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RESEARCH ARTICLE

Using long-term data series to design adequate protected areas that ensure the conservation of inconspicuous small petrel species

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Abstract

1. Marine protected areas (MPAs) are widely used tools for conservation and management. Their correct delimitation is challenging, especially when the target species are small, elusive and inconspicuous, as little data are generally available to adequately assess their distribution at sea. Therefore, currently designated MPAs may not effectively cover key areas for small seabirds, particularly during migration and wintering seasons.
2. We used ensemble species distribution models (ESDMs) on a 15-year time-series data set of at-sea census along the Atlantic Iberian arc to predict the potential distribution of the smallest European seabird, the European storm-petrel (*Hydrobates pelagicus*), and compare it with official marine special protection areas (SPAs).
3. Occurrence of European storm-petrel was related to shifts in sea surface temperature, and to small distances from the coast over the continental shelf.
4. Most relevant area for the species in the Atlantic Iberian arc was west-central Portugal to north-western coast of the Iberian Peninsula, with an additional key area in the Gulf of Cádiz. Both zones host significant SPAs, but they inadequately cover key areas for European storm-petrels. Our findings support extending marine SPAs in the Atlantic Iberian arc to ensure their effective protection.
5. The distribution of the species expands over the years, varying in both size and location. These changes might be attributed to dynamic oceanographic variables, such as sea surface temperature and biomass of micronekton, which seem to play a significant role in their foraging behaviour.

6. *Synthesis and applications*. Our study highlights the importance of analysing long time series and ESDMs to design adequate protected areas, which ensure the conservation of small and highly mobile species such as storm petrels. Our results should be considered by decision-makers to prioritise and update marine protected areas, while incorporating the dynamic nature of the ocean within an ecosystem-based approach.

KEYWORDS
At-sea census, ensemble species distribution modelling, European storm-petrel, Iberian Peninsula, important bird area, marine protected areas, seabird conservation

1 | INTRODUCTION

Marine protected areas (MPAs) are considered a powerful tool to conserve the oceans through the management of human activities (Watson et al., 2014). As evidence of their importance, the numbers of MPAs have been steadily increasing over the past few decades (Sala et al., 2018), with varying objectives and levels of protection, ranging from 'no-take' reserve areas to zones with multiple objectives (Lambert et al., 2017). Currently, there is a broad consensus within the scientific community and growing political understanding that by 2030, at least 30% of the global ocean should be designated as fully or highly protected areas, while the remaining 70% should be sustainably managed (Grorud-Colvert et al., 2021; Laffoley et al., 2022). Relevant international conservation institutions such as the Convention on Biological Diversity (CBD) and the European Union's Biodiversity Strategy for 2030 have called for a significant increase in the MPA coverage, aiming to raise it from its current level of almost 8%–30% of the marine area by 2030 (i.e. '30X30' initiative).

Seabirds are a fundamental piece of the marine ecosystem and should be protected within MPAs (Ronconi et al., 2012) as they play an important role in structuring and connecting pelagic marine food webs as top predators and highly mobile consumers (Bestley et al., 2020). Seabirds have extensive travel ranges and occupy the top of the food chain, making them highly sensitive to any subsequent changes. As a result, they act as excellent indicators of the overall health of marine ecosystems (Hazen et al., 2019; Paiva, 2022). However, seabirds are among the most threatened vertebrate groups and therefore require significant conservation attention (Dias et al., 2019; Phillips et al., 2023). To enhance their protection and conservation status, European Union enforces their member states, through the Birds Directive (Directive 2009/147/EC), to designate areas of special importance for the conservation of endangered bird species as special protection areas (SPAs). These areas are part of the Natura 2000 network, with Marine SPAs specifically targeting seabird conservation. However, it is widely acknowledged that only a small fraction of MPAs are deemed effective in achieving their conservation objectives (Jones & Long, 2021; Vrooman et al., 2022), primarily due to governance issues, such as the lack of a standardised framework, limited survey data, insufficient financial support or inadequate public engagement (Zeng et al., 2022).

The ideal delimitation of an effective MPA is challenging due to its large dimensions, dynamic biological processes, lack of clear barriers and sociopolitical economic interests (Beal et al., 2021; Davies et al., 2021). However, the design and management of MPAs heavily rely on quality baseline ecological information, particularly regarding species distribution and habitat use (Abecasis et al., 2014; De la Cruz, Rodríguez-García, et al., 2022). When protecting areas for seabird conservation, delimiting their boundaries becomes more challenging due to the birds' high mobility, variable environmental preferences, seasonality and the need for extensive data collection (Arcos et al., 2012; Arroyo et al., 2020; Ramírez et al., 2017). This complexity becomes more evident when the target species are small and inconspicuous, such as European storm-petrels *Hydrobates pelagicus* (hereafter ESP) (Critchley et al., 2020).

The ESP is a mostly black, less than 40 cm wingspan seabird, is a transequatorial migrant with two recognised subspecies, *H. p. pelagicus* and *H. p. melitensis* (Carboneras et al., 2021). The nominal subspecies breeds in the northeast Atlantic, ranging from southern Iceland and northwest Norway to the British Isles, northwest France, northwest Spain and the Canary Islands. In contrast, the *H. p. melitensis* subspecies is endemic to the Mediterranean Sea (Carboneras et al., 2021; Lago et al., 2019). Globally, the species is classified as Least Concern by the IUCN (Birdlife International, 2022). However, the Mediterranean subspecies faces greater conservation concerns as it comprises less than 10% of the total population and is restricted to a few predator-free islands in the Mediterranean basin (Lago et al., 2019; Sanz-Aguilar & Lago, 2021). Both subspecies can be found in the Atlantic Iberian arc during specific periods of the year (Carboneras et al., 2021; Militão et al., 2022) and at least 15 SPAs have been declared in the area with the aim of protecting the ESP among other seabird species (Arcos et al., 2009; BOE, 2014; Pereira et al., 2018; Ramírez et al., 2008).

Main conservation threats faced by ESPs include predation by Yellow-legged gull (*Larus michahellis*), the introduction of invasive mammals into their breeding grounds, loss of nesting habitat, resource depletion, human disturbance during breeding or the increased frequency of extreme weather events (revised in Sanz-Aguilar & Lago, 2021). The creation, expansion or improvement of MPAs together with effective management plans have been shown to address the main threats facing the species, such as managing

invasive carnivores or limiting fishing to prevent resource depletion or bycatch (Handley et al., 2020; Hays et al., 2020; Pichegru et al., 2012). Additionally, ESP seem to be highly sensitive to the intake of plastic (De Pascalis et al., 2022) and oil spills, which seem to negatively affect the species at both individual and population levels (Zuberogoitia et al., 2016). Other human activities at sea, such as bycatch, have a significant impact on the species, and storm petrels have been reported as bycatch mainly on trawl and gillnet fishing gears (Pott & Wiedenfeld, 2017). However, as they are the smallest and most cryptic pelagic seabirds, storm petrels are often not correctly identified by fishermen (Oliveira et al., 2015). Finally, the increasing number of offshore wind farms poses a threat to the species, as it may result in collisions with wind turbines and attraction to safety lights (Bolton, 2021).

To identify the distribution of the target species and thereby delimit the important areas to be protected, a variety of different techniques of species distribution models (SDM) have been widely used (Krüger et al., 2017). Among them, ensemble species distribution models, stacking multiple SDMs, provide better predictive performance compared with a single model approach (Pereira et al., 2018; Schmitt et al., 2017). Data for modelling seabird distribution are mainly collected using at-sea surveys and seabird tracking (Lascelles et al., 2012); however, GPS devices are still relatively limited in providing data for the smallest petrel species (Pereira et al., 2022). Much of the information collected through marine surveys is usually carried out in annual campaigns with standardised protocols and methodologies, which gives us the possibility of evaluating the temporal change and the consistency of the species distribution over the years, which is not always stable in migratory seabirds (Paiva et al., 2010). In addition, the analysis of long time-series databases can improve knowledge about the spatial distribution of seabird species because it includes interannual variability, and by increasing the sample, we can obtain better model performance with more reliable and robust results (De la Cruz, Ramos, et al., 2021).

In this scenario, we hypothesise that the designated SPAs in the Atlantic Iberian arc may not effectively cover the key distribution areas of ESP over time. For this, we analysed a 15-year time-series of at-sea surveys monitoring the Atlantic Iberian coastal marine region, generating ensemble species distribution models (ESDMs) to predict the distribution of ESP and measuring the overlap with the current SPAs network.

2 | MATERIALS AND METHODS

2.1 | Study area

The spatial distribution of the ESP was studied in the Atlantic Iberian arc (Spain and Portugal), between 35° N and 45° N, and 1° W and 11° W over a period of 15 years (2005–2019). The studied area was within the 2000 m isobath, where most of the SPAs with interest for the ESP are located, currently hosting 17 SPAs (Figure 1).

2.2 | Occurrence data (at-sea bird sightings)

The area has been the subject of annual multidisciplinary oceanographic studies carried out by the Spanish Institute of Oceanography (IEO-CSIC), AZTI (Marine Research), Conservation, Information and Study on Cetaceans (CIRCE) and Coordinator for the Study of Marine Mammals (CEMMA) in collaboration with the Spanish Ornithological Society (SEO/BirdLife) and the Portuguese Institute of the Sea and the Atmosphere (IPMA) in collaboration with the Portuguese Society for the Study of Birds (SPEA). Taking advantage of these regular surveys, seabird censuses were conducted using visual line transect protocols (European Seabird At Sea (ESAS), 'Snap-shot' and Distance Sampling methodologies) and summed up into survey units as a continuous 180° forward scan (Buckland et al., 2001; Camphuysen & Garthe, 2004; Tasker et al., 1984). In order to standardise different unit survey efforts, all census units were regrouped into units of 10-min duration (vessel speed during census time was constant). Moreover, we used all birds flying or resting on the water to maximise sample number and positive occurrences in an inconspicuous species.

To be effective, a SPA must cover the entire annual cycle of a species, and because breeding, wintering and migratory ESPs use the Atlantic Iberian arc across the year (Militão et al., 2022; Sanz-Aguilar & Lago, 2021), we analysed ESP occurrences during the overall period 2005–2019, without season differentiation. In addition, to consider the annual variability between the most suitable zones, we evaluated the consistency of the ESP distribution across the years by analysing the annual distribution separately.

2.3 | Environmental predictors

Based on the previous literature, a set of static and dynamic variables that characterise suitable habitat for ESPs and other seabirds was used (De la Cruz, Ramos, et al., 2021; Hedd et al., 2018; Pereira et al., 2018). Furthermore, since the distribution of ESPs is conditioned by the distribution of their prey (small pelagic fish, small crustaceans and fish larvae; Albores-Barajas et al., 2011), we used the distribution of zooplankton and micronekton biomass as a proxy for the distribution of ESP prey. Bathymetric data, distance to coast, distance to shelf break and slope were extracted and derived from EMODnet (https://emodnet.ec.europa.eu/en). Chlorophyll *a* concentration, productivity, sea surface temperature, biomass of zooplankton and biomass of micronekton were provided by Copernicus Marine Service (https://marine.copernicus.eu/es) (Table S1). In order to analyse the consistency of the environmental variables throughout the years, and therefore possible variations in the distribution of the species, yearly averages of the dynamic variables were extracted annually to analyse the annual models, while to compute the global model, an average of time-series of environmental variables data was extracted for the entire study period (2005–2019) to represent the present environmental conditions (Sun et al., 2022). Collinearity between predictors and potential spatial autocorrelation is described in supplementary material (Table S2).

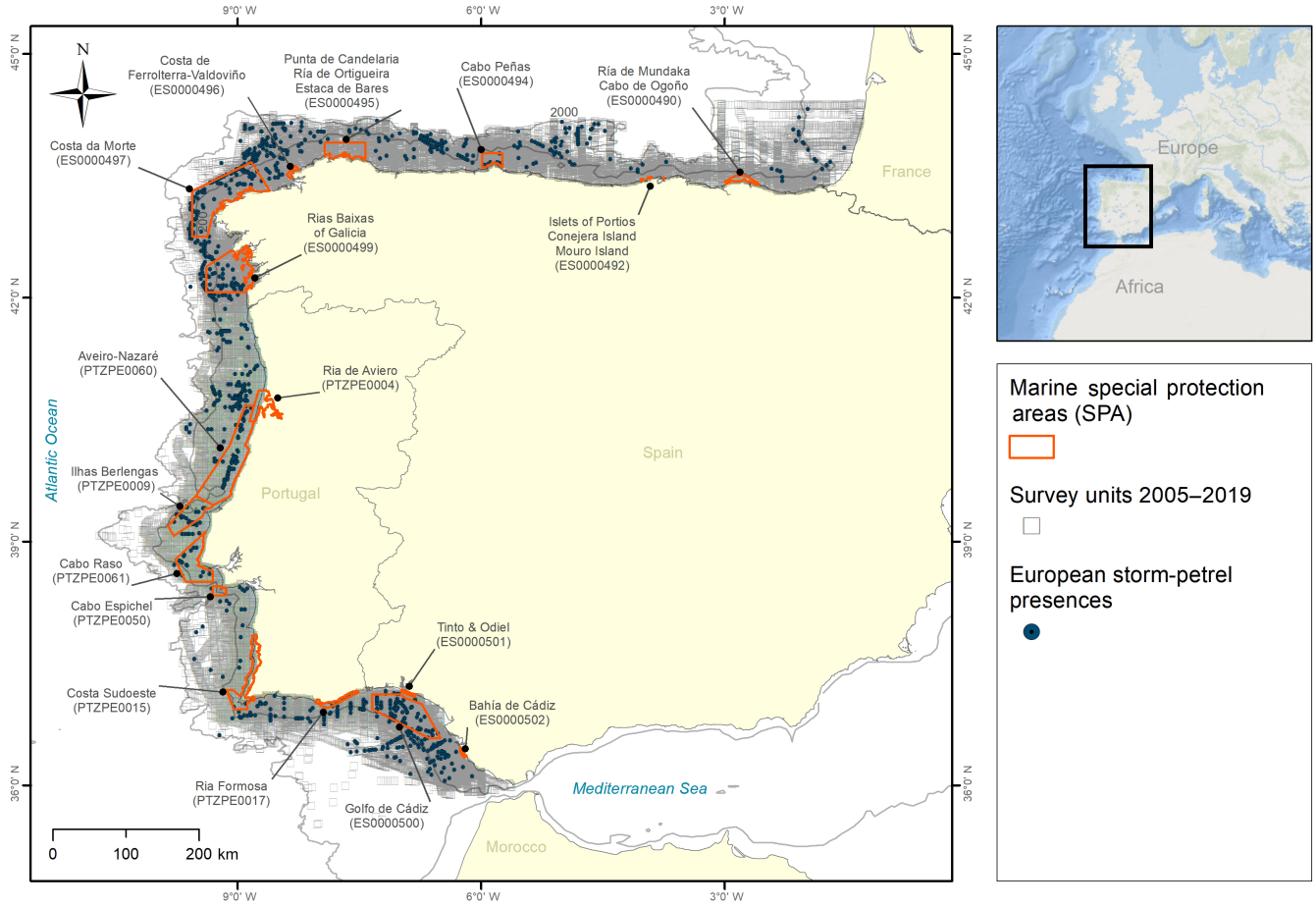

FIGURE 1 Study area overview. The orange squares indicate the marine special protection areas (SPA) in the Atlantic Iberian arc. Grey squares indicate the 10-min survey units and blue spots indicate those survey units with European storm-petrel presences. The isobaths of 200 and 2000 meters are also shown.

2.4 | Ensemble species distribution models

Seven modelling algorithms within an ensemble modelling technique were used to assess the ESP potential distribution in the study area. We used the ensemble modelling implemented in the 'SSDM' R package (Schmitt et al., 2017) applying the following modelling algorithms: generalised linear model (GLM); generalised additive model (GAM); multivariate adaptive regression splines (MARS); generalised boosting model (GBM); classification tree analysis (CTA); random forest (RF); maximum-entropy approach (MAXENT); artificial neural networks (ANN) and support vector machines (SVM). Modelling parameterisation is detailed in the supplementary material.

The area under the receiver operating characteristic curve (AUC) was used to assess the predictive performance of each model. The AUC scores range from 0.5 to 1 as follows: 1.0–0.9, excellent; 0.9–0.8, good; 0.8–0.7, reasonable; 0.7–0.6, poor; and 0.6–0.5, unsuccessful (Araujo et al., 2005; Swets, 1988). The contribution of each variable was calculated based on the Pearson's correlation coefficient between the model with all variables and models where each variable was omitted (Schmitt et al., 2017). Finally, the weighted combination of each different algorithm was assembled into a single model, using only those models with good discriminatory power (AUC ≥0.70), further removing all the models below this threshold.

Ecologists and conservation managers often need to convert continuous measures of species distributions to categorical measures (Cleasby et al., 2020). To facilitate potential decision-making and prioritise the most important areas for the ESP, we constructed the polygon outlining the core areas for the distribution of the ESP following the methodology suggested in Arcos et al. (2012) for creating marine Important Bird Areas, which served as the basis for the present designation of marine SPAs across a significant portion of the study area. This methodology involved the establishment of specific categorical thresholds as follows: To define the core areas, we employed prediction values from the models, using the overall model for the general core area and annual models for specific yearly core areas. Initially, values below 0.1 probability threshold were excluded, designating the remaining as the presence area. Next, we subdivided the range of values within the presence area (0.1–1.0) into two thresholds: the first, positioned at the midpoint (values below 0.450), identified medium suitability areas, while the second threshold divided the upper range by its midpoint, classifying values above 0.775 as optimal suitability zones. The range between 0.450 and 0.775 denoted good suitability zones. This method ensured that only cells

with optimal suitability, indicating probabilities of presence equal to or greater than 0.775, were incorporated into the core areas.

2.5 | Dynamic ESP core areas over time

To evaluate the distribution dynamics of the ESP, we compared the annual core area with the overall core area. First, we calculated the polygon encompassing the highest probability of occurrence for each annual model of species distribution (>77.5%) and then we calculated its area and analysed the variation in the size of the annual core areas over the years, using a model generalised linear (GLM) fitted with a Poisson error distribution. Similarly, to assess the consistency of the annual core areas over time, we first calculated the annual area that falls within the overall core area, determined the percentage it represents with respect to the overall core area, and then evaluated its change over time (2005–2019) using a linear model (LM). Furthermore, we conducted a comparative analysis between the annual averaged values of the key predictors in the ESP distribution within the study area and the expansion of its core area. This analysis was performed using a generalised linear model (GLM) fitted with a Poisson error distribution, enabling us to gain insights into the potential fluctuations and trends in these variables over time.

The GLM and LM analyses were performed using the R *stats* package (R Core Team, 2023). The average response curves of the individual algorithms of the ensemble model were obtained using the Maxent software (Phillips et al., 2006) and plots built with functions within the *ggplot2* and *plotmo* R libraries (Milborrow, 2022; Wickham, 2016).

3 | RESULTS

We analysed 61,358 10-min survey units in the 2005–2019 period, in which 991 presences of ESP were found (Figure 1). Sampling effort was generally homogeneous among years, with an average of 4091 ± 1210 survey units per year (Table 1). Surveys were carried out in every month throughout the years, although monthly effort was not homogeneous, with less information in some months (Table 1). ESP were detected in the Atlantic Iberian arc mainly from July to November, exceeding 85% of the presences. Very few ESP were detected from January to April (0.02% of total presences) (Table 1).

3.1 | Ensemble ESP distribution models performance

Annual and overall ESDM show reasonably good predictive performance with values always higher than 0.713 (Table 2). The overall model showed an acceptable predictive performance when discriminating suitable habitats from unsuitable ones with an AUC score of 0.756 (Table 2). In general, the predictive performance of the ESDM showed higher AUC scores than the individual algorithms analysed,

TABLE 1 Number of 10-min survey units analysed per month and year.

Year/month	January	February	March	April	May	June	July	August	September	October	November	December	Total
2005	189 (1)	1293 (0)	46 (0)	1098 (0)	1014 (0)	101 (0)	2127 (102)	7 (0)	156 (0)	24 (0)	972 (0)	60 (0)	7087 (103)
2006	20 (0)	13 (0)	98 (0)	1270 (0)	581 (3)	134 (34)	14 (0)	148 (0)	134 (6)	575 (20)	1554 (26)	0 (0)	4541 (89)
2007	11 (0)	414 (0)	244 (0)	1803 (0)	325 (2)	31 (0)	232 (3)	0 (0)	0 (0)	157 (0)	811 (34)	239 (0)	4267 (39)
2008	394 (0)	634 (0)	165 (0)	1390 (3)	524 (12)	63 (1)	110 (22)	7 (0)	0 (0)	1146 (38)	0 (0)	0 (0)	4433 (76)
2009	0 (0)	0 (0)	342 (0)	1530 (1)	0 (0)	80 (0)	87 (0)	0 (0)	0 (0)	0 (0)	75 (21)	217 (31)	2331 (53)
2010	0 (0)	0 (0)	104 (0)	2227 (1)	548 (5)	0 (0)	212 (16)	57 (0)	337 (2)	188 (0)	165 (3)	0 (0)	3838 (27)
2011	0 (0)	908 (6)	962 (0)	1164 (4)	907 (8)	57 (5)	72 (0)	192 (1)	292 (9)	789 (70)	224 (18)	0 (0)	5567 (121)
2012	38 (0)	0 (0)	117 (0)	568 (0)	110 (0)	413 (3)	0 (0)	466 (0)	601 (18)	335 (14)	0 (0)	0 (0)	2648 (35)
2013	99 (1)	742 (0)	664 (0)	667 (0)	751 (1)	30 (0)	0 (0)	312 (25)	466 (9)	280 (18)	457 (9)	0 (0)	4468 (63)
2014	0 (0)	0 (0)	890 (0)	1178 (0)	480 (0)	0 (0)	134 (2)	36 (0)	780 (22)	358 (18)	0 (0)	188 (4)	4044 (46)
2015	0 (0)	0 (0)	257 (0)	1145 (0)	369 (0)	14 (0)	90 (1)	184 (10)	609 (18)	272 (7)	23 (0)	10 (0)	2973 (36)
2016	13 (0)	20 (0)	1020 (0)	576 (5)	179 (0)	0 (0)	15 (0)	175 (5)	610 (66)	19 (0)	186 (1)	168 (1)	2981 (78)
2017	0 (0)	0 (0)	434 (0)	645 (0)	1358 (0)	358 (1)	230 (0)	441 (19)	483 (60)	371 (17)	165 (0)	156 (0)	4641 (97)
2018	0 (0)	72 (0)	199 (0)	535 (0)	1175 (1)	0 (0)	0 (0)	237 (5)	376 (25)	79 (0)	549 (0)	0 (0)	3222 (31)
2019	482 (0)	1066 (0)	168 (0)	948 (1)	245 (0)	0 (0)	0 (0)	205 (3)	1116 (92)	87 (1)	0 (0)	0 (0)	4317 (97)
Total	1246 (2)	5162 (6)	5710 (0)	16,744 (15)	8566 (32)	1281 (44)	3323 (146)	2467 (68)	5960 (327)	4680 (203)	5181 (112)	1038 (36)	61,358 (991)

Note: European storm-petrel presences are shown in parentheses.

TABLE 2 Summary evaluation and metrics of annual ensemble specie distribution model (ESDM) and overall (2005–2019) ESDM for the European storm-petrel in the Atlantic Iberian arc.

Year	AUC	Omission.rate	Sensitivity	Specificity	Prop.correct	Kappa
2005	0.810	0.209	0.791	0.829	0.828	0.114
2006	0.730	0.260	0.740	0.720	0.721	0.070
2007	0.785	0.230	0.770	0.800	0.800	0.063
2008	0.713	0.293	0.707	0.719	0.718	0.052
2009	0.836	0.168	0.832	0.841	0.841	0.189
2010	0.773	0.276	0.724	0.818	0.817	0.046
2011	0.721	0.281	0.719	0.723	0.723	0.074
2012	0.786	0.247	0.753	0.814	0.813	0.108
2013	0.719	0.282	0.718	0.720	0.720	0.054
2014	0.716	0.265	0.735	0.696	0.696	0.037
2015	0.729	0.270	0.730	0.724	0.724	0.049
2016	0.795	0.219	0.781	0.808	0.807	0.170
2017	0.754	0.245	0.755	0.754	0.754	0.109
2018	0.750	0.249	0.751	0.749	0.749	0.053
2019	0.760	0.246	0.754	0.765	0.765	0.110
Overall model (2005–2019)	0.756	0.241	0.759	0.754	0.757	0.482

Abbreviations: AUC, area under the receiver operating characteristic curve; Omission.rate, percentage of test locations that falls into pixels not predicted as suitable for the species; Sensitivity, true presence rate; Specificity, true absence rate; Prop.correct, proportion of correctly predicted occurrences; Kappa, Cohen's kappa coefficient from the confusion matrix.

which achieved an average AUC of 0.720 ± 0.091 for the annual models and an average AUC of 0.748 ± 0.054 for the overall model.

Among all the analysed algorithms in the annual models, GAM, RF and MAXENT, showed a higher predictive power (average AUC > 0.750), while CTA and SVM showed a lower average predictive power <0.700. GBM and ANN algorithms did not converge for the annual models due to lack of enough positive occurrences each year (Table S4). On the contrary, the best individual algorithms of the overall model were RF, SVM, MARS, GAM and MAXENT (AUC > 0.750) (Table S5).

The most influential environmental variables driving ESP distribution differed among both annual and overall models (Table 3). Since the SSDM package does not provide the response curves of the explanatory variables, we obtained this information from two of the best ESDM algorithms, extracting 10 replicates of the GAM model from the ensembled model and 10-run MAXENT model with the same parameterisation as ESDM (Figures S1 and S2). The sea surface temperature was the most important variable in the overall model and also in 5 out of 15 years in the annual ESDM. The probability of occurrence of ESP in relation to sea surface temperature showed two peaks with high probability, a first one around 13°C and a second one around 18°C, decreasing this probability between them (Figures S1 and S2). The distance to coast showed the second highest importance value in the overall ESDM and also in 5 out of 15 years, with a maximum probability of finding ESP near the coast up to 25 km, and decreasing beyond this distance (Figures S1 and S2). The third most important variable in the overall ESDM was the biomass of micronekton in the epipelagic layer, showing a higher probability of ESP in a range between 1 and 2.5 mg m^{-2} approximately. However, the significance of micronekton concentration in the overall model is not evident when considering each year independently. Here, bathymetry appears to carry greater importance. Lastly, although with less relative weight in the models, the probability of occurrence of storm petrels showed a positive relationship with the zooplankton concentration.

3.2 | Overall distribution

The overall model showed a predicted projection with a high probability of occurrence of ESP in the northwest coast of the Iberian Peninsula and in the Gulf of Cádiz (Figure 2a). The area with highest probability of occurrence was located in the northern half of the Portuguese coast and the Spanish Galician coast, with values close to 0.90. Additionally, the model predicts highly suitable zones throughout the entire Gulf of Cádiz, with occurrence probabilities exceeding 0.65 in both Portuguese and Spanish waters. Notably, the areas surrounding the Golfo de Cádiz SPA show occurrence probability values above 0.75 (Figure 2a). The uncertainty map for the overall ESDM indicates minimal variation and close agreement among the different algorithms employed, with values below 0.12 (Figure 2b).

In the northwest region of the Iberian Peninsula, four SPAs clearly overlap with the most suitable areas predicted by the overall ESDM for the ESP, namely Ilhas Berlengas, Nazare-Aveiro, Rías Baixas of Galicia and Costa da Morte. However, several patches located in the northern Portuguese coast and the Galician coast (south and northeast of Costa da Morte SPA) and some patches between Punta de Candelaria-Ría de Ortigueira-Estaca de Bares, are core areas for the ESP that fall outside the protection of any marine SPAs (Figure 3a).

TABLE 3 Relative importance of the environmental variables (%) applied to annual and overall (2005–2019) ESDM for the European storm-petrel in the Atlantic Iberian arc.

Year	Bat	CHL	D_Coast	D_Shelf	Micronekton	Slope	SST	Zooplankton
2005	9.82	6.77	6.47	5.01	24.93	15.19	21.08	10.73
2006	11.16	8.45	16.52	11.31	15.59	8.85	14.98	13.14
2007	16.85	31.20	9.00	5.16	8.73	4.09	10.27	14.70
2008	11.96	8.25	12.00	18.59	15.32	6.42	9.87	17.59
2009	18.04	6.49	26.71	8.22	13.25	5.87	10.29	11.14
2010	12.93	19.20	5.92	5.38	7.53	11.12	25.58	12.33
2011	19.26	8.22	7.99	16.53	11.25	6.15	20.70	9.89
2012	8.30	7.10	31.46	15.66	9.51	8.53	13.80	5.64
2013	9.95	10.23	24.05	10.93	19.10	8.91	6.89	9.93
2014	14.82	21.53	26.51	5.93	6.46	14.23	7.26	3.26
2015	18.63	5.13	9.13	14.71	10.23	12.86	23.03	6.27
2016	14.40	22.42	4.43	13.06	11.95	18.97	10.62	4.16
2017	19.55	12.05	6.13	8.94	11.83	8.62	24.65	8.24
2018	22.10	8.20	18.03	7.63	10.69	9.00	16.23	8.11
2019	21.95	7.09	8.10	12.77	9.98	9.11	23.16	7.84
Overall model (2005–2019)	9.81	6.42	17.99	4.51	14.71	5.18	33.46	7.92

Note: Values shaded in grey in importance gradient by rows (years and overall), white indicating low importance and dark grey high importance.
Abbreviations: Bat, Bathymetry; CHL, Chlorophyll-*a*; D_Coast, distance to coastline; D_Shelf, distance to shelf break; Micronekton, mass content of epipelagic micronekton, 2–20 cm, that inhabits permanently the epipelagic layer; Slope, seabed terrain slope; SST, sea surface temperature; Zooplankton, mass content of zooplankton in the epipelagic layer.

In the Spanish side of the southern region of the study area, the Golfo de Cádiz SPA presented appropriate habitat for the ESP. However, the core areas for the species lied outside the boundaries of this protected area, both to the west and southeast of it. Furthermore, in the southern Portuguese region off the Algarve coast, the Costa Sudoeste SPA, which is the only protected area of interest for the ESP, did not sufficiently cover the suitable area found in this region for the species (Figure 3b).

3.3 | Annual distribution

The predicted projections from the annual models revealed areas where the average maximum probability of finding ESP was 0.67 ± 0.11. These areas ranged from zones with a maximum occurrence of 0.87 in 2008 to 0.44 in 2014. The size of the ESP core area varied notably on an annual basis, with a coefficient of variation of 0.82 and an average size of 906.64 ± 1016.790 km^2 (Table S6). Despite this variability, the size of the core areas demonstrated a positive trend over the years, with an average annual increase of 2.84 ± 4.32% (GLM area ~ year, $\beta = 0.014$, $p < 0.001$) (Figure S4a).

When assessing the consistency of the annual models based on the overlap with the overall core area polygon, the majority of the annual ESDMs (9 out of 15) indicated suitable habitat within the core area polygon. However, in 2014 and 2015, the most suitable areas were located entirely outside the overall core area polygon (Figure S3). The zones identified as core areas each year exhibited varying degrees of overlap rate with the overall core area (average 0.40 ± 0.33) (Table S6). Nevertheless, there appears to be a trend of increasing overlap over the years (LM overlap ~ year, $\beta = 0.036$, $R^2 = 0.172$, $p = 0.069$) (Figure S4b).

Regarding the influence of dynamic oceanic factors on the habitat suitability, Figure S5 illustrates the annual variations of the most relevant variables on the distribution of the ESP, as well as the corresponding extent of the core area for each year. Throughout the study period, both variables exhibited minor fluctuations: sea surface temperature ranged from 14.5°C in 2016 to 15.5°C in 2009, while biomass of micronekton varied between 2.3 g m^{-2} in 2016 and 3.4 g m^{-2} in 2018. Remarkably, our analyses revealed a significant inverse relationship between the values of these variables and the size of the core areas. In years with lower sea surface temperature values and biomass of micronekton concentrations, the key areas tended to be more extensive (Figure S6; Table S7).

4 | DISCUSSION

4.1 | Identifying long-term key areas for European storm-petrel in a dynamic ocean

In this study, we used a 15-year time-series database of at-sea census to identify the most suitable areas of the Atlantic Iberian arc for the European smallest seabird, the ESP. Our results identified two main distribution hotspots of the species. The main area was located off

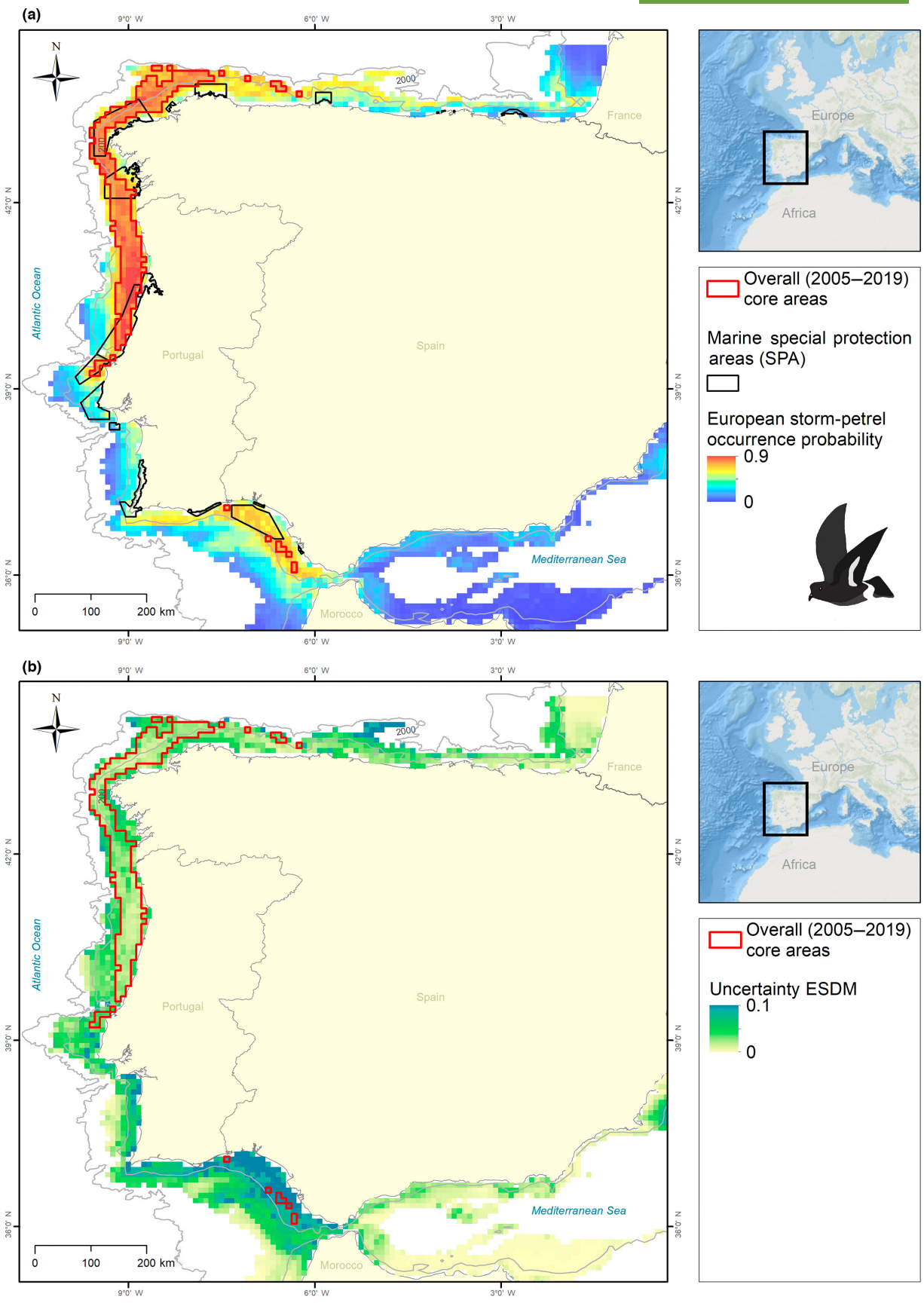

FIGURE 2 (a) Overall (2005–2019) ensemble model projection of the European storm-petrel distribution together with occurrence probability in the Atlantic Iberian arc. (b) Uncertainty map representing the between-methods variance. The core area polygon is depicted (areas with a probability of occurrence higher than 77.5%).

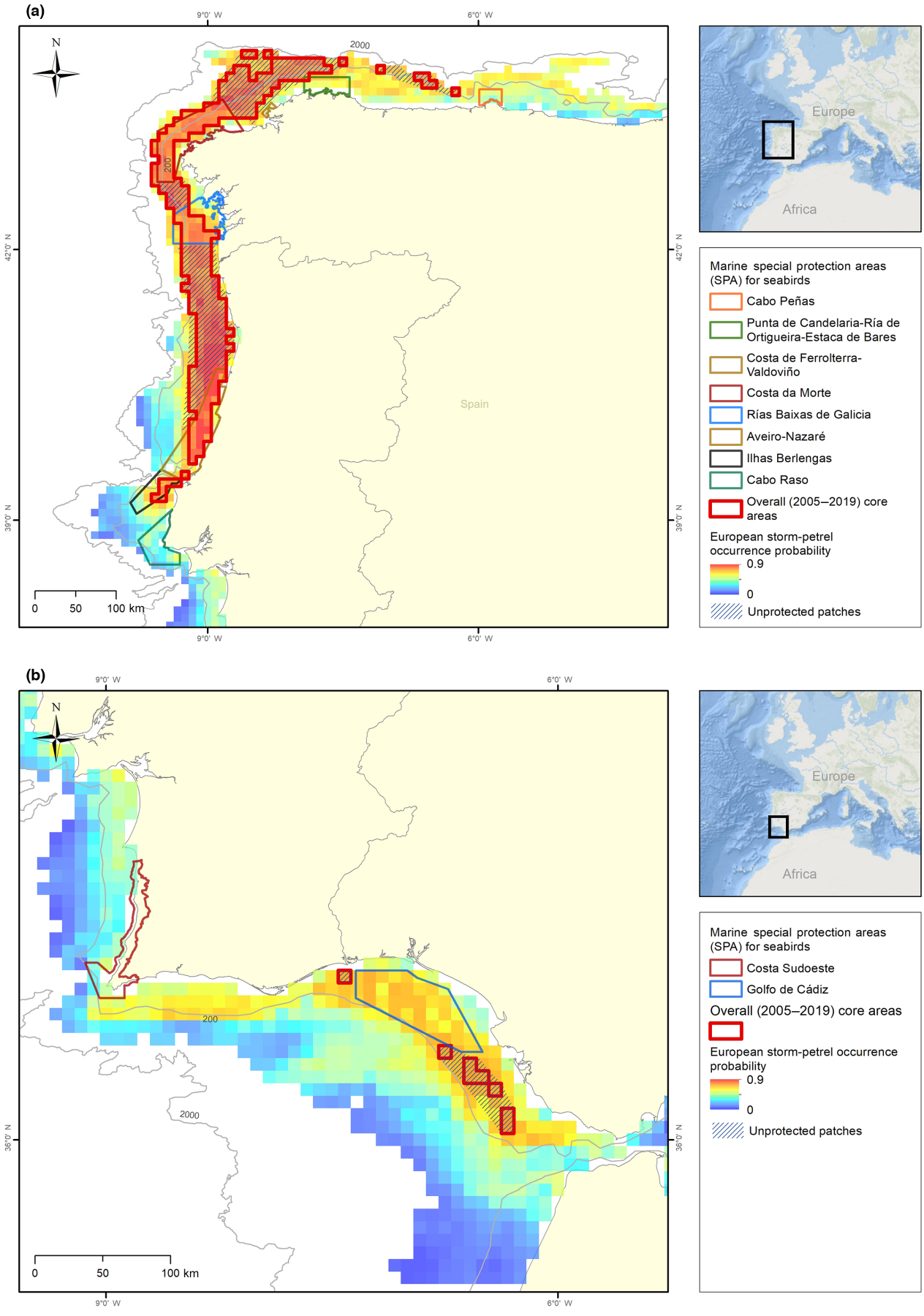

FIGURE 3 (a) North-central and (b) South Atlantic Iberian arc zoom area with the most suitable areas for the European storm-petrel and the declared marine special protection areas. Highly suitable unprotected patches are marked with hatched areas.

the northern half of the Portuguese coast and the Spanish Galician coast, and a second area was identified in the Gulf of Cádiz. Previous studies have highlighted the central and northern region of Portugal as congregation areas for both migratory birds breeding in the north of the Peninsula and those breeding in the North Atlantic in their migration movements towards the African coasts (Sanz-Aguilar & Lago, 2021). Moreover, the area has been recognised as important habitat for the reproduction of other storm petrel species (such as the Band-rumped storm-petrel *Hydrobates castro*), and for other migratory and wintering species in this area (Meirinho et al., 2014).

A second important core area for the ESP was located in the Gulf of Cádiz, in the southern part of our study region. This zone has recently been identified as one of the most important wintering areas for Mediterranean ESP (Militão et al., 2022). Additionally, the Gulf of Cádiz has been revealed as a key area for a significant number of seabird species that feed in this area outside the breeding season, including the critically endangered Balearic shearwater *Puffinus mauretanicus* (Arroyo et al., 2020).

Among oceanographic variables, sea surface temperature was the most influential dynamic variable in explaining the distribution of this species in our study area. Sea surface temperature has been reported as one of the key drivers shaping the evolution of life history strategies in seabirds, as it directly affects primary productivity patterns and thus availability of food resources to top predators (Velarde et al., 2019). Most marine birds typically associate with areas of colder waters, often associated with fronts and upwellings, where higher biological productivity is usually higher (Serratosa et al., 2020). However, in our study, the model results showed two temperature peaks with a high probability of occurrence, around 13°C and 18°C, respectively, which could suggest segregation within the storm petrel population. It has been demonstrated that different species of small petrels can partition their niches into zones with different temperatures to maximise their feeding efficiency and reduce interspecific competition (Quillfeldt et al., 2015). In our study, the presence of individuals from different breeding populations at different distances and at different times of the annual cycle could explain the occurrence of the species in two distinct periods with very different temperatures, which could be related with two waves of species presence in our study area in different seasons. Indeed, the key marine areas identified in this study congregate birds that breed in the north of the Peninsula and those breeding in the North Atlantic in their migration movements towards the African coasts (Sanz-Aguilar & Lago, 2021), but also birds of the Mediterranean subspecies, which winter in the Iberian Atlantic coasts (Lago et al., 2019; Militão et al., 2022). Unfortunately, the lack of regular campaigns throughout all seasons, as well as the relatively low conspicuousness of the species, made it challenging to conduct models which take into account potential intra-annual variability.

On the contrary, storm petrels were more likely to be found at a distance between 20 and 30 km from coast, which coincides with the continental shelf in most of the study area, where nutrients are more abundant and accessible due to the strong upwelling in the continental shelf break (Bolton, 2021; Serratosa et al., 2020). The third most important variable in the overall model was the biomass of micronekton. However, contrary to expectations, our results indicate that the probability of finding storm petrels decreases with the highest concentration of micronekton. This phenomenon may be attributed to the overall model being based on averaged values over the entire study period across a broad range of micronekton values, and the annual variability in the variable's distribution potentially masking this overall significance. This suggests that another food source, such as small pelagic fishes, their eggs or larvae, or other species within the zooplankton (showing a positive correlation in our results), could better explain the distribution of storm petrels (Aguado-Giménez et al., 2016; Albores-Barajas et al., 2011; Carreiro et al., 2020). In addition, the species exhibits an opportunistic scavenging behaviour, consuming the leftover by other marine top predators or even being attracted to fishery discards (Medeiros-Mirra, 2010). Hence, further investigations are necessary to establish a relationship between the distribution of these seabird species and their potential prey. Recent studies suggest that incorporating prey distribution as an explanatory variable significantly improves the predictive accuracy of species distribution models (De la Cruz, Ramos, et al., 2022).

4.2 | Dynamic changes in the distribution of European storm-petrel over time

Our results revealed notable variation in the species' distribution area over the years, in terms of both size and location. This is a common feature observed in migratory seabird species, as they often exhibit remarkable flexibility in their distribution within a broad area during their movements (Beal et al., 2023; Paiva et al., 2010; van Bemmelen et al., 2017). The spatiotemporal variation of resources is considered the most likely cause for the lack of consistency in the distribution areas of seabird species (Fauchald, 2009). Moreover, differences in energy requirements throughout the species' life cycle, as well as factors such as sexual or population segregation and individual foraging strategies, can contribute to variations in the species' distribution area (Bolnick et al., 2003; Franklin et al., 2022; Navarro et al., 2009; Reisinger et al., 2020). Additionally, it is worth noting that the suitable habitat appears to expand in area over the years, which may indicate broader changes in the distribution of the species' prey or an increase in the species' adaptive capacity and dietary plasticity (Bedolla-Guzmán et al., 2021; Carreiro et al., 2020).

Considering all these circumstances, it becomes evident that the distribution of European storm-petrels is shaped by the dynamic nature of the ocean. The interplay between oceanic dynamics and temporal variations in predictor variables seems to play a significant role in determining the size of the storm petrels' most frequented areas. Our findings demonstrate that in years with higher sea surface temperatures and increased micronekton concentrations, storm petrels concentrate their foraging activities within smaller areas. These results could be explained by two plausible hypotheses. First, at the mesoscale level, higher sea temperatures could lead to less productive areas (Grémillet & Boulinier, 2009), resulting in food availability being likely restricted

to isolated patches (Weimerskirch, 2007), where micronekton also concentrated. These isolated patches may be the ones exploited by storm petrels, explaining their preference for small and concentrated foraging areas. Additionally, the high concentrations of potential prey as micronekton could facilitate a consistent usage of a relatively small proportion of the potential foraging area (Bolton, 2021), with shorter and more efficient feeding periods and consequently, they would not need to extensively search larger areas, resulting in energy savings during foraging activities (Weimerskirch et al., 2003).

4.3 | Strategising MPAs for European storm-petrel conservation

Studying the distribution of seabirds offers us tools to delineate MPAs that will better protect the marine environment in a general framework. In the current scenario of deterioration of the marine environment, the designation of new protected and important areas for birds or the expansion of existing ones, to include important foraging and wintering areas or connecting the existing ones are required (Gilmour et al., 2022; Sanz-Aguilar & Lago, 2021). Such proposals to expand the SPAs in the study area are aligned with the objectives advocated by the Convention on Biological Diversity (CBD), the International Union for Conservation of Nature (IUCN) and the European Union (EU) of expanding the protected areas network to recover and protect habitats and species, and thereby achieving the target of 30% of MPAs by 2030 to improve biodiversity as a whole (Davies et al., 2022; Vrooman et al., 2022).

The application of environmental niche modelling techniques for habitat selection has been extensively used in the marine environment to identify core conservation areas (Lascelles et al., 2016; Ronconi et al., 2012). Nonetheless, in many instances, data analysed to identify the range of a species or delimit these core areas were collected over a limited period of time and, under these circumstances, may lead to protect area boundaries that are not as precise as they should be, nor do they reflect the entire annual cycle (Arroyo et al., 2020; Critchley et al., 2018). Hence, the analysis of long time-series greatly improves the accuracy of the analysis and allow to evaluate the species' distribution changes, incorporating the dynamism of the ocean (Araújo & Guisan, 2006; Patterson et al., 2021). In addition, counting at sea elusive seabirds as ESPs can be difficult given their small size and dark colour (Bolton, 2021; Critchley et al., 2020). For those inconspicuous seabird species, an increase in the number of sampling years may be key to accurately map their distribution at-sea, which allows considering the interannual variability linked to environmental changes. Moreover, the use of complementary methodology such as GPS devices, would improve the knowledge on the distribution of these species (Bolton, 2021). Currently, the small size of seabirds like the ESP still greatly limits the use of most GPS devices, but technological progress in its miniaturisation is offering recent and novel results (Lago et al., 2019; Militão et al., 2022).

While this species is not currently considered particularly threatened, it serves as an example of specialised marine top predator and, consequently, identifying its key habitats can greatly aid in the conservation of food webs in oceanic area. These important areas identified for the ESP in the Atlantic Iberian arc were located from west-central Portugal to the north-western coast of the Iberian Peninsula. Currently, up to 15 SPAs have been declared in this area to protect seabirds. However, there are important patches of European storm-petrel core areas in this zone that are unprotected, mainly on the northern coast of Portugal. In addition, these key areas were not recognised in previous marine spatial plans, and consequently there is a lack of designation of MPAs in these regions (Araújo et al., 2017; Araújo, Correia-Rodrigues, et al., 2022; Pereira et al., 2018). Furthermore, all Atlantic coast of Iberia is an important migratory flyway for seabird species breeding in northern Europe and moving to lower latitudes during the winter (Araújo, Rodrigues, et al., 2022; Arcos et al., 2009; Paris et al., 2021). The relevance of this coast for numerous seabird species, including the European storm-petrel, has been highlighted in different forums and international projects (Aranda et al., 2021), suggesting the need to create a 'migratory corridor' which connects the already declared SPAs in the area.

A secondary important core area for the ESP was located in the Gulf of Cádiz. This is an important area for seabirds, with five SPAs designated under Birds Directive (2009/147/EC) as part of the Natura 2000 network. Additionally, in this area, a candidate MPA in the Southern coast of Portugal has been proposed for nonbreeding and migratory species (Pereira et al., 2018). However, our study demonstrates that the current protected areas in the Gulf of Cádiz do not cover the entire suitable area for the species. The deficiency in the Golfo de Cádiz SPA has already been highlighted for species such as the critically endangered Balearic shearwater, where an extension to the southeast of the current limits of the SPA has been proposed (Arroyo et al., 2020). This extension, along with a westward extension covering part of the Portuguese coast, would also cover the core areas for the European storm-petrel.

In this scenario, our research supports the efforts leading to the expansion of the Iberian Atlantic arc SPAs, and help to identify where to apply strict management measures that favour the conservation of the ESP and other seabird species. The expansion of the MPAs network together with efficient enforcement of management measures have demonstrated their success in different areas and marine species limiting human activities as fishing or mitigating bycatch (Augé et al., 2018; De la Cruz, Bastos, et al., 2021; Edgar et al., 2014; Hays et al., 2019). Hence, the expansion and connection of the MPAs network should improve spatial planning in the development of offshore wind energy, which are known to affect seabird species (Garthe et al., 2023; Kelsey et al., 2018).

This expansion proposal would result in larger SPAs. However, there is a worldwide debate about the advantages and disadvantages of small, highly protected MPAs and large MPAs with multiple purposes and uses (Kelleher, 1999). While small highly protected marine areas, that is marine no-take areas, remain critical for conservation purposes, large MPAs will complement and enhance these conservation efforts (Toonen et al., 2013). Recent created larger MPAs helped achieve global protection objectives, as large areas

often contain diverse ecosystems and habitats, which interact ecologically and allow a more holistic conservation approach (Wilhelm et al., 2014). In addition, large MPAs can extend their boundaries between different countries (as would be our case) to promote joint protection policies (Christie et al., 2017; García-Barón et al., 2019), or even allow for some human uses in particular areas, such as regulated fishing or sustainable tourism (Maestro et al., 2019). Conversely, monitoring larger MPAs is unquestionably more expensive and complex due to the required time, number of resources and costly technology to adequately monitor vast areas. Nonetheless, the urgent need to conserve our seas and coasts and achieve the agreed biodiversity targets means that the expansion of our proposed SPAs will undoubtedly offset the difficulties of surveillance, law enforcement, and control of large MPAs.

4.4 | Limitations of the data and models

Although our models did not offer an excellent performance (AUC ~0.750), predictions with such values indicates useful applications (Swets, 1988), especially when the target species is difficult to detect. In addition, recent studies with deployed geolocators in ESP support our results, with tracked individuals using the same core area in the Gulf of Cádiz (Militão et al., 2022).

Our models mainly represent the periods between July and November, which coincides with the reproductive and migratory season of the breeding ESPs of the Spanish colonies, and with the migratory season of ESPs from higher latitudes that cross our study area (Carboneras et al., 2021; Sanz-Aguilar & Lago, 2021). Because fewer surveys were conducted during the winter months (December and January), the results of our models might be biased towards these months with more sampling effort. However, this period is likely representative for the wintering period of the Mediterranean subspecies, of which several individuals cross the Strait of Gibraltar towards the Atlantic from August to late December (Militão et al., 2022).

Furthermore, the algorithms used in the ensemble models offered very robust predictions as evidenced by the low values of the uncertainty map (<0.1). However, the highest values of this uncertainty occurred in the candidate's zones to be expanded in the area around the Golfo de Cádiz SPA, so this information must be taken with caution. Such relatively high level of uncertainty might be related to the small sample size gathered over a few months in that area (March or December), or due to a very low or null presence during certain months (January or March).

Despite these limitations, we consider our results to be sufficiently robust to characterise the at-sea habitat of ESPs throughout the year. Our study is the first to utilise a very extensive long-term data set (15 years) collected during all months of the year on a representative large spatial scale (>150,000 km^2) to effectively assess the coverage of MPAs for the distribution of the ESP. Our findings emphasise the need to expand and enforce MPAs effectively to conserve this small marine predator and other seabird species, thus enhancing spatial planning for at-sea conservation.

AUTHOR CONTRIBUTIONS

Andrés De la Cruz and Gonzalo M. Arroyo conceived the ideas; Andrés De la Cruz, Jorge M. Pereira, Vitor H. Paiva, Jaime A. Ramos and Gonzalo M. Arroyo designed methodology; Andrés De la Cruz, Jorge M. Pereira, Vitor H. Paiva, Nuno Oliveira, Hany Alonso, Camilo Saavedra, José Antonio Vázquez, Isabel García-Barón and José Manuel Arcos provided the data; Andrés De la Cruz and Jorge M. Pereira analysed the data; Andrés De la Cruz led the writing of the manuscript; all authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

Vitor H. Paiva is an associate editor of *Journal of Applied Ecology*, but took no part in the peer review and decision-making processes for this paper. The rest of the authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

European storm-petrel occurrence data are available via the Dryad Digital Repository https://doi.org/10.5061/dryad.jh9w0vtfz (De la Cruz et al., 2023).

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SUPPORTING INFORMATION

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

Table S1: Bivariate Pearson rank correlations between environmental predictors included as variables analysed in the models.

Table S2: Univariate summary of generalised additive models (GAM) ordered by Akaike's information criterion (AIC).

Table S3: Static and dynamics environmental variables applied for the ensemble species distribution models.

Table S4: Summary evaluation and metrics of annual ensemble specie distribution model (ESDM) for the European storm-petrel in the Atlantic Iberian arc.

Table S5: Summary evaluation and metrics of the overall ensemble (2005–2019) specie distribution model (ESDM) for the European storm-petrel in the Atlantic Iberian arc.

Table S6: European storm-petrel core area size comparison and overlap rate (0–1) with the overall core area (2005–2019) over the years in the Atlantic Iberian arc.

Table S7: Explanatory generalised lineal models obtained to study the relationship between the overall European storm petrel core area size (km^2) and the most important dynamic variables: SST (Sea Surface Temperature) and MNK (Biomass of Micronekton) throughout the study period (2005–2019) based on the AIC criteria and the and explained deviance percentage.

Figure S1: Overall MAXENT model response curve showing the predictor variables.

Figure S2: Overall GAM model response curve showing the predictor variables.

Figure S3: Annual ensemble distribution model of the European storm-petrel distribution together with occurrence probability in the Atlantic Iberian arc.

Figure S4: Relationship between (a) European storm-petrel core area size comparison and (b) overlap rate with the global core area (2005–2019) over the years in the Atlantic Iberian arc.

Figure S5: Variation of the mean values of the primary dynamic predictors of the European storm-petrel distribution in the study area, depicted by different colours: sea surface temperature in blue, micronekton in green (the standard deviation is depicted in grey), along with the species' core area throughout the study period.

Figure S6: Partial effects of the best GLM model when analysing the relationship between the size of the European storm-petrel core area throughout the study period and its main dynamic predictors (sea surface temperature and micronekton concentration).

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