreases in the future projections, suggesting a widespread reduction in highly suitable habitats.

Annual projections of each suitability class (HS, MS, LS, and NS) from 2000 to 2050 (Figure 4) reveal a significant negative trend ($p < 0.05$, Mann–Kendall test) for HS and MS. Conversely, NS shows a significant positive trend, indicating an expansion of unsuitable areas.

Interannual variability is evident, with short-term fluctuations in suitability areas following fluctuations in environmental predictors. Despite these fluctuations, the overall trend indicates a progressive decline in suitability and a concomitant increase in completely unsuitable areas. The consistent decline in HS and MS across all thresholds and projections emphasises the potential vulnerability of *C. cylindracea* to future environmental change as more regions become increasingly inhospitable for its establishment.

3.4 | Model response curves

Figure 5 shows how the predicted occurrence of *C. cylindracea* varies in response to four key environmental variables—biozone, maximum temperature, minimum water velocity and substrate type—while all other predictors are held at their mean values. Overall, the species shows a higher probability of occurrence in shallow, infralittoral waters (top left), but also tolerates deeper zones. In terms of temperature (top right), suitability peaks at around 24°C and drops sharply beyond 27°C, indicating a relatively strict thermal upper limit. The minimum water velocity (bottom left) shows a moderate optimum at near-zero velocities, with suitability steeply decreasing at moderate velocities. Response to the substrate (bottom right) shows a moderate preference for more complex surfaces, such as mixed sediments and *Posidonia oceanica* meadows. Taken together, these patterns confirm that *C. cylindracea* retains a broad ecological tolerance but exhibits remarkable optima for temperature and water movement.

4 | DISCUSSION

4.1 | Evaluation of MaxEnt model performance and selection criteria

In this study, seven selection criteria were evaluated for their ability to identify models that perform better in an independent presence/absence dataset. To evaluate their abilities, we used TOPSIS analysis to create an overall score that takes into account the simple metrics, the weighted metrics, and the absolute difference between the two scores. The underlying logic is that we want to increase the level of detail in our assessment while minimising the risk of a biased valuation due to the weighting system. In this regard, applying the CRITIC method to estimate the data-driven importance of each criterion in the TOPSIS calculation helped to strengthen the ecological signal by minimising collinearity and avoiding a subjective hierarchy of criteria. The introduction of weighted metrics led to unexpected results that illustrate the complexity of interpreting model performance in the context of machine learning. The performances of most models change, in some cases drastically, between cross-validation and the independent dataset, and between weighted and unweighted metrics. This change is significant as it alters the ranking of the models and thus the model selected.

These differences are interpreted as an artificial increase in model performance due to biases in the data and the individual evaluation procedure, rather than an improved fit (Townsend Peterson et al., 2007). The Kiviat plots in Figure 2a–c represent the performances as areas. A visual comparison makes it clear that the model selected by TOPSIS performs more consistently than the others despite the weighting system and dataset used.

4.2 | Annual projections and temporal trends in suitability

The use of high-quality data at fine time scales enabled the production of annual suitability maps for the period from 2000 to 2050. The Mann–Kendall test can provide insight into the direction of the future suitability trend, although the assumption of no species adaptation requires a cautious interpretation of the strength of this trend. We interpret the results as an indication that the spread of the species is likely to be limited, despite some fluctuations in the currently suitable areas. The smooth annual oscillation is reminiscent of the 'persistence phase' for the 'natural fluctuation' invasion model, as defined in Boudouresque and Verlaque (2012). The highlighted annual fluctuations are of particular interest for management purposes as they indicate years when the environmental pressure on the species may be particularly high or low. This indication could help prioritise eradication and restoration activities, increasing the cost-effectiveness of measures (Bogich et al., 2008).

4.3 | Impact of threshold uncertainty on suitability classification

The suitability classification strongly depends on the threshold value (Liu et al., 2013). By extracting the *maxSSS* thresholds estimated by the fitted models for each partition, we can evaluate how the classification results change depending on the threshold variability, which provides an additional measure of the uncertainty of the predictions.

Changes in the threshold can have a significant impact on the classification results if the peaks of the probability density have similar values or if the threshold has a high degree of uncertainty. This effect can be seen in Figure 3 when comparing the c,g suitability maps.

This could be particularly important for management and decision-making, as cautious approaches should be favoured when there is a high degree of threshold uncertainty. Conversely, low uncertainty allows for greater confidence in the limits of the suitability classes and thus a relatively known margin of safety.

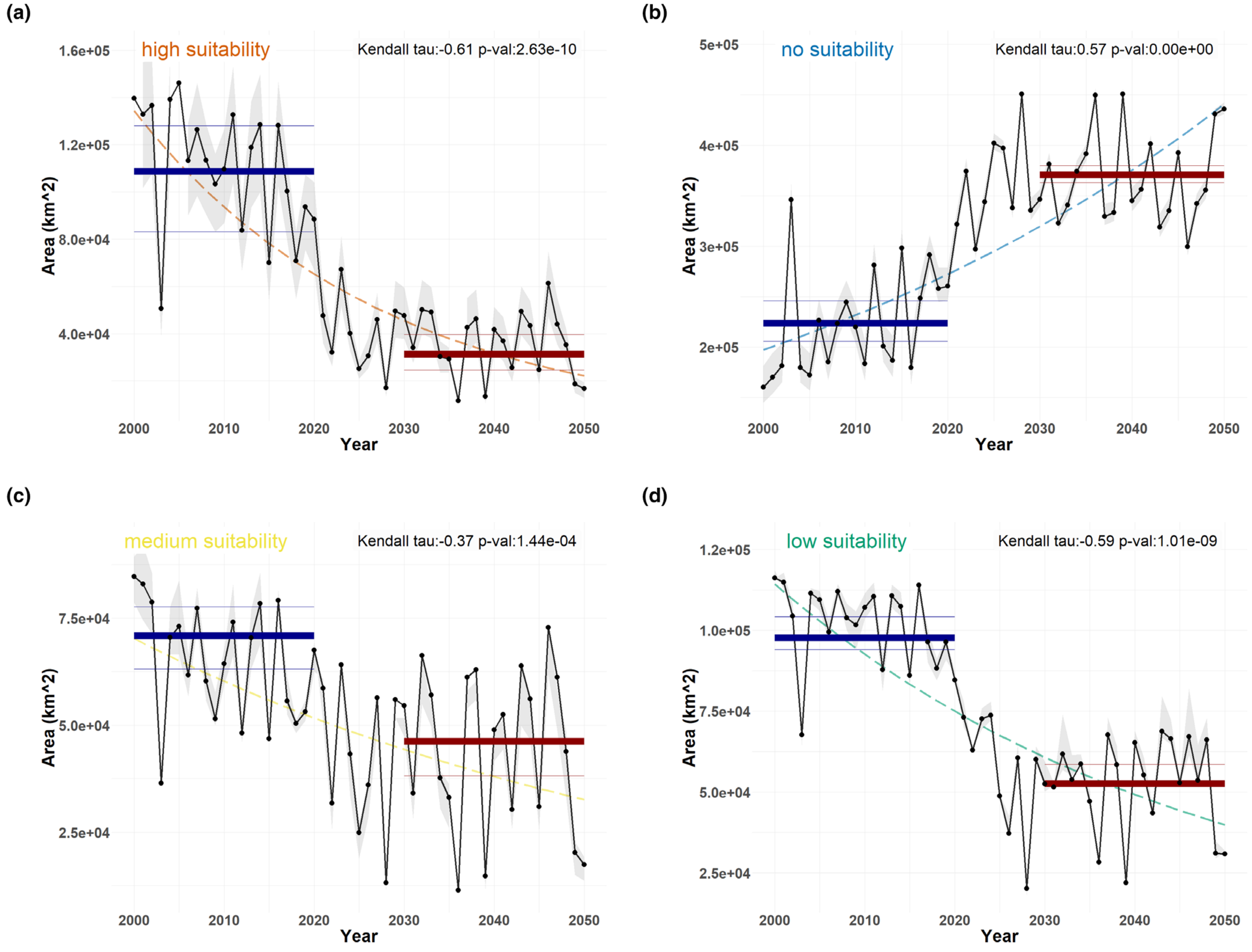


FIGURE 4 Area (km^2) for High (a), No (b), Medium (c) and Low (d) suitability classes as predicted by projecting the model to each available year. The grey area shows the variability associated with threshold uncertainty. Red and blue horizontal lines indicate the area (thick) predicted for present and future scenarios, respectively. The thin lines show the variability of the scenarios due to threshold uncertainty. The dashed line is the exponential fit. The text shows the results of the Mann–Kendall trend test.

4.4 | Response curves and species ecological preferences

In this study, we explicitly aim for ecologically meaningful results by selecting biologically relevant predictors that we can easily compare with the results from the field and mesocosm experiments.

While MaxEnt generates a statistical model that best explains the data patterns in the training set, this does not necessarily guarantee ecologically interpretable results, especially in cases of extreme overfitting (Phillips & Dudík, 2008). However, estimated response curves that are consistent with known species–environment relationships argue in favour of successful model training.

Figure 5 shows the response curves for the most important variables. The preference for shallow waters, but the ability to survive and thrive at greater depths, is consistent with observations (Cantasano et al., 2017). The relationship with the substrate reflects the species' ability to colonise all types of sediments, with a preference for complex substrates that facilitate anchoring (Bulleri et al., 2011; Piazzi et al., 2016). Caronni et al. (2021) investigated the influence of water motion and temperature on gametogenesis and spawning of *C. cylindracea*. The number of fertile thalli (FT) and releasing thalli (RT) is already disturbed at a low water velocity, with high success rates only occurring at 'no water movement'. The study found an optimum temperature of 24°C and a strong negative effect on the RT/FT ratio at 30°C. It is worth noting that analysing the response curves is also useful to identify potential problems in the data and therefore in training. As discovered by Santamaría et al. (2021), a cryptic, filamentous form of *C. cylindracea* emerges at temperatures above 28°C, which can survive and return to its original form when the stressful conditions disappear. The cryptic form has a completely different thallus, indicating a strong correlation between the probability of detection and temperature, which could undermine the validity of the estimated response and thus the predictions.

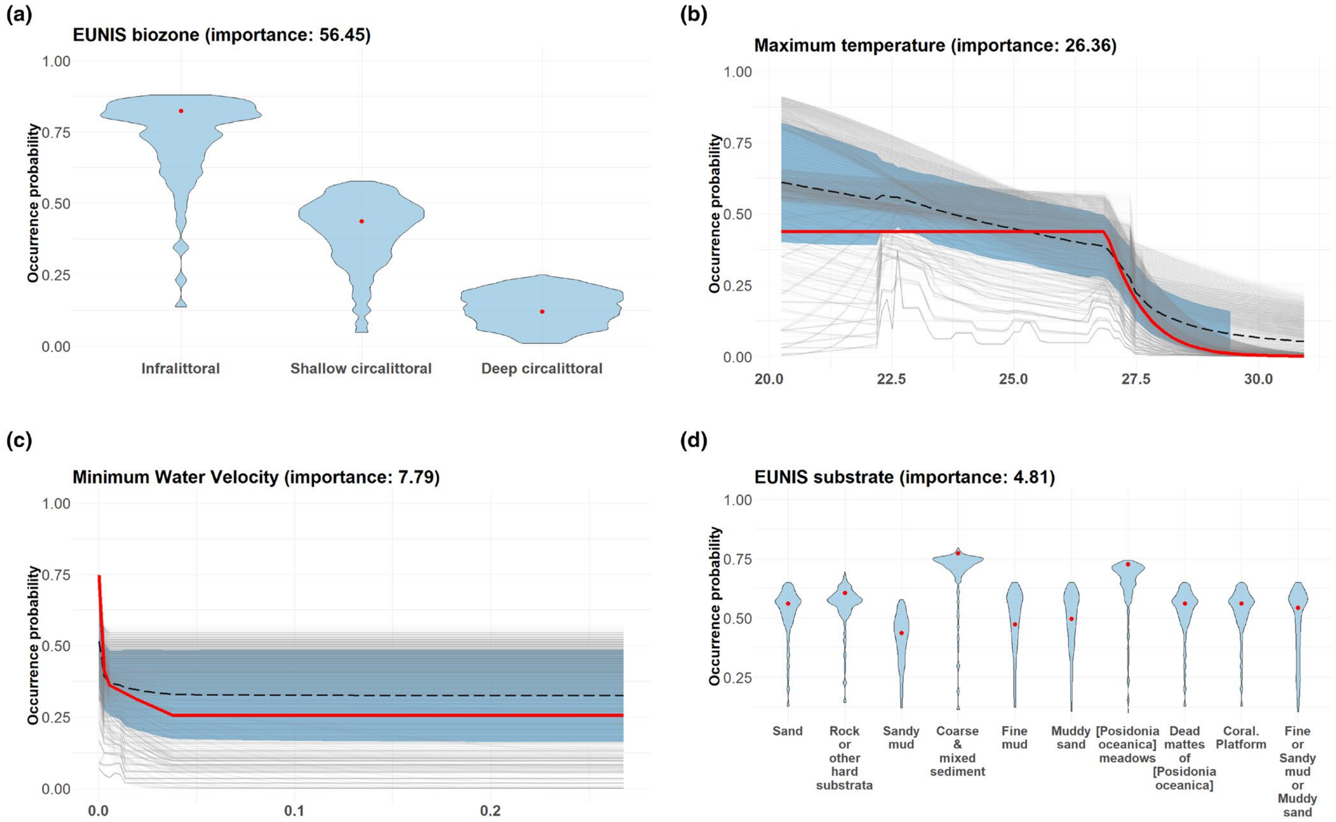


FIGURE 5 Response curves for biozone (a), maximum temperature (b), minimum water velocity (c) and substrate (d). The red lines/points signal the selected model response, grey lines are the other models. The dashed line is the 'mean' response curve, light-blue area shows ± 1SD.

5 | CONCLUSIONS

In this study, we developed and applied a robust ecological niche model (ENM) framework using MaxEnt and successfully demonstrated its usefulness in predicting the spread of the invasive species *Caulerpa cylindracea* in the Mediterranean region. The aim was to maximise both the predictive accuracy and ecological validity of the projections while minimising sampling bias and overfitting.

5.1 | A robust model selection process

Our study shows that relying solely on traditional evaluation metrics in presence-only, correlative ENMs leads to a biased and unreliable characterisation of performance and can result in suboptimal model selection.

Applying different weighting schemes and relative measures (delta metrics) broadens the evaluation landscape and introduces a useful redundancy that helps to separate the true signal of the metrics from artefacts related to data structure and bias.

Our results support the view that the integration of site-weighted metrics should become standard practice in ENM applications.

In particular, the use of ecologically relevant ancillary data—such as species abundance—to weight performance metrics improves model evaluation.

In line with the work of Radosavljevic and Anderson (2014) and Moreno-Amat et al. (2015), our approach emphasises the need for a multi-criteria approach to model selection. Building on this perspective, TOPSIS analysis provides a robust and unbiased method for determining the best performing model among the candidates. A well-defined ideal solution allows TOPSIS to synthesise multiple, potentially biased metrics into a robust and objective ranking framework. This method not only overcomes the limitations of relying on any single metric, but also provides a transparent, reproducible and flexible solution for model selection in applied studies.

In addition, the integration of the CRITIC method into our TOPSIS analysis further strengthens the overall robustness of the performance evaluation. CRITIC objectively calibrates the weighting of each criterion based on the statistical variance and correlations between criteria, thereby reducing the undue influence of metrics that may be biased by the structure of the validation datasets.

5.2 | An objective solution for risk assessment

The framework presented in this study offers significant potential as a practical tool for invasion risk management, particularly through its emphasis on objectivity and quantification of uncertainty.

The fully data-driven nature of our model selection process represents a significant advance in objective decision-making for invasion risk assessment. This objectivity is particularly valuable in management contexts where decisions must be defensible and reproducible. The framework's ability to systematically evaluate multiple model configurations while balancing complexity and ecological validity provides managers with robust, evidence-based predictions that can serve as the basis for intervention strategies.

A key strength of the framework is its comprehensive treatment of uncertainty. The integration of mobility oriented parity (MOP) analysis with objective thresholds (see 2.7) and the sensitivity analysis on classification provides a spatially explicit assessment of the reliability of predictions. This enables managers to:

- Identify areas where model predictions are most reliable.
- Assess the spatial distribution of the model's uncertainty.
- Plan future sampling and/or monitoring projects in highly uncertain areas to iteratively improve the assessment process.

The four-level suitability classification system in combination with the threshold uncertainty analysis provides a clear basis for prioritising intervention areas in the context of multiple scenarios. The annual projections and trend analysis allow management efforts to be prioritised over time, which can improve the cost-effectiveness of control measures (Bogich et al., 2008).

The adaptability of the framework to different management contexts is enhanced by its transparent, modular structure. While our case study focussed on *C. cylindracea* in the Mediterranean region, the methodology can also be applied to other invasive species and regions, provided that sufficient data are available and model assumptions are not violated (See 5.4).

5.3 | Insights on invasion spread

In our study, the annual changes in predicted suitability for *C. cylindracea* in the Mediterranean were examined to gain insights into the spread of the invasion.

Although suitability shows a negative trend due to the adverse effects of the rising temperature, sexual reproduction can give rise to new genotypes that favour the invasion profile, as noted by Caronni et al. (2021). The analysis showed that the Adriatic Sea is a new hotspot for the species. This observation is consistent with the results of Iveša et al. (2015), which investigated the *C. cylindracea* spread in this region between 2004 and 2014.

In summary, our dynamic suitability predictions shed valuable light on the potential spread of *C. cylindracea* and expand the possibilities for utilising ENM results. The comprehensive methodological analysis sets a standard for future research in model evaluation and selection in the context of machine learning-based ENM techniques.

5.4 | Limitations

While the methodology presented in this study is comprehensive, it is based on several assumptions and has limitations that should be taken into account when interpreting the results and planning future research. In this section, we briefly discuss the most important of these.

A major limitation of our approach is the considerable amount of data required. The methodology is highly dependent on the availability of high-quality occurrence data, especially from the independent test sites with abundance measurements for validation. While this enabled a robust model evaluation in our case study, it may limit the applicability of the full framework to well-studied species or regions with extensive monitoring programmes. Future research will focus on exploring alternative validation approaches and utilising other ancillary data for cases where abundance is not available.

The scalability of our approach requires more efficient hyperparameter exploration strategies (e.g. Gobeyn et al., 2019). The 'brute-force' evaluation of the hyperparameter space and the complex validation procedure ensure the identification of an optimal solution but are extremely resource-intensive. This can make it difficult to apply the framework to very large datasets.

Presence-only ENM studies based on machine learning algorithms make strong assumptions (i.e. species in equilibrium, no correlation between predictors and species detection) that are often violated (Elith et al., 2011; Yackulic et al., 2013). Invasion dynamics in the real world involve complex relationships that go beyond mere suitability and are often neglected in correlative ENMs. Factors such as the adaptability of invasive species, evolutionary changes and the intricate role of human activities not only alter the invasion trajectory but also distort the patterns in the data we use to train our models to an unknown extent. An example was presented in Section 4.4 regarding the cryptic form of *C. cylindracea*. Another example is the assumed correlation between abundance and suitable conditions, which may only apply to benthic organisms.

AUTHOR CONTRIBUTIONS

All authors together discussed the ideas and conceived the methods. Marco Fianchini collected and analysed the data. All authors discussed the results. Marco Fianchini and Donata Melaku Canu wrote the first version of the manuscript. All authors contributed critically to manuscript drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All processed data, fitted MaxEnt models and the complete code used to reproduce the results of this study are publicly available on Zenodo at: https://doi.org/10.5281/zenodo.15591894 (Fianchini, 2025).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1. Additional documentation of environmental variable processing, model calibration and validation procedures, and performance assessment metrics.

Figure S1. Boxplot of variable importances, ordered by descending median value. Black and red numbers represent, for each variable, the median and the selected model importance values, respectively.

Figure S2. Environmental calibration and testing space.

Figure S3. Presence and absence weights for the RCMED test set. The dashed line indicates the value assigned to each point if no weighting is applied. Colours from blue to yellow indicate the abundance value (left) and the number of proximal presence sites in the Spatial Auto Correlation range from absence sites (right).

Figure S4. Spider diagram showing the partial TOPSIS scores across six metric groups for the best performing model configurations. The black outline represents the top-ranked model (*fc.H_rm.7*). The diagram shows how different model configurations achieve different levels of performance in different metric groups.

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