Proceedings of the 6th International Conference on Biological Engineering and Medical Science
DOI: 10.54254/2753-8818/2026.36410

Future Habitat Suitability of Sphyrna lewini in the Galápagos

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Abstract. This research study aims to analyze the consequences of climate change on the spatiotemporal distribution of Critically Endangered scalloped hammerhead shark (Sphyrna lewini) in the Galápagos Marine Reserve (GMR) using MaxEnt modelling and CMIP6 scenarios (SSP1-2.6, SSP3-7.0, and SSP5-8.5). Results show that the distribution of S. lewini is mainly controlled by two predictors, which are phytoplankton concentration (phyc) and silicate (si), confirming the bottom-up control process. Under all scenarios, the core highly suitable areas are predicted to contract and become fragmented substantially, especially under SSP1-2.6 scenario. While SSP5-8.5 suggests an expansion of marginal habitats, this likely reflects forced dispersal into less favorable environments due to rising thermal stress. Notably, suitability centroids are projected to shift toward the eastern sectors of the GMR, increasing the species' exposure to industrial fishing beyond current protected boundaries. Stable eastern regions are identified as critical climatic refugia that warrant prioritized protection. These results emphasize the urgent need for dynamic ocean management and transboundary conservation corridors to ensure the long-term persistence of migratory shark populations in the Tropical Eastern Pacific.

Keywords: Climate change, marine biology, wildlife conservation

1. Introduction

Marine ecosystems possess exceptional biodiversity and resource wealth. Despite offering numerous ecological advantages for humans, marine ecosystems have been adversely affected by human interference such as overfishing, degradation of habitat and marine pollution [1]. Over exploitation has triggered severe population declines of apex predators, disrupting the balance of marine food webs and reducing the ecological resilience of ocean systems simultaneously [2]. Climate change intensifies existing oceanic pressures by changing oceanography parameters including warmer sea surface temperature, decreased pH of seawater, and decreasing oxygen levels. This impacts negatively on marine productivity and life cycles of species migration [3].

The scalloped hammerhead shark (Sphyrna lewini) is a highly mobile apex predator essential for regulating marine food chains. Mostly, the species inhabits coastal and pelagic regions, with juveniles occupying the inshore nurseries such as mangrove and estuarine regions, and adults congregating at oceanic islands. It is because of its characteristic life history features, which include live-bearing and low fecundity, that the species becomes very susceptible to human disturbance. Globally, wild populations of S. lewini have declined by over 80%, resulting in its classification as a

DOI: 10.54254/2753-8818/2026.36410

Critically Endangered species on the IUCN Red List [4]. The sharks migrate to track shifting prey aggregations and suitable thermal zones, yet how their migratory ranges will respond to severe future climate warming remains poorly understood [5].

The Galápagos Marine Reserve (GMR) is a globally significant biodiversity hotspot, whose complex upwelling systems make it disproportionately sensitive to anthropogenic global warming. Despite its ecological importance, research focusing on the specific shifts in S. lewini habitat suitability within the GMR under future climate scenarios is still limited [6]. This study employs Ecological Niche Models (ENMs), specifically like the MaxEnt algorithm, to quantify the relationship between species occurrence and environmental predictors [7]. By integrating high-resolution data from the Bio-ORACLE system and the latest CMIP6 emissions scenarios, future distribution shifts are predicted and climate refugia for the target species are delineated [8].

MaxEnt will be utilized in this study to analyze the suitability and future prediction of habitat of S. lewini in the Galapagos Islands both in current conditions and three climate scenarios of CMIP6 (SSP1-2.6, SSP3-7.0, SSP5-8.5) for two periods: mid-century (2050-2060), and end-of-century (2090-2100). The following three main objectives of research will be set: (1) to predict the present suitability of habitat of S. lewini, (2) to predict the suitability of habitat of S. lewini in the future, and (3) to determine the environmental variables with maximum impact on the distribution range of S. lewini. The results obtained by us will help to fill an important gap in the knowledge about the future distribution ranges of S. lewini and its conservation in the Galapagos Islands.

2. Materials and method

2.1. Species occurrence data

The study focuses on the distribution range of S. lewini in the eastern Pacific Ocean, specifically on the Galapagos Marine Reserve. Georeferenced occurrence records of S. lewini are retrieved from the Global Biodiversity Information Facility [9]. All raw occurrence datasets undergo standardized preprocessing prior to subsequent statistical modeling. Data cleaning procedures include removing duplicate coordinate records, filtering geographic points falling outside the defined study boundary, and eliminating erroneous geospatial outliers. To mitigate spatial sampling bias, spatial thinning is implemented via the R package spThin (version 0.2.0), retaining only one valid occurrence point within each 0.5 km radius grid cell [10]. After preprocessing, a total of 209 geographically independent valid occurrence points of S. lewini are retained for modeling analysis (See Figure 1). These cleaned records serve as the primary input dataset for all downstream MaxEnt simulations. Finally, the filtered occurrence points are visualized in ArcGIS 10.8 software (ESRI, Redlands, CA, USA) based on the World Geodetic System 1984 (WGS84) geographic coordinate system.

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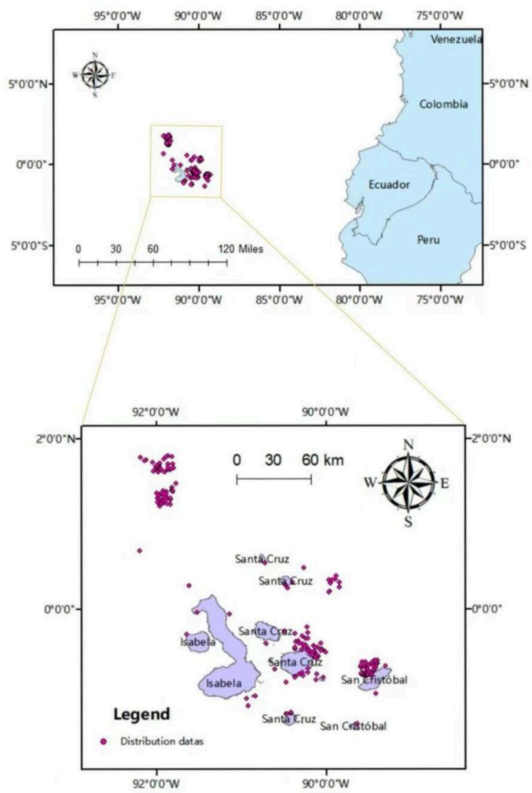

Figure 1. The geographic distribution of Sphyrna lewini in the Galapagos Marine Reserve

2.2. Environmental data

The study used environmental data from the Bio-ORACLE database (https://www.biooracle.org/) to predict the potential distribution of S. lewini. Present-day variables (2010–2020) and future projections under three climate scenarios (SSP1-2.6, SSP3-7.0, and SSP5-8.5) were gathered for two time periods: midcentury (2050–2060) and end-century (2090–2100).

Given that the scalloped hammerhead is a highly mobile pelagic species, we initially considered a suite of surface oceanographic layers, including phytoplankton concentration (phyc), silicate (si), dissolved oxygen (O_2), seawater salinity (so), depth (swd), current speed (sws), and seafloor topography (See Table 1). The selection of a biologically relevant calibration area is fundamental to reducing spatial bias in ecological niche modeling (ENM). To delineate the geographic scope of our model, we utilized the Marine Ecoregions of the World (MEOW) classification system. Only ecoregions with confirmed occurrence records were included in the calibration area to ensure biological realism.

Table 1. Description of environmental variables used in the MaxEnt model

Variable Code	Environmental Variable	Units	Data Source
phyc	Phytoplankton concentration	mg.m-3	Bio-ORACLE v3.0
si	Silicate concentration	mol.m-3	Bio-ORACLE v3.0
O2	Dissolved oxygen	Mol.m-3	Bio-ORACLE v3.0

Table 1. (continued)

swd	Sea water depth	m	Bio-ORACLE v3.0
so	Sea water salinity	PSU	Bio-ORACLE v3.0
sws	Sea water speed	m.s	Bio-ORACLE v3.0
Terrain	Terrain characteristics	-	Bio-ORACLE v3.0

Prior to model training, collinearity among all predictor layers is quantified to eliminate redundant variables. A stepwise multicollinearity diagnosis is conducted using the vifstep function integrated in the R package usdm to screen the original 12 environmental predictors. A strict Variance Inflation Factor (VIF) cutoff value of 5 is applied to exclude highly correlated predictors. Seven ecologically meaningful environmental variables are retained for the final MaxEnt simulation, ensuring all input predictors provide non-overlapping biological information (See Figure 2).

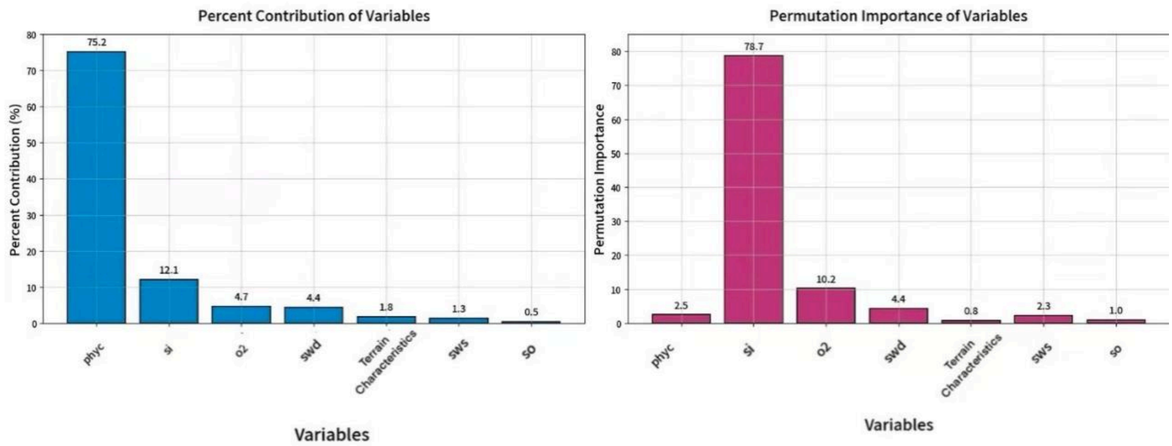

Figure 2. The relative influence of environmental factors on the potential distribution of Sphyrna lewini in the Galapagos Marine Reserve, as derived from the ecological niche models

2.3. Ecological Niche Modelling (ENM)

Based on recent findings in the area of Distribution Modelling, an Ecological Niche Model (ENM) was constructed using accurate coordinates data (see Figure 1) and important environmental variables (see Figure 2). During the process of creating the first model, a series of improvements to increase the effectiveness of the model's operation were implemented. The data points regarding the species' occurrence were split into ten groups using cross-validation technique in order to minimize the influence of spatial autocorrelation. Additionally, the Maxent model parameters were optimized up to 5,000 iterations.

MaxEnt version 3.4.4 was used to generate a habitat suitability model of S. lewini because it is a very efficient algorithm designed for the modeling of presence-only data within marine ecosystems. This algorithm was set up to output a logistic format; the probability of presence ranging between 0 to 1. To achieve the best prediction performance, the study optimized the model parameters by testing different combinations of Regularization Multipliers (RM) and Feature Classes (FC). For S. lewini, the optimal parameterization was determined to be RM = 1 with linear, quadratic, and

DOI: 10.54254/2753-8818/2026.36410

product (lqp) feature classes. These settings were selected to ensure model stability and significance during the 10-fold cross-validation process. Furthermore, we utilized the Jackknife test to evaluate the relative importance of each environmental variable in determining the shark's distribution.

To evaluate the model's performance, the Area Under the Receiver Operating Characteristic Curve (AUC) was utilized, with values interpreted as outstanding (≥0.9), moderate (0.8–0.9), or poor (≤0.8). The paper predicted the suitable habitats for S. lewini under current conditions and six future climate scenarios (SSP1-2.6, SSP3-7.0, and SSP5-8.5 for the years 2050 and 2100). Future projections were based on the standardized future climate layers provided by the Bio-ORACLE v3.0 database, which represent an integration of multiple climate model outputs. The raw ASCII outputs from MaxEnt were converted into GeoTIFF format using the 'ASCII to Raster' tool in ArcGIS 10.8. To standardize the maps, we employed the 'Reclassify' tool (Spatial Analyst), using the Natural Breaks method to partition the continuous probability values into four discrete categories. To simplify the ecological interpretation, these categories were grouped and labeled as: (a) low suitability, (b) moderate suitability, and (c) high suitability (See Figure 3)."

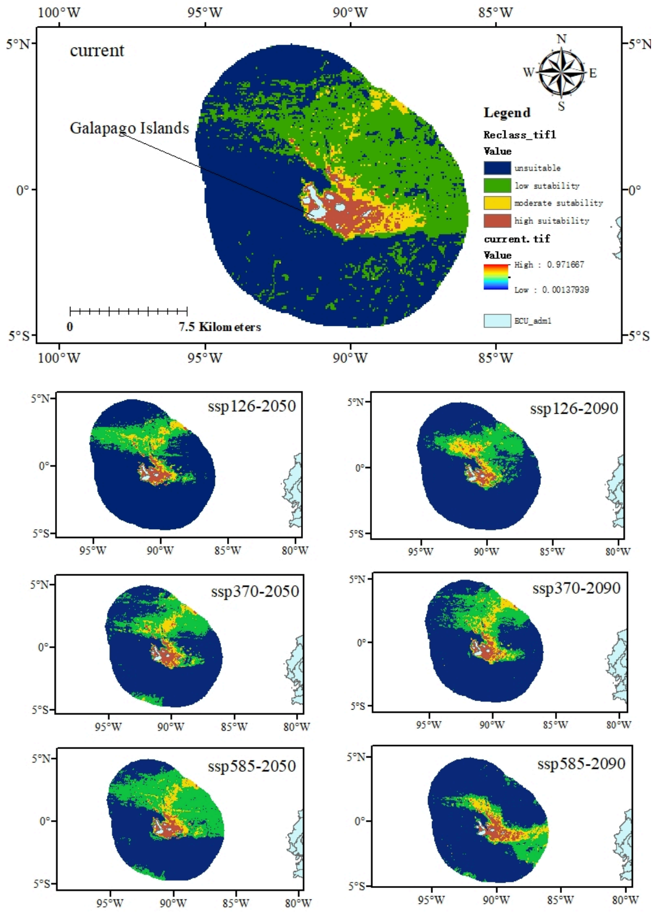

Figure 3. Predicted potential suitable areas for Sphyrna lewini under various climate change conditions within the Galapagos Marine Reserve. Maps show the status quo and three possible futures under different development pathways by 2050-2060 and2090-2100 beyond (i.e., SSP1-2.6, SSP3-7.0 and SSP5-8.5)

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3. Results

3.1. Model performance

The finalized MaxEnt model demonstrated high reliability, achieving an average test AUC of 0.877 under current environmental conditions. The model maintained stable and excellent predictive performance across all future climate scenarios, with AUC values ranging from 0.918 to 0.957 (See Table 2; See Figure 4). These metrics validate that the modeling framework is robust and highly applicable for spatial predictions within the Galápagos Marine Reserve.

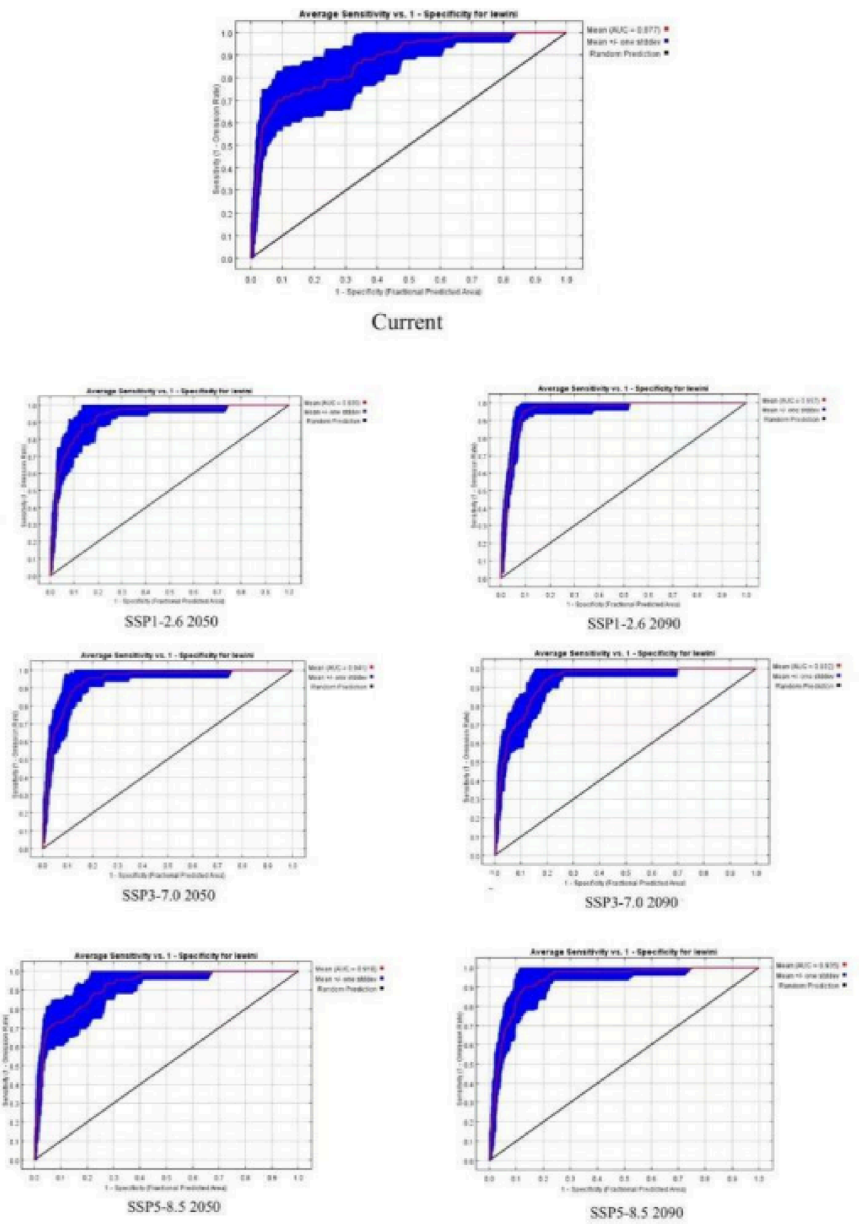

Figure 4. Receiver operating characteristic (ROC) curve averaged over 10 replicate runs for the MaxEnt model of S. lewini. The red line represents the mean AUC, and the blue shading indicates the standard deviation

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3.2. The relative contribution of environmental predictors

To examine the importance of the environment factors for the spatial distribution of S. lewini , the contribution values and permutation importance were assessed using MaxEnt software output and Jackknife analysis (See Figure 2; Figure 5). As shown in the result, the concentration of phytoplankton (phyc) had the highest percent contribution value (75.2%) among the environmental variables in the model building. On the other hand, si (silicate) possessed the highest permutation importance value (78.7%), which indicates that it is the most important factor for predicting the stability of the model. The other variables included dissolved oxygen (o2) and swd (sea water depth) had a smaller percent contribution value (4.7% and 4.4%, respectively). This finding implies that primary productivity (phyc) and nutrients availability (si) are the two main factors for habitat suitability in the Galápagos Marine Reserve (Figure 6).

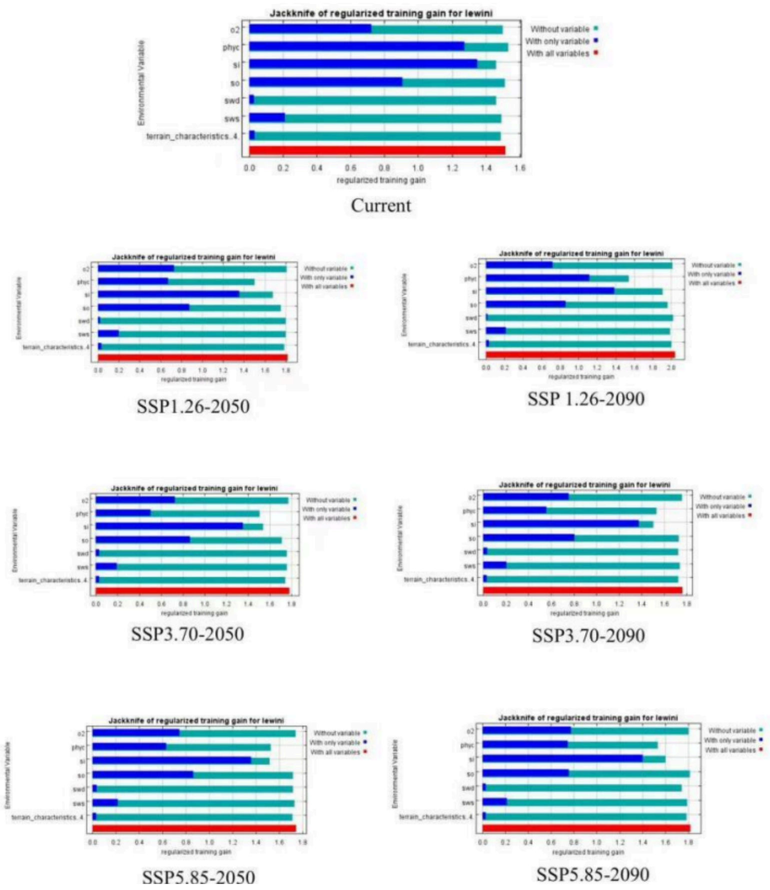

Figure 5. Jackknife test results for evaluating the relative importance of environmental variables in the S. lewini distribution model. Blue bars indicate the gain achieved using only the specific variable; the teal bar indicates the total gain when all variables are included

Table 2. The distribution of records for S. lewini, as well as the assessment indicators including area under the curve (AUC)

Period	Scenario	No. of Records	AUC
Current	Present-day (2010–2020)	209	0.877

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Table 2. (continued)

2050–2060	SSP1-2.6	209	0.935
2050–2060	SSP3-7.0	209	0.941
2050–2060	SSP5-8.5	209	0.918
2090–2100	SSP1-2.6	209	0.957
2090–2100	SSP3-7.0	209	0.932
2090–2100	SSP5-8.5	209	0.935

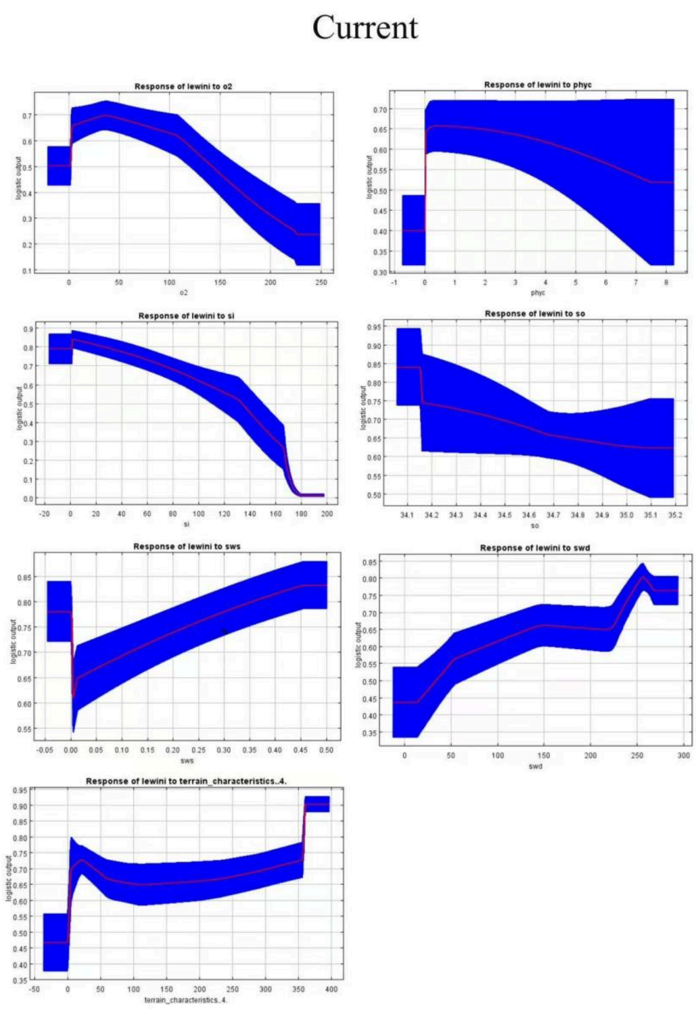

Figure 6. Response curves showing the relationship between environmental predictors and the habitat suitability for S. lewini. Red lines indicate the mean response of 10 replicate runs, and blue shading represents the standard deviation

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3.3. Potential distribution ranges under current climatic conditions

The MaxEnt model reveals distinct distribution patterns for S. lewini under current climatic conditions (2010–2020) based on the analyzed environmental variables. From geographical analysis (see Figure 3), it is shown that the highly suitable regions (Red areas) occupy around 32,248 km². The core areas are mainly found in the coastal and island regions of the Galápagos archipelago, especially those located centrally and eastwards due to the abundance of nutrients and favorable temperatures in these locations. This aligns with the ecological preferences of the species in the region.

The Medium Suitable Area (yellow spaces) serves as a transitional zone with an approximate size of 38,962 km². The medium suitable areas act as continuous barriers for the high suitability core areas and therefore the species is relatively uniformly distributed in the middle part of the Galapagos Marine Reserve. For the poor Suitable Areas (green spaces), it has a much larger coverage of 265,742 km² and extends to distant pelagic areas.

Such patterns illustrate the ecological relevance of shelf and slope nutrient habitats near the Galápagos Islands (Figure 3). Such habitats show a high amount of clustering in their concentrations of optimal habitats due to close relation to local maximum values of phycotrophic abundance and silica in the variable importance graph (Figure 2). Presently, when considering such a distribution, it is mainly dependent on such productive or nutrient habitats that arise due to the Galapagos Upwelling System. Habitat area estimates for all suitability classes are summarized in Table 3.

Table 3. Predicted habitat areas (km²) of S. lewini in the present and future periods

Scenario	Period	Highly Suitable	Medium Suitable	Low Suitable	Unsuitable
Current	Present	32,248	38,962	265,742	501,455
SSP1-2.6	2050	24,059	42,166	143,528	628,659
	2090	21,652	43,644	140,048	633,063
SSP3-7.0	2050	25,934	48,972	178,825	566,505
	2090	25,595	53,715	163,640	595,456
SSP5-8.5	2050	26,734	51,005	287,426	1,803,340
	2090	31,046	111,003	648,371	1,804,572

3.4. Predicted shifts under climate change scenarios

Future projections of habitat suitability based on different scenarios of future climate change (SSP1-2.6, SSP3-7.0, and SSP5-8.5) reveal considerable changes in the spatial pattern of S. lewini (Figure 3; Table 3). In the low-emission scenario SSP1-2.6, considerable reduction in core high-quality habitats will take place. In the 2090-2100 time frame, the area of highly suitable habitat will be reduced to 21,652.4 km² from the current value of 32,247.6 km². Particularly, the highly suitable habitat regions that were earlier connected around the archipelago will fragment (Figure 3d), which means that even moderate warming may lead to localized habitat loss in key areas for the species.

The situation under the scenario of extreme emissions (SSP5-8.5) demonstrates a much more complicated reaction of the system. The high suitability region will stay almost unchanged and will be equal to about 31,046.4 km² until the 2090-2100 decade. Nevertheless, the model foresees considerable growth of moderately and unsuitably areas that would total more than 750,000 km²

(Figure 3f; Table 3). It means the expansion of regions where the animal lives due to an increase in sea temperature.

In all possible future cases, it becomes clear that the habitats become displaced from their initial locations. In particular, there is a gradual displacement of the center of habitat suitability to the outer parts of the Galápagos Marine Reserve. This will most certainly affect the survival environment of S. lewini. To address these problems, better methods of adaptive management strategies need to be considered for protecting the habitat of this species.

Notably, despite the overall contraction of highly suitable areas, the study's overlapping analysis of all climate scenarios identifies specific regions primarily located in the eastern and northern sectors of the GMR as persistent high-suitability zones. They have maintained their stability in environmental conditions through both SSP1-2.6 and SSP5-8.5 scenarios and can thus function as climatic refugia for S. lewini.

4. Discussion

4.1. Ecosystem function and environmental drivers

As a critically endangered apex predator, Sphyrna lewini is an indispensable species in contributing to the structure and balance of the ecosystem of the Tropical Eastern Pacific. The study's analysis identifies phytoplankton concentration (phyc) and silicate (si) as the dominant environmental determinants that influences its distribution(Figure 2). The substantial contribution of phyc (75.2%) provides robust empirical support for the "bottom-up" control mechanism within the Galápagos Marine Reserve (GMR). The implication here is that the range of S. lewini is not arbitrary but rather depends on areas of high primary productivity, which are necessary to support large concentrations of forage fish and squid that the sharks feed on [11, 12].

More precisely, due to high silicate concentration, the existence of localized nutrient upwelling leads to the emergence of biogeochemical "hot spots," which are vital for the existence of the studied species [13]. Modern research has emphasized the role of climate-driven changes in primary productivity, which directly control the residency and foraging behavior of large pelagic predators [11, 12]. The nutrient-rich areas are crucial for foraging and represent the arena where the interaction of nutrient-dense and cool upwelling currents and high sunlight create an intensive food chain required by hammerhead sharks.

4.2. Climate-induced range shifts and vulnerability

The multi-scenario projections derived from CMIP6 data offer a sobering perspective on the long-term sustainability of S. lewini. There is a trend of habitat fragmentation and loss seen in most, if not all, possible future developments (Figure 3; Table 3). In the case of the SSP1-2.6 scenario, the highly suitable habitat area will shrink to around 21,652.4 km² in the years 2090 to 2100. This loss of suitable habitat is representative of a broader, systemic decline in specialized marine habitats caused by the synergistic effects of ocean warming and deoxygenation [14].

The key factor here is that although the high emission scenario (SSP5-8.5) delineates a huge shift towards low suitability areas, this implies that the increase in temperature of the water can create thermal windows for S. lewini to move out of the traditional core areas. This is a misleading range expansion because instead of being a true range expansion it is rather forced migration to unsuitable places for the species. A dispersed distribution makes these species more vulnerable to any danger because a dispersed community is hard to manage. The warming climate will force the sharks to go

DOI: 10.54254/2753-8818/2026.36410

into deeper water and higher latitudes where they might face phenological mismatching with seasonal prey species.

4.3. Conservation implications and management strategies

The spatial analysis reveals that the most critical habitats are currently nested within the GMR, but their predicted shift toward the boundaries of the Exclusive Economic Zone poses a significant management challenge (Table 3). As these "suitability centroids" move toward the GMR's periphery, the sharks will be increasingly exposed to unregulated anthropogenic threats, such as industrial longline fishing and illegal, unreported, and unregulated (IUU) fishing activities [2].

Since S. lewini cannot perceive political or administrative borders, static Marine Protected Areas (MPAs) have become increasingly outdated in the face of rapidly changing climate. In order to reduce the risk of these impacts, we suggest moving towards Dynamic Ocean Management. This involves the use of satellite tracking and predictive modeling in order to move the boundary line in accordance with the movement of the species. Moreover, "climate refuges," which stay the same regardless of the scenario of SSP (Figure 3), should receive the highest level of protection to ensure they remain as resilient nurseries for future generations.

4.4. Model limitations and future directions

Even though the performance of the MaxEnt models in this study was in a good situation (AUC > 0.9), it is imperative to understand that there are some uncertainties associated with correlative modeling. This modeling requires the use of presence-only data from the global databases, GBIF, and OBIS. To enhance scientific reasoning for policy-making, this study suggests the inclusion of Acoustic and Satellite Telemetry data, which will help obtain a high resolution understanding of the vertical habitat usage and fine-scale movement of the sharks [15]. Moreover, even though the abiotic variables have been used in this study, it is essential to include the biotic variables to make the biological projection more realistic, such as inter-specific competition and prey density map. Incorporation of socio-ecological variables, like fishing intensity and maritime traffic density, will definitely lead to holistic approach in adaptive conservation planning.

5. Conclusion

In this research paper, the impacts of climate change on the Spatial Distribution patterns of the Critically Endangered Scalloped hammerhead shark (Sphyrna lewini) in the Galapagos Marine Reserve have been estimated using Maximum Entropy Modeling approach. The general results of the study show that the distribution pattern of this species has been mainly determined by the synergism of the primary production and nutrient. In particular, the environmental predictors like phyc (phytoplankton concentration) and si (silicate) have proven to be the most influential factor, consistent with a bottom-up ecological control mechanism.

Under different CMIP6 emission scenarios (SSP1-2.6, SSP3-7.0, and SSP5-8.5), projections demonstrate a concerning trend: the main core habitats of this species are expected to shrink significantly or become fragmented by the end of this century. While the extreme-emission scenario (SSP5-8.5) reveals a complex system response characterized by a spatial expansion of marginal habitats, this 'range expansion' may be misleading; in reality, the population becomes increasingly vulnerable as it is forced into less favorable environments due to rising seawater temperatures and shifts in the pelagic environment.

In the light of the discussed above patterns of spatial and temporal variability, one may state that S. lewini will most probably invade those areas which are currently beyond the borders of protection systems. It implies certain consequences, including the danger of intensification of the exploitation of sharks and possible conflicts between the migration and historical ranges of sharks. For these reasons, it is crucial to develop a dynamic system of marine management in combination with creating transboundary conservation zones based on new migration routes of S. lewini. At the same time, it is necessary to ensure the protection of climatically stable areas in the east and north of the GMR, which will serve as refuges for sharks in the future. Thus, taking into account the continuous transformation of the structure of marine biodiversity under the influence of climate change, the current paper serves as a theoretical basis for management and protection of the studied populations of sharks in the Tropical Eastern Pacific region.

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