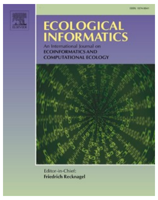
Ecological Informatics 95 (2026) 103727

Contents lists available at ScienceDirect

Ecological Informatics

journal homepage: www.elsevier.com/locate/ecolinf



Global climatic impact on the sea kraits living near the tectonic plate boundaries

Il-Kook Park [a,b], Yucheol Shin [c,d], Il-Hun Kim [a], Daesik Park [e,f,*]

[a] Marine Biodiversity Division, National Marine Biodiversity Institute of Korea, Seocheon 33662, Republic of Korea
[b] Research Institute of Agriculture and Life Sciences, Seoul National University, Seoul 08826, Republic of Korea
[c] Richard Gilder Graduate School, American Museum of Natural History, New York, NY 10024, USA
[d] Department of Herpetology, Division of Vertebrate Zoology, American Museum of Natural History, New York, NY 10024, USA
[e] Department of Science Education, Kangwon National University, Chuncheon 24341, Republic of Korea
[f] Interdisciplinary Program in Earth Environmental System Science & Engineering, Kangwon National University, Chuncheon 24341, Republic of Korea

ARTICLE INFO

Keywords:
Climate change
Distribution range
Ecological niche model
Habitat requirement
Marine reptile
Tectonic plate boundary

ABSTRACT

Rapid climate change threatens marine ecosystems, and understanding the distribution patterns and habitat requirements of marine organisms is crucial for their conservation. All eight species of sea kraits (genus *Laticauda*), amphibious marine reptiles, have distributions constrained within areas in the Indo-Pacific region, although their unique distribution patterns remain unclear. To define the distribution patterns and habitat requirements of sea kraits, 454 occurrence points across 8 species and 7 macro-environmental variables were analyzed. Additionally, ecological niche models were built to predict the potential distributions of sea kraits and the impact of climate change in the 2090s. Our findings indicate that sea krait habitats are primarily located near tectonic plate boundaries and centered around the equator, with interspecific differences mainly influenced by sea surface temperature. Ecological niche models predicted a considerable decrease in the habitable areas for sea kraits by the 2090s, primarily around the equatorial region with the highest species richness and diversity. However, the models also predicted minor expansion in Japan and Korea to the north and New Zealand to the south. Despite such predictions, cold subarctic Oyashio Current from the North Pacific and long-distance travel to potential refugia in New Zealand in the south may restrict their expansion. These findings indicate that the specific habitat requirements of sea kraits may limit their ability to cope with climate threats across their ranges, suggesting that climate change poses a significant threat to the entire genus with a unique ecology and restricted distribution range.

1. Introduction

Rapid rises in sea temperatures accompanying marine heatwaves and changes in sea salinity occurred in many oceans globally, causing severe ecological and economic damages, including mass deaths and migration of marine life (D'Amen et al., 2023; Hansen et al., 2006; QGIS.org, 2024; Smale et al., 2019). For example, habitat shifts in latitude or ocean depth were observed in approximately two-thirds of North Sea fish species (Kleisner et al., 2017; Perry et al., 2005), and sea turtles are increasingly exploring alternative foraging and nesting sites (Park et al., 2025; Pike, 2013). Although highly migratory species can respond relatively quickly to habitat disturbances, species with low vagility and strict habitat requirements often struggle to cope with rapidly changing habitat conditions that exceed their tolerance. This phenomenon was observed in marine benthos, corals, seaweeds, and seagrasses (Anderson et al., 2022; Birchenough et al., 2015; Waycott et al., 2009).

Understanding species distribution patterns and habitat requirements can provide essential information for effectively managing and conserving species in the face of climate change (Dawson et al., 2011). However, elucidating the patterns of distribution and habitat requirements of marine organisms is challenging because climatic, geographical, and biological factors have complex and interacting influences. Although sea temperature, salinity, currents, and depth can broadly characterize the habitats of marine organisms (Brischoux et al., 2012; Kerswell, 2006; Mascle and Biscarrat, 1978), species distributions cannot be explained solely by oceanic or climatic factors in many cases. In this regard, geographical factors can provide further insights into understanding distribution (Keith et al., 2013). The tectonic plate

---

* Corresponding author.
E-mail address: parkda@kangwon.ac.kr (D. Park).

https://doi.org/10.1016/j.ecoinf.2026.103727
Received 3 September 2025; Received in revised form 29 December 2025; Accepted 17 March 2026

boundary is one of the key geographic factors that explains the distribution of marine organisms. As complex seafloor topographies created by tectonic plate collisions could provide unique habitats for various marine organisms, areas near tectonic plate boundaries have been hypothesized to harbor high marine biodiversity in the Phanerozoic Eon (Zaffos et al., 2017). Coral reefs are estimated to have changed their distribution in response to the movement of tectonic plate boundaries 100 million years ago (Keith et al., 2013; Leprieur et al., 2016).

Only 8 sea krait species (genus *Laticauda*; subfamily Laticaudinae) are known among 73 marine snakes globally (Gherghel et al., 2016; Heatwole et al., 2017; Uetz et al., 2023). These species are amphibious and have a restricted distribution in the western Pacific and northeastern Indian Ocean centered around the equator (Gherghel et al., 2016; Heatwole et al., 2017; Patrón-Rivero et al., 2024). The equatorial region has the largest population and species diversity of sea kraits, but is predicted to experience the most severe rise in temperature due to climate change (Ramírez et al., 2017). Therefore, the disturbance of existing core habitats by climate change could accelerate serious threats to sea krait populations, exacerbating a steady decline in sea krait populations that has already been observed over the past 40 years (Bonnet et al., 2014; Heatwole, 1997). Nevertheless, research on the potential impacts of climate change on this unique and range-restricted genus is scarce.

To cope with climatic threats, understanding the distribution patterns and habitat requirements of sea kraits has to precede (Tovar et al., 2022). Previous studies have investigated the influence of diverse environmental factors on determining the global distribution patterns of sea kraits, including precipitation (Lillywhite and Tu, 2011), salinity (Brischoux et al., 2012), sea and air temperatures (Heatwole et al., 2016), minerals (Patrón-Rivero et al., 2024), coral reefs (Heatwole et al., 2017), and prey abundance (Gherghel et al., 2018). Additionally, as sea kraits primarily forage in coral reef areas, their distribution has been explained by the Coral Triangle, extending through Southeast Asia and Melanesia (Heatwole and Cogger, 2013, Heatwole et al., 2017). Nevertheless, the regional distribution patterns of all sea krait species remain unclear. For instance, sea kraits are not found near the coasts of China, eastern Indochina, or Australia, despite the conditions above being suitable for them in these regions (Gherghel et al., 2018, 2019; Heatwole et al., 2016).

To investigate the distribution of sea kraits, we hypothesized that, in addition to previously known variables, tectonic plate boundaries may have critical importance in determining their habitats. Accordingly, we aimed to 1) determine the macro habitat requirements of all sea krait species, 2) compare the interspecific differences, and 3) predict global range shifts and habitat disturbances under future climate change scenarios. This study aims to evaluate the current and future conservation status of sea kraits to offer guidelines for effective conservation and management strategies following climate change. Furthermore, our findings warn potential threats posed by climate change to unique and limited marine species.

2. Methods

2.1. Location data collection

We collected location data for eight sea krait species: yellow-lipped sea krait (*Laticauda colubrina*), blue-banded sea krait (*L. laticaudata*), Chinese sea snake (*L. semifasciata*), dwarf sea krait (*L. frontalis*), New Caledonian sea krait (*L. saintgironsi)*, Guinea's sea krait (*L. guineai*), flat-tail sea krait (*L. schistorhynchus*), and Crocker's sea snake (*L. crockeri*). Location data were collected from field surveys, literature, and online databases. First, we conducted field surveys in the Republic of Korea, Japan, and the Philippines from 2014 to 2024. Second, we obtained location data from published literature (Cogger et al., 1987, Cogger and Heatwole, 2006; Gherghel et al., 2016; Heatwole et al., 2016). Finally, we downloaded data from iNaturalist (https://www.inaturalist.org/) and GBIF (https://www.gbif.org/) [Accessed on January 8th, 2025]. To increase reliability, we utilized data collected since 2000, including the year of observation, observer information, and coordinates with more than five decimal places of accuracy. Additionally, we excluded erroneous datapoints based on Gherghel et al. (2016) and Heatwole et al. (2016). Lastly, to reduce spatial autocorrelation and bias between location data, we used only one randomly selected coordinate within a 50-km radius of each location data point (Anderson and Raza, 2010; Boone and Krohn, 1999). The final dataset composed of 454 occurrence points for all 8 species of sea kraits: 271 for *L. colubrina*, 99 for *L. laticaudata*, 40 for *L. semifasciata*, 17 for *L. frontalis*, 17 for *L. saintgironsi*, 4 for *L. guineai*, 4 for *L. schistorhynchus*, and 2 for *L. crockeri*. It should be noted that a small number of fewer than five locations each from *L. guineai*, *L. schistorhynchus*, and *L. crockery* indicate relatively narrow distribution ranges, not their small population sizes.

2.2. Environmental variable selection

To determine the habitat characteristics of sea kraits, we analyzed topographical, geographical, and oceanic variables known to be essential for sea krait habitat. First, as topographical variables, we selected sea depth (m) and slope (°), considering that sea kraits are benthic foragers mainly using shallow seas less than 100 m deep with diverse and complex seafloor structures (Brischoux et al., 2007; Liu et al., 2012). Second, we analyzed distance to shore (DTS, km) and distance to the tectonic plate boundaries (DTP, km) as geographical variables. Amphibious sea kraits mainly use near-shore habitats, as they not only use the sea as a foraging ground, but also use land for thermoregulation and oviposition (Gherghel et al., 2016; Heatwole et al., 2016). Additionally, preliminary visualization of species distribution suggested that sea kraits are closely distributed along tectonic plate boundaries (TPBs) in the Indo-Pacific region (Fig. 1). Third, as oceanic variables, we selected annual mean values of sea surface temperature (SST_{mean}) between 2010 and 2020, the mean values of the hottest month (SST_{max}), and annual ranges (SST_{range}) of sea surface (°C) and air temperatures (AIT_{mean}, AIT_{max}, and AIT_{range}). The sea krait location data were collected over the period 2000–2024, while the range of current climatic variables was from 2010 to 2020. Despite this temporal mismatch, we used a wider time period for the location data collection to increase the sample size of sea krait locations. We also selected annual mean sea surface salinity (SSS, ‰), which is closely related to the water intake of sea kraits (Brischoux et al., 2012; Kidera et al., 2013). Additionally, because rainfall provides a major freshwater source for sea kraits, the annual mean cloud coverage (%) was used as a substitute for precipitation (Gherghel et al., 2018; Lillywhite and Tu, 2011). As high collinearity between variables can distort model predictions, we excluded variables with Pearson correlation coefficients greater than 0.7 (Dormann et al., 2013). Consequently, seven variables were used for all analyses: depth, slope, DTS, DTP, SST_{max}, SST_{range}, and SSS (Supplementary Material 1).

All variables except DTS and DTP were downloaded from Bio-ORACLE (https://www.bio-oracle.org/index.php; Assis et al., 2024) [Accessed on January 10th, 2025]. The DTS and DTP were calculated as the distance from the land map sourced from the Database of Global Administrative Areas (https://gadm.org/) and TPB data downloaded from ArcGIS Hub (https://hub.arcgis.com/maps/), respectively. The spatial resolution for all the variables used was ~5.5 km × 5.5 km. Although this resolution is too coarse to capture fine-scale environmental conditions, it is effective for analyzing large areas exceeding 100 million km^2 of the entire sea krait distribution range, reasonable given that the climate does not vary significantly within 5.5 km. We provided the values of each environmental variable for all sea krait locations in Supplementary Material 1.

2.3. Interspecific comparison in oceanic variable usage

Based on selected environmental variables, we aimed to determine the distribution patterns of each sea krait species. *Laticauda colubrina*, *L. laticaudata*, and *L. semifasciata* consisted of sufficient samples over 30 for statistical analysis, whereas the five remaining species (*L. frontalis*, *L. saintgironsi*, *L. guineai*, *L. schistorhynchus*, and *L. crockeri*) consisted of fewer than 20 samples with narrow distributions. Therefore, we did not conduct individual species tests for the five species; instead, we treated these five species as one complex, considering that they all occur within narrow areas at similar latitudes and climates near small islands in Melanesia (hereafter referred to as the five-*Laticauda* complex [FLC]). The analysis for the FLC does not reflect the specific habitat characteristics of each species; instead, it presents the overall distribution pattern of the five species. Therefore, we note that the analysis for FLC was conducted to predict the potential effects of climate change on habitat disturbance and range shift for these five sea krait species combined, rather than to predict the distribution of each species.

First, we conducted a one-way analysis of variance (ANOVA) to compare the habitat environmental variables among the four *Laticauda* groups, including *L. colubrina* ($n = 271$), *L. laticaudata* ($n = 99$), *L. semifasciata* ($n = 40$), and FLC ($n = 44$), after verifying the normality of data using the Kolmogorov-Smirnov test. To compare the differences between each group, we additionally conducted the Bonferroni test as a post hoc analysis. Statistical significance was defined as a $p < 0.05$.

Second, we conducted the principal component analysis (PCA) to determine which variables mainly affect the distribution patterns of each species. Before performing PCA, we evaluated the suitability of our data for PCA by performing the Kaiser-Meyer-Olkin (KMO) test and Bartlett's test. The KMO and Bartlett's test values were 0.576 (moderate) and significant (Chi-Square = 811.644, $P < 0.001$), respectively, suggesting that this data set was appropriate for conducting PCA (Shrestha, 2021). However, it should be noted that the KMO value barely exceeds the minimum criteria for PCA analysis. As PCA results, we only provided the principal components (PCs) with an eigenvalue of 1 or more. For the intergroup discrimination pattern, we created the loading score plot, created based on the two most important PCs, and 50% ellipsoids were centered around the median of each group. We used the "prcomp" function in R software (R Core Team, 2021) for PCA.

2.4. Building ecological niche models

We generated individual ecological niche models (ENMs) for *L. colubrina*, *L. laticaudata*, *L. semifasciata*, and FLC. We did not build individual ENMs for five *Laticauda* species with fewer than 20 location data points, since at least 30 presence data points are required to build reliable models (Barbet-Massin et al., 2012; Valavi et al., 2022). For ENM algorithms, we selected three machine learning methods: random forest, boosted regression tree (BRT), and maximum entropy (MaxEnt). Random forest has high predictive power (especially in interpolation) even with little presence data, and BRT and MaxEnt are known to have the most reliable modeling performance compared to other algorithms (Heikkinen et al., 2012; Valavi et al., 2022). We first generated single algorithm models and used these models to generate ensemble models using the *biomod2* package (Guéguen et al., 2025) in R software v.4.2.2 (R Foundation for Statistical Computing, Vienna, Austria; R Core Team, 2021). The ensemble method can enhance model performance by overcoming the shortfalls of individual modeling algorithms (Grenouillet et al., 2011; Park et al., 2023; Valavi et al., 2022).

To evaluate the performance of the ENMs, we used the area under the curve (AUC), true skill statistic (TSS; Allouche et al., 2006), and continuous Boyce index (CBI, Hirzel et al., 2006). The AUC is a

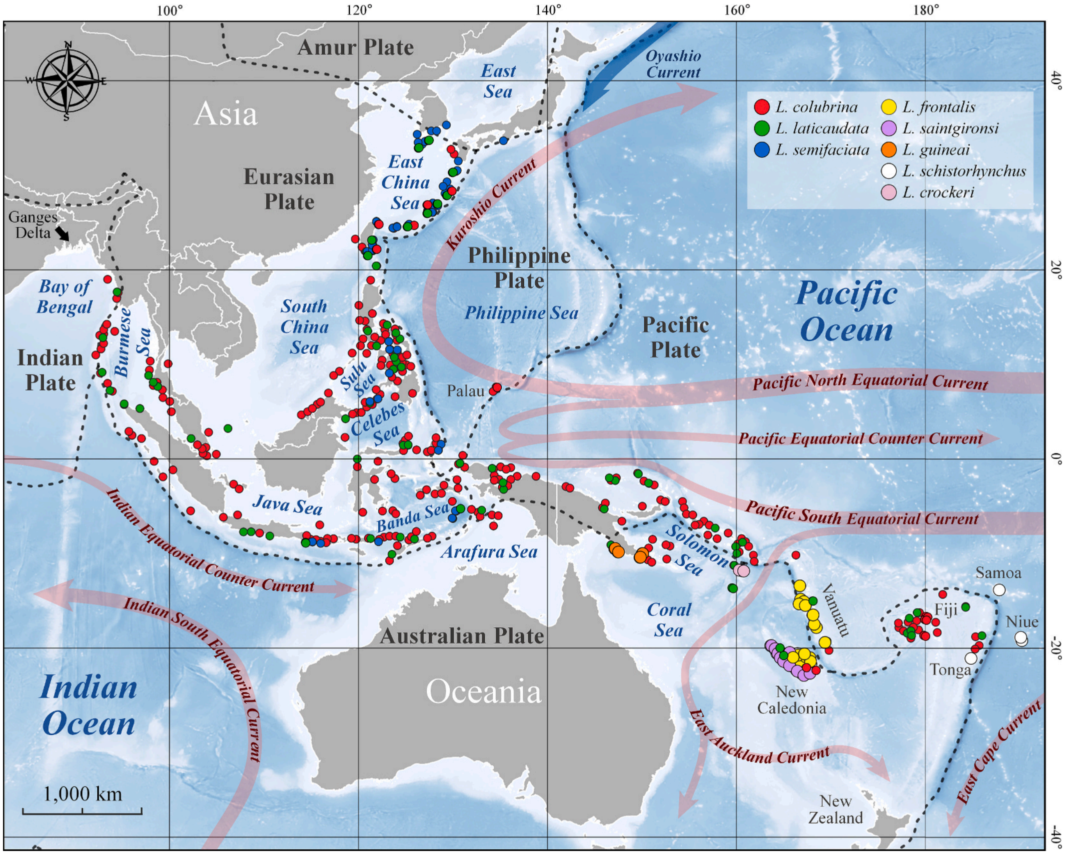


Fig. 1. Global distribution of the eight sea krait species (genus *Laticauda*). The dotted lines indicate the tectonic plate boundaries. Red and blue arrows indicate warm and cold currents, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

threshold-independent metric for measuring the discriminatory capacity of ENMs, with values closer to 1 and 0.5 representing high and poor discriminatory capacities, respectively (Fielding and Bell, 1997). The TSS is a threshold-dependent metric with a range between −1 and 1, where values close to 1, 0, and − 1 indicate good predictive performance, performance no better than that of random prediction, and performance worse than random prediction, respectively (Allouche et al., 2006; Guisan et al., 2017). Unlike AUC and TSS, CBI does not rely on absence data and ranges from −1 to 1. Positive value indicates good model performance, values near zero mean performance no better than random predictions, and negative values suggest incorrect predictions (Hirzel et al., 2006). While we used the TSS to select a subset of models from the total set of fitted single models for the ensemble step, following the standard *biomod2* workflow, we also calculated the AUC and CBI to ensure that each of these selected models consisted of high scores across various metrics. Additionally, we assessed the importance of each variable using percent contribution. For the quantitative assessment of habitable areas for sea kraits, we also converted the continuous model prediction outputs into binary maps using the 10th percentile of training presence threshold, which conservatively presents the species distribution based on presence data (Jiménez-Valverde and Lobo, 2007). The pixels with predicted suitability values above and below the threshold were treated as habitable and unhabitable, respectively.

2.5. Future projection based on oceanic change

To predict the habitable areas of sea kraits under future climate change, we used the current sea surface and air temperature data and averages for each future decade from the 2020s to the 2090s (e.g., 2020s = average between 2021 and 2030; 2090s = average between 2091 and 2100). Future climate prediction was based on the Coupled Model Intercomparison Project Phase 6 under the Shared Socioeconomic Pathway (SSP) scenarios. According to the 6th IPCC Assessment Report (Parmesan et al., 2022), the SSP2–4.5 and 5–8.5 forecast intermediate and high emissions scenarios and climate warming, respectively (O'Neill et al., 2014). All future variables, built by ensembling numerous Earth System models provided by the Coupled Model Intercomparison Project Phase 6, were downloaded from Bio-ORACLE (https://www.bio-oracle.org/index.php; Assis et al., 2024) [Accessed on January 10th, 2025]. When projecting the models to future conditions, we only changed the values of $\mathrm{SST_{max}}$, $\mathrm{SST_{range}}$, and SSS according to SSP scenarios, and kept the geographic variables (depth, slope, DTS, and DTP) constant. We thus generated eight future ENMs four sea krait groups (three individual species ENMs and FLC). We calculated the change in habitable areas in future predictions using the percentage of the total habitable area, percentage of stable habitats, percentage of range expansion (gain), and percentage of range contraction compared to that of the present. We mainly discuss the results for SSP5–8.5 in the 2090s, where the most severe climate changes were predicted. We also used the multivariate environmental similarity surfaces (MESS) to assess the extrapolation risk of future model projections (Elith et al., 2010; Park et al., 2024). We presented only the MESS results for SSP5–8.5 in the 2090s as the main results.

We managed and analyzed the spatial data and created maps using QGIS v.3.34 (QGIS.org, 2024; https://qgis.org/). Statistical analyses were conducted in R v.4.2.2 (R Foundation for Statistical Computing, Vienna, Austria; R Core Team, 2021) and data were visualized using the *ggplot2* package (Wickham, 2016). We provide the details of modeling procedures as an ODMAP protocol (Supplementary Material 2; Zurell et al., 2020). The full ENM workflow and R codes can be found in a dedicated GitHub repository (https://github.com/yucheols/seasnakenm/tree/main/codes).

3. Results

3.1. Distribution pattern and habitat environments

The distribution of sea kraits ranged from 22.8466°S to 35.3155°N and from 92.2083°E to 169.8251°W (Fig. 1). Sea kraits were found at an average distance of 265.2 ± 231.7 km (ranging from 0 to 1474.4 km) from TPBs. Most sea krait occurrence points (95.0%) were within 700 km of TPBs (Fig. 2). The 22 remaining occurrences (5.0%) were more than 700 km away from the TPBs and were recorded near the Sulu and Celebes Seas. The mean SST and AIT across all sea krait occurrences were 28.0 ± 2.1 °C and 26.0 ± 2.4 °C, respectively. Under the SSP 2–4.5 scenario, temperatures in the habitats of sea kraits were predicted to increase by, on average, 1.4 °C (SST) and 1.5 °C (AIT) by the 2090s. Under the SSP 5–8.5 scenario, the average predicted temperature increase was 3.0 °C and 3.3 °C for SST and AIT, respectively (Fig. A.1). See Supplementary material 1 for additional information on other environmental variables at occurrence locations.

3.2. Differences in environmental variables between sea krait groups

The interspecific differences in variables were significant for DTP ($F = 6.815$, $P < 0.001$), $\mathrm{SST_{max}}$ ($F = 61.562$, $P < 0.001$), $\mathrm{SST_{range}}$ ($F = 54.503$, $P < 0.001$), and SSS ($F = 28.571$, $P < 0.001$), while depth, slope, and DTS were not significantly different among the four groups ($Ps > 0.05$). In the post-hoc test results, *L. colubrina* was mainly distributed in areas with the highest $\mathrm{SST_{max}}$ and smallest $\mathrm{SST_{range}}$, *L. semifasciata* was distributed in areas with the highest $\mathrm{SST_{range}}$, and FLC was distributed in areas with the lowest $\mathrm{SST_{max}}$ and the highest SSS (Fig. 3). *Laticauda laticaudata* generally had a similar range of habitat requirements to those of other species.

The first three PCs explained 71.2% of the total variance in environmental data (Table 1). PC1 had high loadings of the absolute value in oceanic variables such as $\mathrm{SST_{max}}$ and SSS, and PC2 showed high loadings of depth, slope, and DTS. Lastly, PC3 had a high loading of $\mathrm{SST_{range}}$. The principal variables for each species were $\mathrm{SST_{max}}$, DTS, and DTP for *L. colubrina*, $\mathrm{SST_{range}}$ for *L. semifasciata*, and SSS for FLC. *Laticauda laticaudata* showed even distributions of all seven variables. In the PCA score plot, 50% ellipsoids had overlapping areas among all four sea krait groups, except between *L. colubrina* and FLC (Fig. 4).

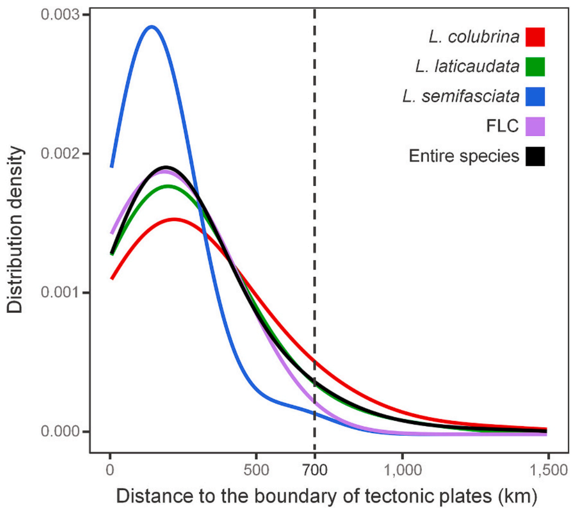


Fig. 2. Distance from the location of sea kraits (*Laticauda* spp.) to the tectonic plate boundary and the distribution density based on the distance to the boundary. The dotted line indicates 700 km, in which 95% of sea kraits were distributed.

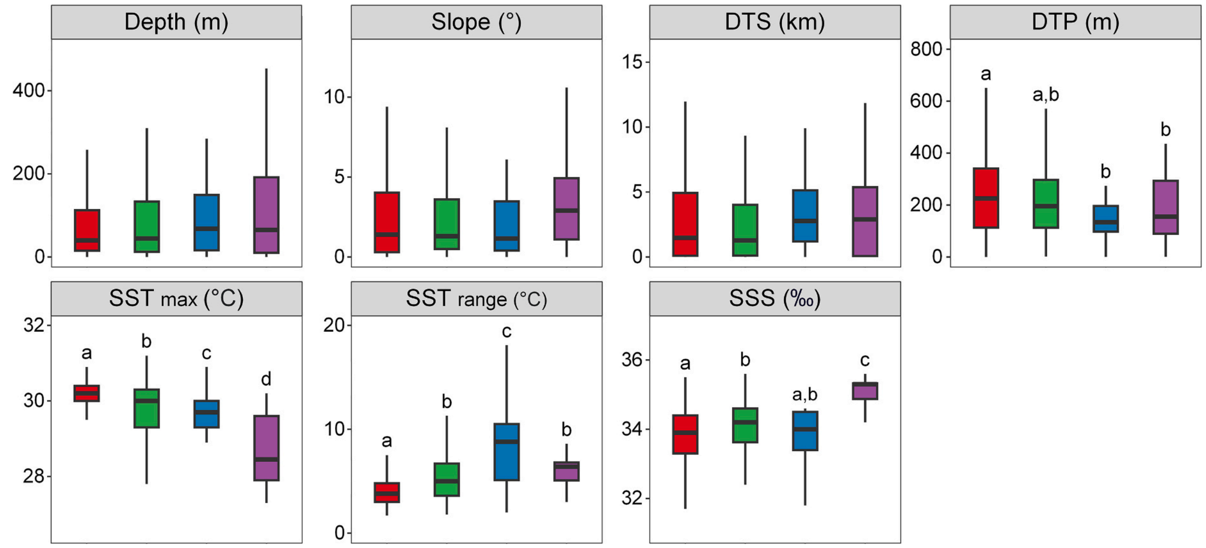


Fig. 3. Interspecific differences in seven environmental variables of *L. colubrina* (red), *L. laticaudata* (green), *L. semifasciata* (blue), and the five-*Laticauda* complex (purple). In the ANOVA test, DTP, SST_{max}, SST_{range}, and SSS showed significant differences among the four groups ($Ps < 0.05$). Bars marked with distinct letters differ significantly ($p < 0.05$, Bonferroni test). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Results of principal component analysis for sea krait location data based on seven environmental variables. The three principal components (PCs) with eigenvalues greater than one were extracted.

Variable	PC1	PC2	PC3
Depth	−0.221	−0.789	−0.250
Slope	0.345	0.621	−0.335
DTS	0.044	0.630	0.606
DTP	−0.663	−0.044	0.249
SST_{max}	−0.807	0.322	−0.222
SST_{range}	0.586	−0.461	0.530
SSS	0.748	0.113	−0.390
Eigenvalue	2.165	1.737	1.086
Explained	30.9%	24.8%	15.5%

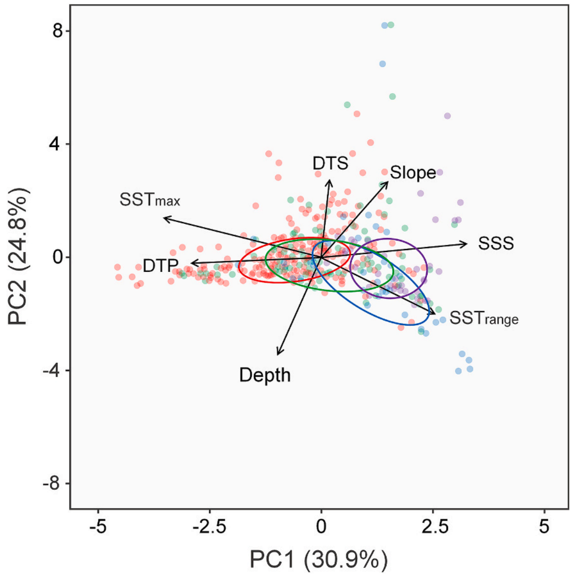


Fig. 4. Principal component analysis based on seven variables for *L. colubrina* (red), *L. laticaudata* (green), *L. semifasciata* (blue), and five *Laticauda*-complex (purple). The ellipsoids represent 50% confidence levels. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.3. Modeling performance and projection

The evaluation metrics of ENMs for *L. colubrina* (AUC = 0.992, TSS = 0.921, and CBI = 0.851), *L. laticaudata* (AUC = 0.986, TSS = 0.823, and CBI = 0.802), *L. semifasciata* (AUC = 0.988, TSS = 0.655, and CBI = 0.659), and FLC (AUC = 0.989, TSS = 0.829, CBI = 0.642) all indicated good model predictive abilities. For *L. colubrina*, *L. laticaudata*, and *L. semifasciata,* DTS had the highest contribution to the models, followed by depth and SST_{max}. On the other hand, in FLC, DTS had the highest variable contribution, followed by SSS and DTP (Table 2). The current habitable areas were 1,740,041 km^2 for *L. colubrina,* 1,814,002 km^2 for *L. laticaudata*, 793,579 km^2 for *L. semifasciata*, and 121,272 km^2 for FLC (Figs. 5 and 6). The largest habitable area for *L. colubrina* and *L. laticaudata* was predicted to be near the equator. The main habitable areas for *L. semifasciata* were distributed near −10°N or 35°N. Lastly, FLC showed the main habitable area between −25°N and − 10°N.

The evaluation metrics of the models built without the DTP for *L. colubrina* (AUC = 0.991, TSS = 0.913, and CBI = 0.847), *L. laticaudata* (AUC = 0.987, TSS = 0.828, and CBI = 0.827), *L. semifasciata* (AUC = 0.986, TSS = 0.636, and CBI = 0.652), and FLC (AUC = 0.993, TSS = 0.835, CBI = 0.651) also indicated good model predictive abilities, and indicated no significant difference from the main results. Nevertheless, the models without the DTP variable resulted in additional predicted habitable areas where sea kraits are not currently distributed, including Indochina for *L. colubrina*; Indochina and northern Australia for *L. laticaudata*; southern China, Indochina, and northern Australia for *L. semifasciata*; and eastern Australia for the rest of the FLC (Fig. 7). This implies that DTP is likely a principal variable in predicting sea krait distribution.

Table 2
Contribution importance of the seven variables to ecological niche models for the four sea krait groups. FLC = five-*Laticauda* species.

Variable	*L. colubrina*	*L. laticaudata*	*L. semifasciata*	FLC
Depth	25.1%	19.6%	25.4%	2.8%
Slope	5.3%	0.8%	0.8%	0.2%
DTS	46.7%	56.3%	39.9%	55.3%
DTP	4.3%	10.0%	18.6%	11.3%
SST max	14.9%	12.1%	12.5%	5.0%
SST range	2.1%	0.2%	2.3%	0.7%
SSS	1.6%	1.1%	0.5%	24.7%

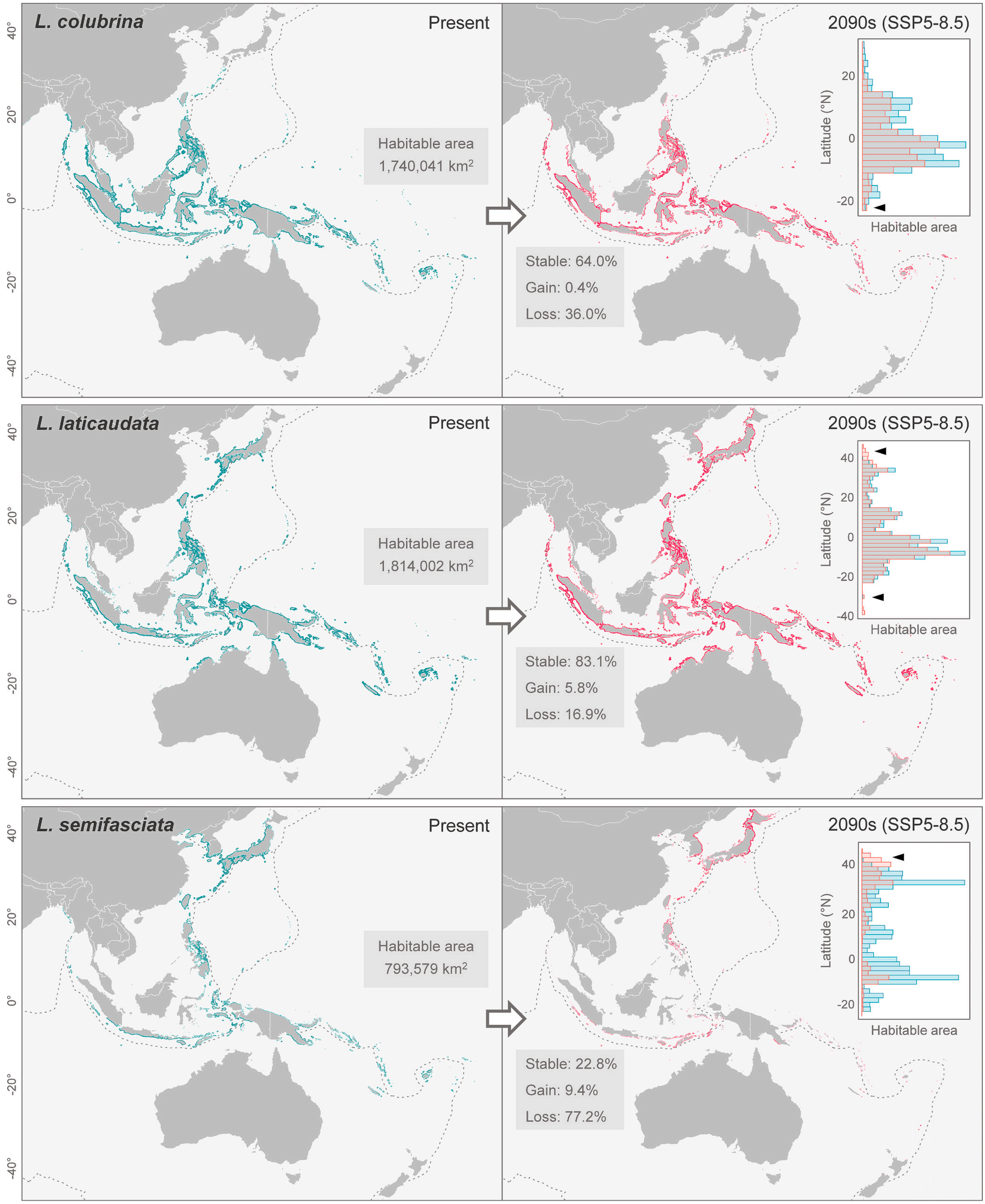


Fig. 5. Prediction of habitable area changes for three sea krait species under SSP5–8.5. The green (present) and red (2090s) zones indicate suitable habitats for each species, and the dotted lines represent the tectonic plate boundaries. The inserted histograms show the distribution of habitable areas along latitudes for the present (green) and 2090s (red). Black triangles in the inserted histograms indicate latitudes where habitable areas will increase in the future. Compared with those of the current habitable areas, three types of future habitable areas were identified: remaining areas in the future (stable), newly expanded areas (gain), and decreased areas (loss). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

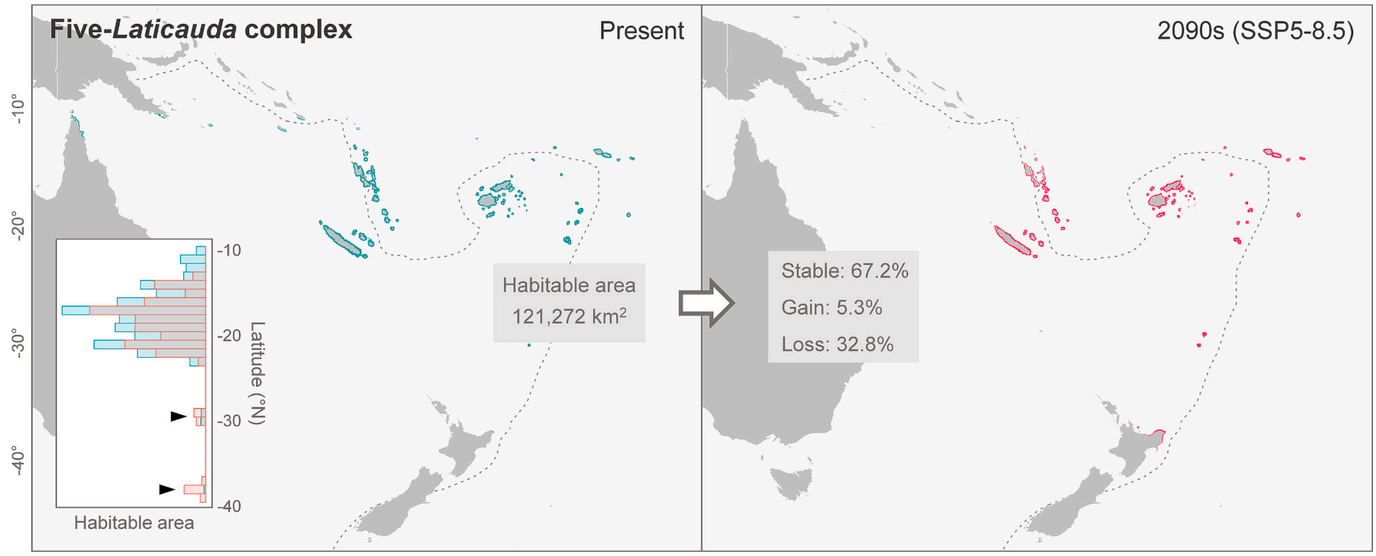


Fig. 6. Prediction of habitable area changes for the five-*Laticauda* complex under SSP5–8.5. The five-*Laticauda* complex includes *L. frontalis*, *L. saintgironsi*, *L. guineai*, *L. schistorhynchus*, and *L. crockeri*. The green (present) and red (2090s) zones and dotted lines indicate suitable habitats for sea kraits and the tectonic plate boundaries, respectively. The inserted histogram shows the distribution of habitable areas by latitude for the present (green) and 2090s (red). Black triangles in the inserted histogram indicate latitudes where habitable areas will increase in the future. Compared with those of the current habitable areas, three types of future habitable areas were identified: remaining areas in the future (stable), newly expanded areas (gain), and decreased areas (loss). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.4. Prediction of change in future habitable areas

Under SSP2–4.5, the habitable areas were predicted to decrease by 48.3% for *L. colubrina*, 25.9% for *L. laticaudata*, 51.2% for *L. semifasciata*, and 31.5% for FLC by the 2090s (Figs. A.2 and A.3). According to SSP5–8.5, habitable areas were predicted to decrease by approximately 35.7% for *L. colubrina*, by 11.1% for *L. laticaudata*, by 67.9% for *L. semifasciata,* and by 27.5% for FLC by the 2090s (Figs. 5 and 6). The four sea krait groups were predicted to decline primarily from the equator to ±20°N. The expansion of habitable areas for *L. colubrina* was not predicted, except for the 0.4% expansion in the south of −20°N. Habitable areas for *L. laticaudata* were predicted to expand by ~5.8% north of 40°N near the Korean Peninsula and Japan, and south of −20°N near New Zealand. The new habitable areas for *L. semifasciata* were predicted to increase by 9.4% north of 40°N along the coasts of the Korean Peninsula and Japan. The habitable area of FLC was predicted to decrease at its existing main areas between −10°N and − 23°N, while increasing in the area south of −30°N near New Zealand. The MESS results showed a high extrapolation risk near the equator (between −20°N and 30°N), which decreased toward both poles (Fig. A.4).

4. Discussion

4.1. Distribution pattern and tectonic plate boundaries

Tectonic plate boundaries reasonably explain the global distribution patterns of sea krait species in the Indo-Pacific region. Most sea kraits were distributed along the boundaries of the Eurasian, Philippine, Indian, Australian, and Pacific Plates, and climatically restricted by the cold sea and air temperatures in the south and north. To date, the best explanation for sea krait distribution has been the coral reefs spanning Southeast Asia and Melanesia, called the Coral Triangle (Heatwole et al., 2005, 2017; Heatwole and Cogger, 2013). However, the absence of sea kraits near the coasts of northern Australia and Indochina remains unexplained despite the abundant coral reefs providing major habitats and high suitability, as suggested in earlier studies (Gherghel et al., 2016, 2018, 2019). For example, considering that sea kraits were estimated to have originated in Melanesia about 30 million years ago (Crowe-Riddell et al., 2024; Heatwole et al., 2017), they may have had sufficient time to expand to the northern coast of Australia, including the Great Reef Barrier, which is the richest coral reef globally. However, no sea kraits inhabit this area. This indicates that other environmental factors also play major roles in the habitat requirements of sea kraits, although coral reefs remain a key factor. By including DTP as an environmental variable, our model complemented the observed global distribution of sea kraits along TPBs and improved explanations of their habitat patterns.

Although our study cannot provide a clear explanation for sea krait distribution near TPBs, diverse submarine structures formed by plate collisions may have generated habitats suitable for sea kraits. Hence, we suggested some possible causes. First, the diverse submarine topography created by plate collisions has led to the abundant coral reefs with high biodiversity, hosting 32 of 34 recognized phyla and approximately one-third of all marine organisms (Sobha et al., 2023; Zaffos et al., 2017), which serve as rich foraging grounds for sea kraits (Keith et al., 2013; Leprieur et al., 2016). Additionally, small islands formed by tectonic activity offer terrestrial habitats with few predators (Heatwole et al., 2017). Second, the volcanic environments at TPBs may provide suitable terrestrial habitats for sea kraits. More specifically, various volcanic landforms like tidal caves and volcanic rocks provide safe nesting and basking sites for sea kraits (Bonnet et al., 2014; Guinea, 1986; Mišur et al., 2021; Sauro et al., 2019; Tu et al., 1990). These requirements may clarify the occurrence of sea kraits in the Sulu and Celebes Seas, relatively distant from the TPBs. As the four major plates (the Eurasian, Philippine, Pacific, and Australian Plates) converge, geologically and topographically diverse seabed basin structures were formed and affected the western part of the Sulu and Celebes Seas, approximately 1000 km away from TPBs (Krause, 1966; Mascle and Biscarrat, 1978), resulting in abundant coral reefs and volcanic terrain (DeVantier et al., 2004; Grossmann et al., 2015; Matsuura et al., 2010). Contrastingly, sea kraits are absent in regions with abundant coral reefs but are distant from TPBs, such as the coasts of northern Australia, southern China, and eastern Indochina. A detailed comparison of the habitat characteristics of sea krait habitats near TPBs and the three regions where sea kraits are absent may help to elucidate the habitat requirements of sea kraits.

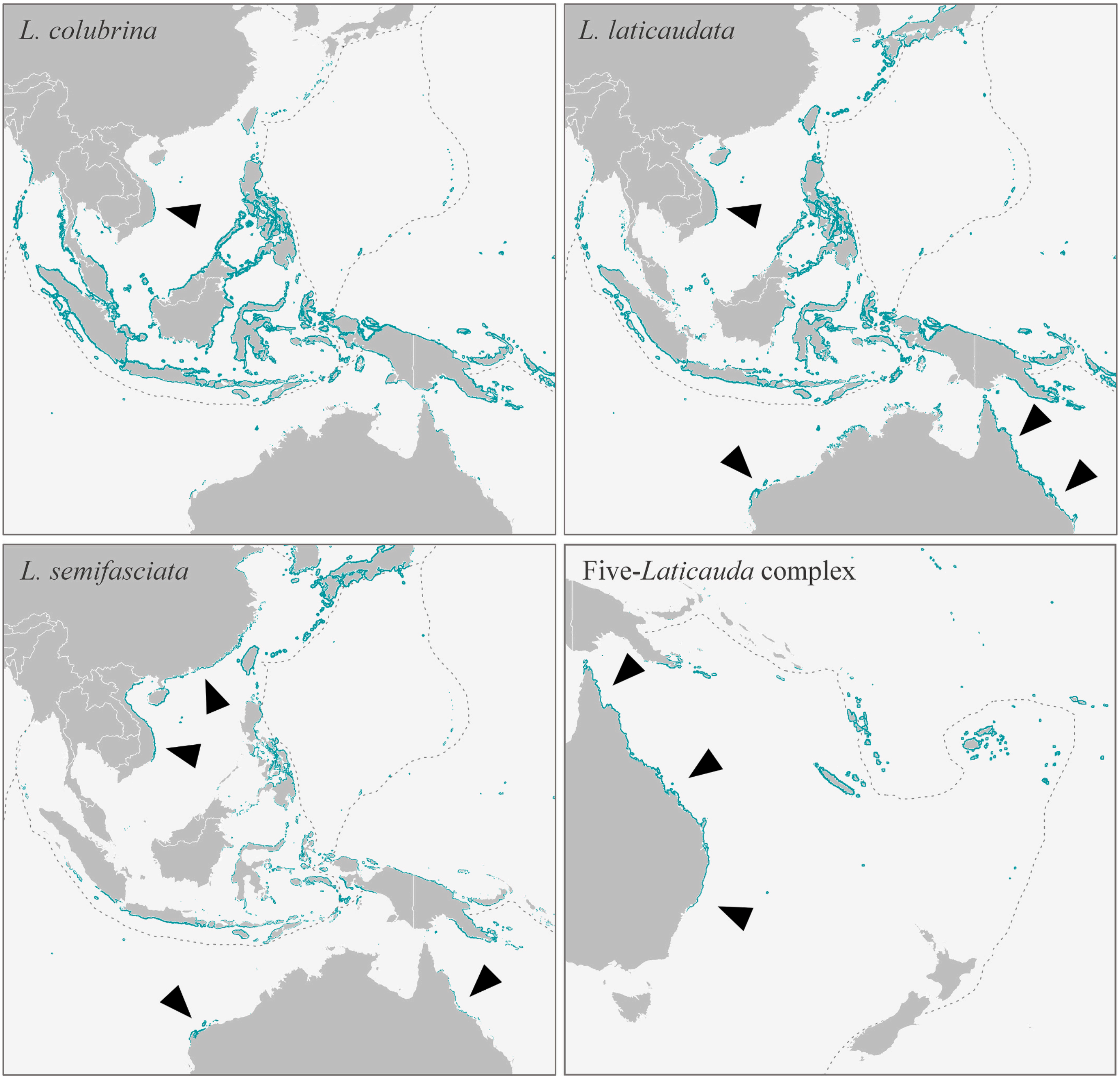


Fig. 7. Ecological niche model results excluding the distance to the tectonic plate boundaries (DTP) as a variable. Green areas represent the habitable areas for each sea krait species. Black triangles indicate additional predicted habitable areas for sea kraits off the coasts of China, Indochina, and Australia, where sea krait occurrences were not confirmed, unlike the modeling results built with DTP. The five-*Laticauda* complex includes *L. frontalis*, *L. saintgironsi*, *L. guineai*, *L. schistorhynchus*, and *L. crockeri*. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4.2. Interspecific differences in habitat use

Sea kraits exhibited distinct latitudinal distribution patterns among species, primarily distinguished by oceanic variables rather than topological and geographical variables. All sea kraits are amphibious and must breathe at the sea surface, which limits their use of the depths (Gherghel et al., 2016; Heatwole et al., 2016), and use land to obtain fresh water because they have limited enough water intake from seawater (Brischoux et al., 2012, 2013). Additionally, sea kraits typically forage in the ocean within 40 km of their terrestrial habitats (Brischoux et al., 2007) and primarily dive in depths of less than 50 m (Cook et al., 2015; Somaweera et al., 2023). Therefore, while subtle differences in habitat requirements exist between species (Gherghel et al., 2016; Heatwole et al., 2016), their topological and geographical requirements may be similar at the macroenvironmental scale. Instead, interspecific differences in habitat use were particularly evident in SST. *Laticauda colubrina* occupied habitats with the highest SST_{max}, followed by *L. laticaudata*, *L. semifasciata*, and FLC, suggesting a gradient of thermal preference among species. Conversely, *L. semifasciata* and *L. colubrina* were distributed in regions with the greatest and the least SSTrange areas, respectively. These distinctions could be closely related to the climatic adaptability among species. First, *L. colubrina* had the highest population densities within ±20°N of the equator. This species appears to be most adapted to warm and stable equatorial climates, but less well adapted to colder and more variable climates further toward the poles. Second, *L. laticaudata*, which has intermediate values in

SSTmax, SSTrange, SSS, and DTP among the sea krait species, has a lower population density than *L. colubrina*. However, it has likely reached a broader distribution by adapting to diverse environmental conditions (Heatwole et al., 2016). Compared to that of *L. colubrina* and *L. laticauda*, *L. semifasciata* has a relatively narrow distribution range, although it appears to have adapted to harsher environments. This species is even found near the Korean Peninsula, the northern limit of all sea krait species (Park et al., 2017a). FLC were distributed in regions with the lowest SST_{max} and highest SSS in our results, but several limitations exist to suggest that they adapted only to this specific climate. The distribution of FLC was restricted to small island groups in the Melanesian region between −10°N and − 20°N (Gherghel et al., 2016, 2018; Heatwole et al., 2017). Considering that all sea krait species diverged about five million years ago (Heatwole et al., 2017; Lane and Shine, 2011), the FLC species appear to have adapted specifically to these particular island environments, rather than a lack of time for dispersal. For example, *L. guineai* appears to be able to spread along the coast, although it was found only near the southern coast of New Guinea Island (Heatwole et al., 2005). Additionally, *L. crockeri* is known to occur only in brackish Lake Tegano on Rennell Island (Cogger et al., 1987). Thus, the limited distribution of FLC may be due to their specific habitat requirements rather than simply adaptation to a narrow climate.

4.3. Climatic threats and dispersal potential

According to the modeling results, the core equatorial habitats of all sea kraits were predicted to decrease significantly under climate change. These habitats are the hottest regions on Earth with high marine biodiversity and are predicted to be most severely affected by climate change (Mellin et al., 2024; Ramírez et al., 2017). The recent steep rise in water and air temperatures in this region could threaten sea krait populations by exceeding their capacity to adapt to high temperatures (Cael et al., 2024; Smale et al., 2019). One of the most serious threats due to rising sea temperatures is the destruction of coral reefs (Heatwole et al., 2017). Following rising sea temperatures, a global decline in coral reefs was observed, with damage expected to be the greatest near the equator (Anderson et al., 2022; Bonnet et al., 2014; Mellin et al., 2024). The decline in coral reefs and connected ecosystems will lead to the destruction of sea krait habitats, which rely on coral reefs as their primary foraging grounds (Brischoux et al., 2007; Heatwole et al., 2017). Additionally, rising sea temperatures increase the oxygen consumption of sea kraits, reducing their diving time for hunting (Dabruzzi et al., 2012) and accelerating the spread of marine parasites and diseases (Karvonen et al., 2010).

Considering the specific habitat requirements of sea kraits, potential climatic refugia are restricted to three regions: Korea and Japan in the north, India in the west, and New Zealand in the south. Our model results suggest that the northern and southern regions are potential refugia. However, these regions appear to have some limitations in terms of successful establishment. First, the northern region may be suitable for the dispersal and establishment of sea kraits, although the area is likely to be small. *L. colubrina* was observed to extend to Kyushu, Japan (32°N), and *L. laticaudata* and *L. semifasciata* to southern Korea (35°N) (Gherghel et al., 2016; Park et al., 2017a, 2017b). Given the proximity of the coasts of the Korean Peninsula and Japan to TPBs, combined with the recent rise in sea temperatures and increased coral populations in the area (Nakabayashi et al., 2019; Vieira et al., 2015), the three aforementioned sea krait species may establish themselves in this region. However, unlike the current habitats surrounded by warm currents, the northern seas of Korea and Japan comprise low sea temperatures due to the influence of the cold Oyashio Current originating from the North Pacific. The sea temperature difference between the north and south of the northern coast of Japan (∼38°N), where the Oyashio and Kuroshio Currents meet, is greater than 10 °C (Isoguchi and Kawamura, 2006; Nishikawa et al., 2020), and steep temperature differences could restrict further northward dispersal of sea kraits. Despite the small establishment area predicted, the northern region could be the most reasonable refugium among the three suggested regions, depending on our model results, recent dispersal observations, and population connectivity with existing habitats.

Second, the southern region may be difficult to reach despite its suitability as a refugium. The only potential refugium for sea kraits in the south is New Zealand, located near the boundary of the Australian and Pacific Plates. However, New Zealand also has some limitations for the dispersal and establishment of sea kraits. The northernmost part of New Zealand (−34°N) is ∼1400 km away from Tonga and New Caledonia (−22°N), located on the southernmost distribution of sea kraits, and has a mean SST that is colder by 6 °C (Assis et al., 2024; Wijffels et al., 2018). Additionally, the southern route to New Zealand differs from the northern route, where many islands, including Taiwan and the Ryukyu Islands, are connected by a continuous chain of islands shorter than 200 km, providing a stepping-stone path for sea kraits. The long distance from their current distribution to New Zealand, without any land area in between, is likely too far for successful dispersal, even if sea kraits ride the East Cape Current. Furthermore, this abrupt transition to a cold southern habitat could prevent their adaptation. Particularly, these obstacles may limit the response of FLC to climate change. Because these species are distributed only in Melanesia between −22°N and − 9°N, rapid climate change could result in catastrophic population declines.

Finally, the western region may not satisfy the habitat requirements for sea kraits, except for climatic conditions. To date, sea kraits have not spread westward to the Bay of Bengal, despite a stable climate and the presence of *L. colubrina* and *L. laticaudata* along the adjacent central coast of Myanmar (Heatwole et al., 2016; Tyabji et al., 2018). The first limitation is likely the absence of TPBs and terrestrial habitats. The boundary between the Indian and Eurasian Plates in the ocean and the coral reefs ends off the coast of Myanmar. Furthermore, no terrestrial habitats are available for sea kraits near the boundary between the Indian and Australian Plates. Therefore, the absence of environments provided by TPBs and terrestrial habitats could restrict the dispersal of sea kraits to the west. The second limitation is that, in the estuary north of the Bay of Bengal, the Ganges Delta, the largest delta globally, discharges a large amount of freshwater and silt into the Bay of Bengal, where mangroves develop (Islam and Gnauck, 2008). Consequently, this region provides environments distinct from those of the known sea krait habitats (Heatwole et al., 2017). Therefore, these environmental limitations in the Bay of Bengal may act as geographic barriers to the westward dispersal of sea kraits.

One significant limitation of our prediction models is that they primarily concentrate on SST. We note that topographic and biological factors not accounted for in our study, such as sea level rise and prey availability, may also lead to a decline in sea krait populations. First, a decline in coastal areas due to sea level rise could devastate the sea krait habitats, as sea kraits rely on coastal areas for basking, freshwater intake, and oviposition (Gherghel et al., 2016; Heatwole et al., 2016). As a relevant example for other marine reptiles, Fuentes et al. (2010) predicted that up to 38% of Australia's largest sea turtle nesting grounds will be inundated due to sea level rise by 2100. Second, destruction of food webs in sea krait habitats may also further contribute to habitat loss. Asch et al. (2018) predicted that local extinction rates of marine fish and invertebrates in tropical coastal areas of the western Pacific would exceed 50% by 2100 due to changes in sea temperature, pH, and dissolved oxygen. This biodiversity loss will severely reduce the prey availability for sea kraits distributed in this area. Therefore, climate change could cause more severe and/or rapid declines of sea krait populations due to factors we could not account for in our predictions and complex interactions between environmental variables.

5. Conclusion

The global distribution pattern of sea kraits is better understood when the topographic characteristics of TPBs are included than when relying solely on climatic and oceanic conditions. This case is an illustrative example of the various climatic, geographic, and topographic factors jointly influencing the habitats and global distributions of marine organisms. Based on these findings, climatic and geographic barriers could limit the practical dispersal and establishment of sea kraits in potential habitats. Climatic threats expand from the equator, forcing the range shift of sea kraits poleward. However, the area of TPBs providing suitable habitats is the widest near the equator (between −10°N and 10°N) and decreases toward the poles. For instance, the TPB areas near Japan and New Zealand are narrower than those at the equatorial habitats, even if sea kraits successfully become established there. Thus, only small areas toward both poles along TPBs may support potential sea krait establishment, whereas large existing habitat areas near the equator would shrink due to climate change. The current distribution range of sea kraits may have already nearly reached the maximum extent suitable for them. Therefore, major habitat disturbances caused by climate change and restricted potential refugia could have catastrophic consequences for all sea krait species. Moreover, considering the ecological role of sea kraits as predators in coral reef areas at high trophic levels, the decline of sea kraits could have widespread negative consequences for the ecosystems of those habitats. These findings suggest that habitat disruption caused by climate change may have a more serious impact on marine biodiversity than previously anticipated, especially for species that have adapted to specific and unique habitats, such as sea kraits.

CRediT authorship contribution statement

Il-Kook Park: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Yucheol Shin:** Writing – review & editing, Writing – original draft, Software, Methodology. **Il-Hun Kim:** Writing – review & editing, Resources, Investigation, Funding acquisition, Data curation. **Daesik Park:** Writing – review & editing, Supervision, Project administration, Conceptualization.

Funding sources

This study was supported by the National Marine Biodiversity Institute of Korea grant (2026E00300) and the National Research Foundation of Korea grant funded by the Ministry of Science and ICT (RS-2026-25472857).

Declaration of competing interest

The authors declare no conflicts of interest.

Acknowledgments

We appreciate Jaejin Park and the Department of Ecology and Conservation of MABIK for their advice and resource support.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoinf.2026.103727.

Appendix B. Appendices

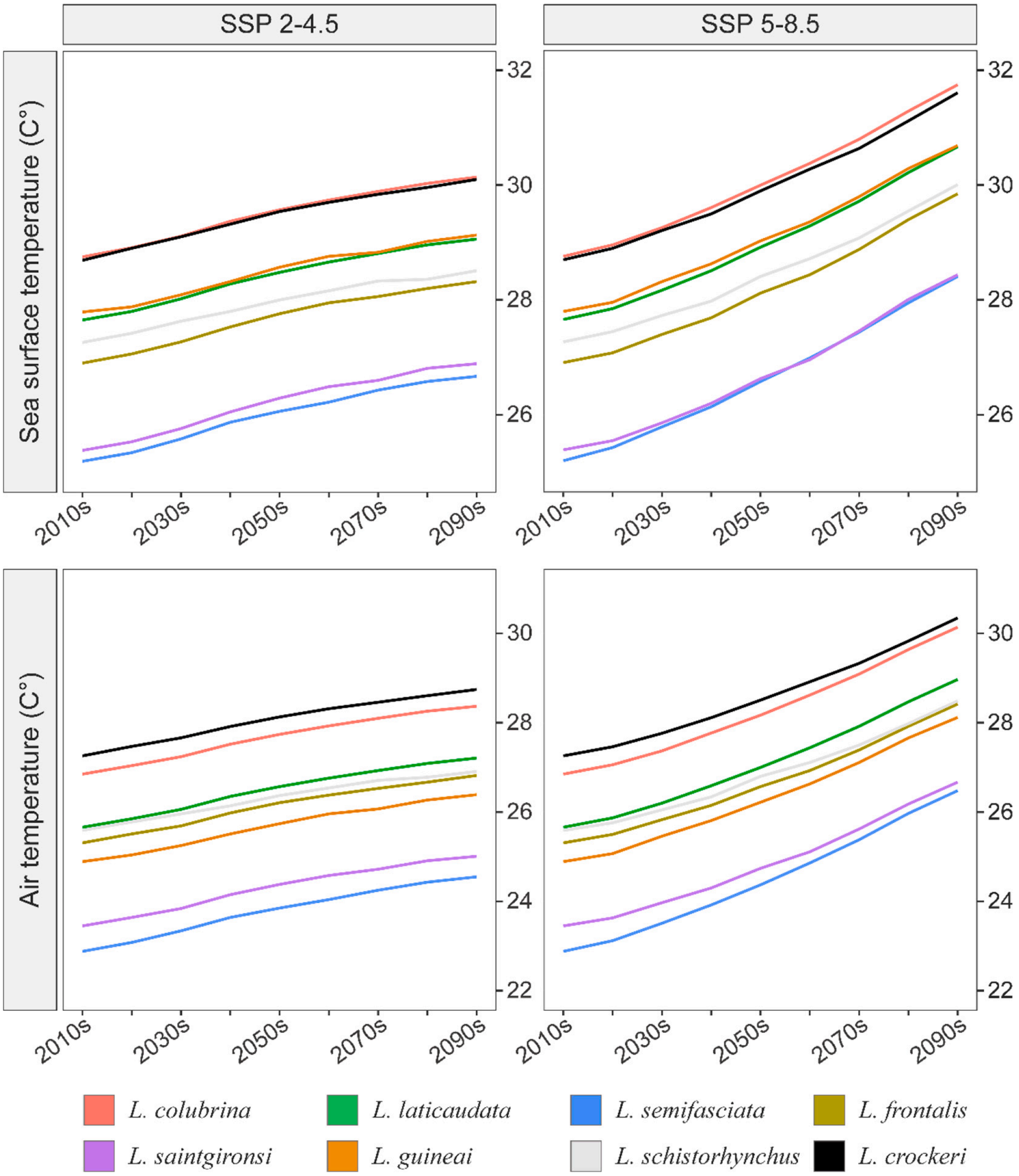


Fig. A.1. Change in sea surface and air temperatures for the location data of sea krait species in two climate change scenarios (SSP2–4.5 and SSP5–8.5). Each line represents the mean temperature in the location data for each sea krait species for each decade from the 2010s (present) to the 2090s.

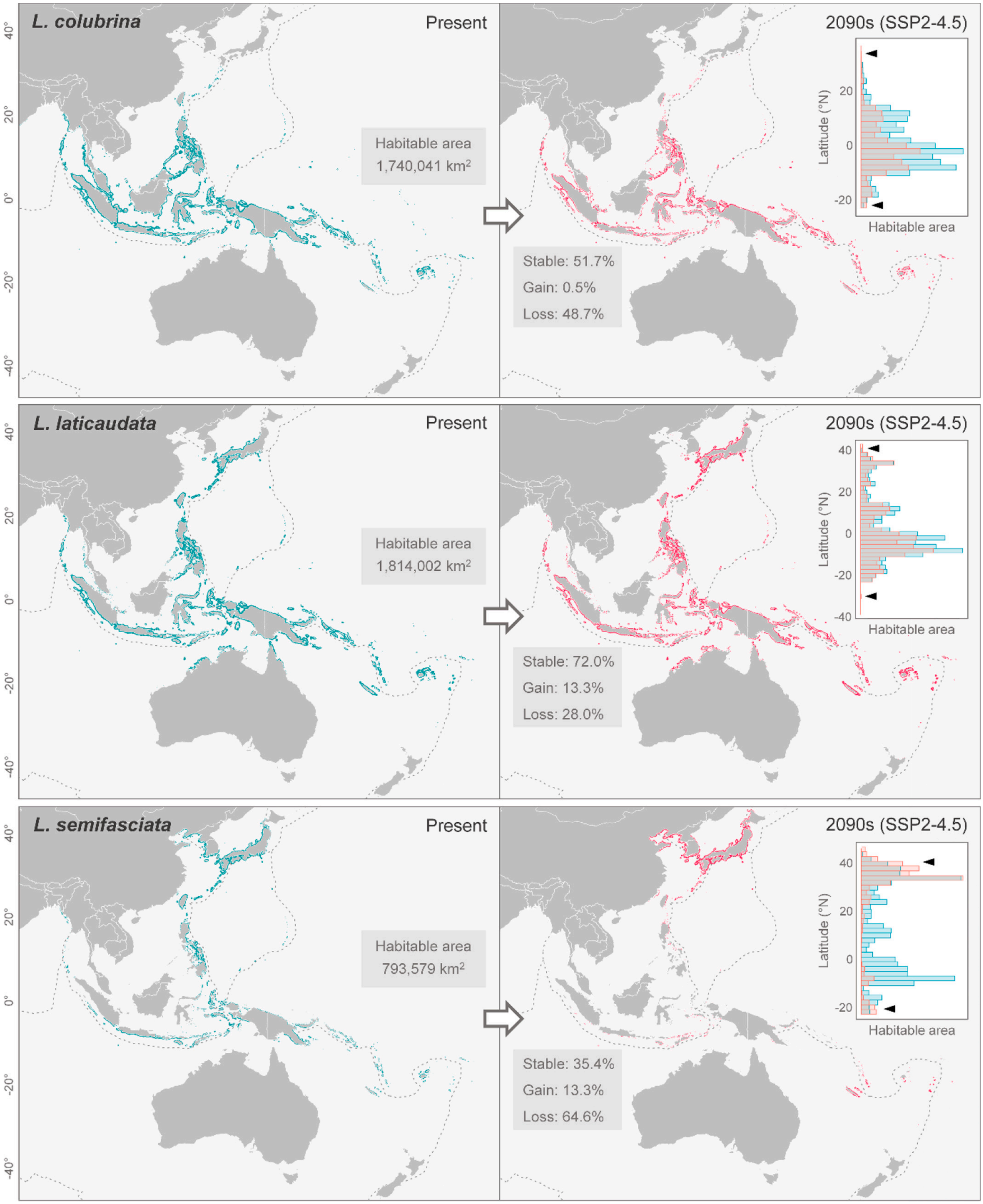


Fig. A.2. Prediction of habitable area changes for three sea krait species under SSP2–4.5. The green (present) and red (2090s) zones indicate suitable habitats for each species, and the dotted lines represent the tectonic plate boundaries. The inserted histograms show the distribution of habitable areas along latitudes for the present (green) and 2090s (red). Black triangles in the inserted histograms indicate latitudes where habitable areas will increase in the future. Compared with those of the current habitable areas, three types of future habitable areas were identified: remaining areas in the future (stable), newly expanded areas (gain), and decreased areas (loss). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

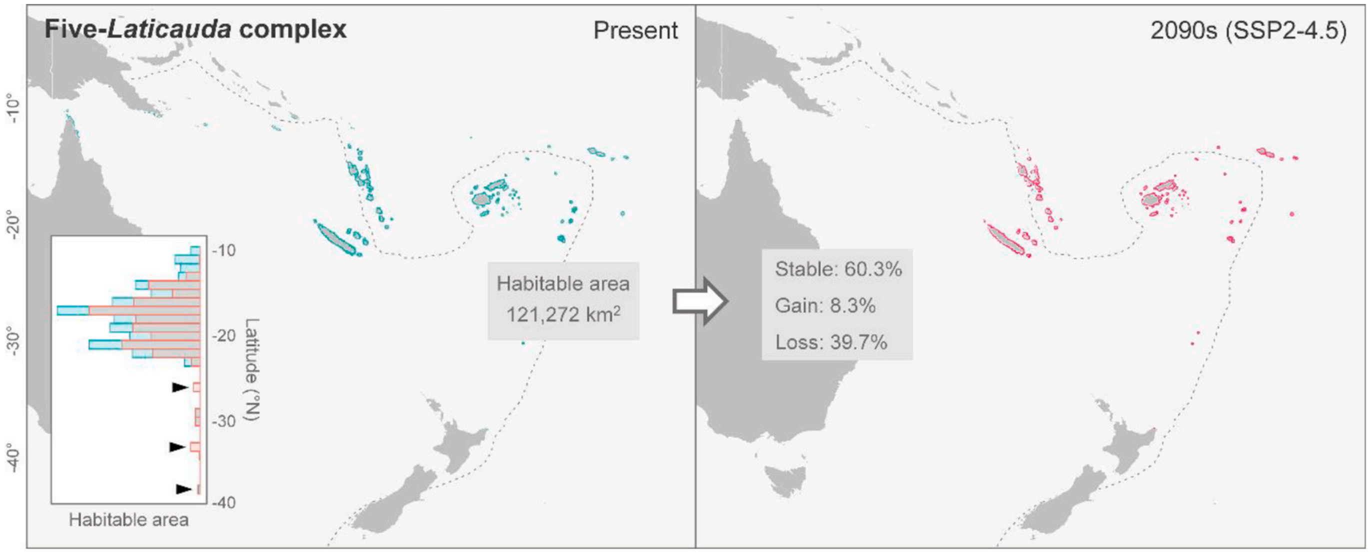


Fig. A.3. Prediction of habitable area changes for the five-*Laticauda* complex under SSP2–4.5. The five-*Laticauda* complex includes *L. frontalis*, *L. saintgironsi*, *L. guineai*, *L. schistorhynchus*, and *L. crockeri*. The green (present) and red (2090s) zones and dotted lines indicate suitable habitats for sea kraits and the tectonic plate boundaries, respectively. The inserted histogram shows the distribution of habitable areas by latitude for the present (green) and 2090s (red). Black triangles in the inserted histogram indicate latitudes where habitable areas will increase in the future. Compared with those of the current habitable areas, three types of future habitable areas were identified: remaining areas in the future (stable), newly expanded areas (gain), and decreased areas (loss). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

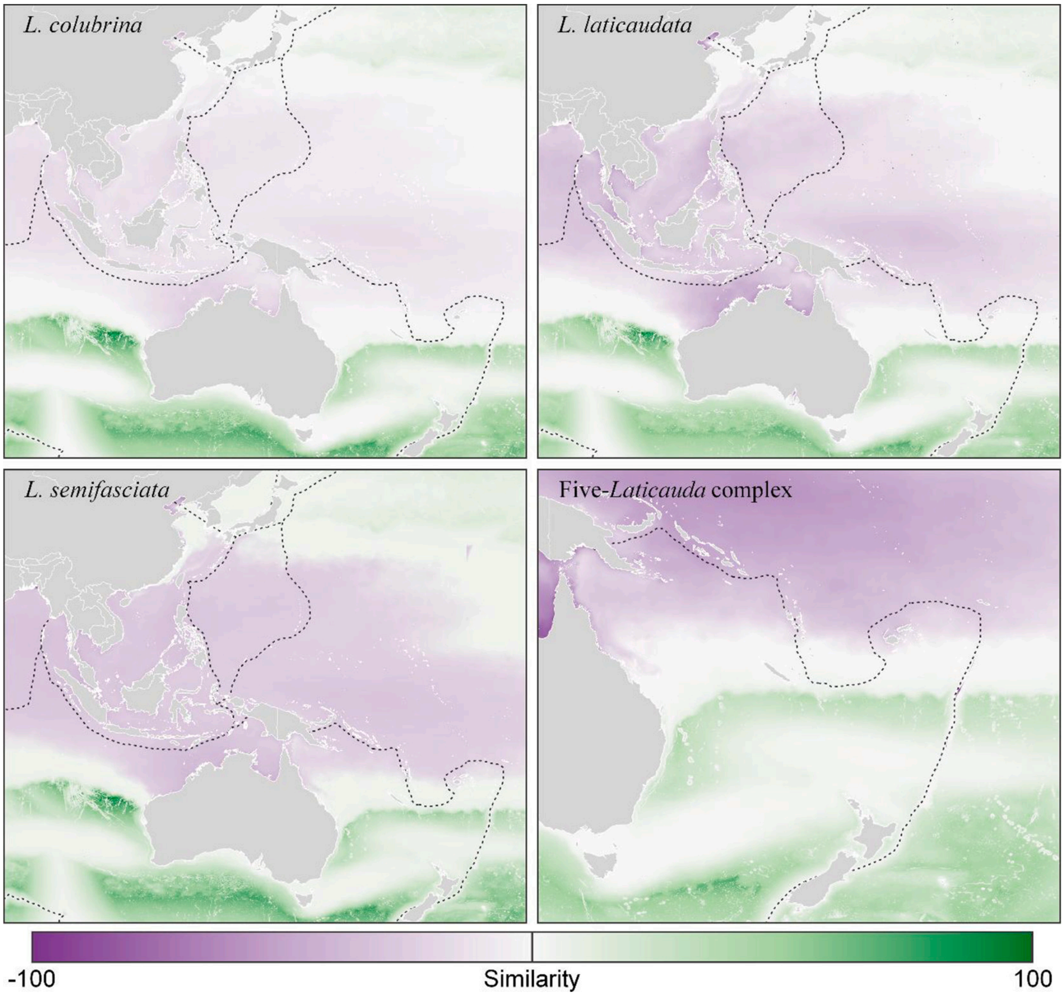


Fig. A.4. Multivariate environmental similarity surfaces (MESS) for the ecological niche model projections of sea kraits. The future projections were conducted for the 2090s under the SSP 5–8.5 scenario. The MESS provides a value ranging from −100 to 100, where negative values represent regions with novel variable values, and larger absolute negative values (purple) represent a greater difference from the present. Zero value (white) represents variable conditions on the verge of falling outside the current range. The positive value (green) represents the similarity between variables from other periods and present variables, and a positive value close to 100 is closer to the present. The five-*Laticauda* complex includes *L. frontalis*, *L. saintgironsi*, *L. guineai*, *L. schistorhynchus*, and *L. crockeri*. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Data availability

All data needed to evaluate conclusions in the paper are present in the paper and/or the Supplementary Materials. The code required to reproduce the results can be found on GitHub (https://github.com/yucheols/seasnakenm/tree/main/codes).

References

Allouche, O., Tsoar, A., Kadmon, R., 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). J. Appl. Ecol. 43, 1223–1232. https://doi.org/10.1111/j.1365-2664.2006.01214.x.

Anderson, R.P., Raza, A., 2010. The effect of the extent of the study region on GIS models of species geographic distributions and estimates of niche evolution: preliminary tests with montane rodents (genus *Nephelomys*) in Venezuela. J. Biogeogr. 37, 1378–1393. https://doi.org/10.1111/j.1365-2699.2010.02290.x.

Anderson, O.F., Stephenson, F., Behrens, E., Rowden, A.A., 2022. Predicting the effects of climate change on deep-water coral distribution around New Zealand—will there be suitable refuges for protection at the end of the 21st century? Glob. Chang. Biol. 28, 6556–6576. https://doi.org/10.1111/gcb.16389.

Asch, R.G., Cheung, W.W., Reygondeau, G., 2018. Future marine ecosystem drivers, biodiversity, and fisheries maximum catch potential in Pacific Island countries and territories under climate change. Mar. Policy 88, 285–294. https://doi.org/10.1016/j.marpol.2017.08.015.

Assis, J., Fernández Bejarano, S.J., Salazar, V.W., Schepers, L., Gouvêa, L., Fragkopoulou, E., Leclercq, F., Vanhoorne, B., Tyberghein, L., Serrão, E.A., Verbruggen, H., De Clerck, O., 2024. Bio-ORACLE v3. 0. pushing marine data layers to the CMIP6 earth system models of climate change researchBio-ORACLE v3. 0. Pushing marine data layers to the CMIP6 eEarth sSystem mModels of climate change research. Glob. Ecol. Biogeogr. 33, e13813. https://doi.org/10.1111/geb.13813.

Barbet-Massin, M., Jiguet, F., Albert, C.H., Thuiller, W., 2012. Selecting pseudo-absences for species distribution models: how, where and how many? Methods Ecol. Evol. 3, 327–338. https://doi.org/10.1111/j.2041-210X.2011.00172.x.

Birchenough, S.N., Reiss, H., Degraer, S., Mieszkowska, N., Borja, Á., Buhl-Mortensen, L., Braeckman, U., Craeymeersch, J., Mesel, I.D., Kerckhof, F., Kröncke, I., Parra, S., Rabaut, M., Schröder, A., Colen, C.V., Hoey, G.V., Vincx, M., Wätjen, K., 2015. Climate change and marine benthos: a review of existing research and future directions in the North Atlantic. Wiley Interdiscip. Rev. Clim. Chang. 6, 203–223. https://doi.org/10.1002/wcc.330.

Bonnet, X., Brischoux, F., Bonnet, C., Plichon, P., Fauvel, T., 2014. Coastal nurseries and their importance for conservation of sea kraits. PLoS One 9, e90246. https://doi.org/10.1371/journal.pone.0090246.

Boone, R.B., Krohn, W.B., 1999. Modeling the occurrence of bird species: are the errors predictable? Ecol. Appl. 9, 835–848. https://doi.org/10.1890/1051-0761(1999)009[0835:MTOOBS]2.0.CO;2.

Brischoux, F., Bonnet, X., Shine, R., 2007. Foraging ecology of sea kraits *Laticauda* spp. in the neo-Caledonian lagoon. Mar. Ecol. Prog. Ser. 350, 145–151. https://doi.org/10.3354/meps07133.

Brischoux, F., Tingley, R., Shine, R., Lillywhite, H.B., 2012. Salinity influences the distribution of marine snakes: implications for evolutionary transitions to marine life. Ecography 35, 994–1003. https://doi.org/10.1111/j.1600-0587.2012.07717.x.

Brischoux, F., Tingley, R., Shine, R., Lillywhite, H.B., 2013. Behavioral and physiological correlates of the geographic distributions of amphibious sea kraits (*Laticauda* spp.). J. Sea Res. 76, 1–4. https://doi.org/10.1016/j.seares.2012.10.010.

Cael, B.B., Burger, F.A., Henson, S.A., Britten, G.L., Frölicher, T.L., 2024. Historical and future maximum sea surface temperatures. Sci. Adv. 10, eadj5569. https://doi.org/10.1126/sciadv.adj5569.

Cogger, H.G., Heatwole, H., 2006. *Laticauda frontalis* (de Vis, 1905) and *Laticauda saintgironsi* n.sp. from Vanuatu and New Caledonia (Serpentes: Elapidae: Laticaudinae)-a new lineage of sea kraits? Rec. Aust. Mus. 58, 245–256.

Cogger, H., Heatwole, H., Ishikawa, Y., McCoy, M., Tamiya, N., Teruuchi, T., 1987. The status and natural history of the Rennell Island Sea krait, *Laticauda crockeri* (Serpentes: Laticaudidae). J. Herpetol. 21, 255–266. https://doi.org/10.2307/1563967.

Cook, T.R., Bonnet, X., Fauvel, T., Shine, R., Brischoux, F., 2015. Foraging behaviour and energy budgets of sea snakes: insights from implanted data loggers. J. Zool. 298, 82–93. https://doi.org/10.1111/jzo.12286.

Crowe-Riddell, J.M., Zdenek, C.N., Sanders, K.L., Rasmussen, A.R., 2024. Sea snakes. Curr. Biol. 34, R795–R815. https://doi.org/10.1016/j.cub.2024.07.101.

Dabruzzi, T.F., Sutton, M.A., Bennett, W.A., 2012. Metabolic thermal sensitivity optimizes sea krait amphibious physiology. Herpetologica 68, 218–225. https://doi.org/10.1655/HERPETOLOGICA-D-11-00077.1.

D'Amen, M., Smeraldo, S., Azzurro, E., 2023. Salinity, not only temperature, drives tropical fish invasions in the Mediterranean Sea, and surface-only variables explain it better. Coral Reefs 42, 467–472. https://doi.org/10.1007/s00338-023-02357-9.

Dawson, T.P., Jackson, S.T., House, J.I., Prentice, I.C., Mace, G.M., 2011. Beyond predictions: biodiversity conservation in a changing climate. Science 332, 53–58. https://doi.org/10.1126/science.1200303.

DeVantier, L., Alcala, A., Wilkinson, C., 2004. The Sulu-Sulawesi Sea: environmental and socioeconomic status, future prognosis and ameliorative policy options. AMBIO 33, 88–97. https://doi.org/10.1579/0044-7447-33.1.88.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., García Marquéz, J. R., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D., Lautenbach, S., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36, 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x.

Elith, J., Kearney, M., Phillips, S., 2010. The art of modelling range-shifting species. Methods Ecol. Evol. 1, 330–342. https://doi.org/10.1111/j.2041-210X.2010.00036.x.

Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ. Conserv. 24, 38–49. https://doi.org/10.1017/S0376892997000088.

Fuentes, M.M.P.B., Limpus, C.J., Hamann, M., Dawson, J., 2010. Potential impacts of projected sea-level rise on sea turtle rookeries. Aquat. Conserv. Mar. Freshwat. Ecosyst. 20, 132–139. https://doi.org/10.1002/arc.1088.

Gherghel, I., Papeş, M., Brischoux, F., Sahlean, T., Strugariu, A., 2016. A revision of the distribution of sea kraits (Reptilia, *Laticauda*) with an updated occurrence dataset for ecological and conservation research. ZooKeys 569, 135–148. https://doi.org/10.3897/zookeys.569.6975.

Gherghel, I., Brischoux, F., Papeş, M., 2018. Using biotic interactions in broad-scale estimates of species' distributions. J. Biogeogr. 45, 2216–2225. https://doi.org/10.1111/jbi.13361.

Gherghel, I., Brischoux, F., Papeş, M., 2019. Refining model estimates of potential species' distributions to relevant accessible areas. Prog. Phys. Geogr. Earth Environ. 44, 449–460. https://doi.org/10.1177/0309133319881104.

Grenouillet, G., Buisson, L., Casajus, N., Lek, S., 2011. Ensemble modelling of species distribution: the effects of geographical and environmental ranges. Ecography 34, 9–17. https://doi.org/10.1111/j.1600-0587.2010.06152.x.

Grossmann, M.M., Nishikawa, J., Lindsay, D.J., 2015. Diversity and community structure of pelagic cnidarians in the Celebes and Sulu seas, southeast Asian tropical marginal seas. Deep-Sea Res. I Oceanogr. Res. Pap. 100, 54–63. https://doi.org/10.1016/j.dsr.2015.02.005.

Guéguen, M., Blancheteau, H., Thuiller, W., 2025. Biomod2: Ensemble Platform for Species Distribution Modeling. R Package (version 4.3-2). https://biomodhub.github.io/biomod2/.

Guinea, M.L., 1986. Aspects of the Biology of the Common Fijian Sea Snake *Latcauda colubrina* (Schneider). University of the South Pacific Suva, Fiji. Thesis.

Guisan, A., Thuiller, W., Zimmermann, N.E., 2017. Habitat Suitability and Distribution Models: With Applications in R. Cambridge University Press, New York.

Hansen, J., Sato, M., Ruedy, R., Lo, K., Lea, D.W., Medina-Elizade, M., 2006. Global temperature change. Proc. Natl. Acad. Sci. 103, 14288–14293. https://doi.org/10.1073/pnas.0606291103.

Heatwole, H., 1997. Marine snakes: are they a sustainable resource? Wildl. Soc. Bull. 25, 766–772. http://www.jstor.org/stable/3783721.

Heatwole, H., Cogger, H., 2013. Provenance errors and vagrants: their role in underestimating the conservation status of sea kraits (Elapidae: Laticaudinae). Pac. Conserv. Biol. 19, 295–302. https://doi.org/10.1071/PC130295.

Heatwole, H., Busack, S., Cogger, H., 2005. Geographic variation in sea kraits of the *Laticauda colubrina* complex (Serpentes: Elapidae: Hydrophiinae: Laticaudini). Herpetol. Monogr. 19, 1–136. https://doi.org/10.1655/0733-1347(2005)019[0001:GVISKO]2.0.CO;2.

Heatwole, H., Lillywhite, H., Grech, A., 2016. Physiological, ecological, and behavioural correlates of the size of the geographic ranges of sea kraits (*Laticauda*; Elapidae, Serpentes): a critique. J. Sea Res. 115, 18–25. https://doi.org/10.1016/j.seares.2016.05.003.

Heatwole, H., Grech, A., Marsh, H., 2017. Paleoclimatology, paleogeography, and the evolution and distribution of sea kraits (Serpentes; Elapidae; *Laticauda*). Herpetol. Monogr. 31, 1–17. https://doi.org/10.1655/HERPMONOGRAPHS-D-16-00003.

Heikkinen, R.K., Marmion, M., Luoto, M., 2012. Does the interpolation accuracy of species distribution models come at the expense of transferability? Ecography 35, 276–288. https://doi.org/10.1111/j.1600-0587.2011.06999.x.

Hirzel, A.H., Le Lay, G., Helfer, V., Randin, C., Guisan, A., 2006. Evaluating the ability of habitat suitability models to predict species presences. Ecol. Model. 199, 142–152. https://doi.org/10.1016/j.ecolmodel.2006.05.017.

Islam, S.N., Gnauck, A., 2008. Mangrove wetland ecosystems in Ganges-Brahmaputra delta in Bangladesh. Front. Earth Sci. China 2, 439–448. https://doi.org/10.1007/s11707-008-0049-2.

Isoguchi, O., Kawamura, H., 2006. Oyashio seasonal intensification and its effect on subsurface temperature variation off the Sanriku coast. J. Geophys. Res. Oceans 111, C10006. https://doi.org/10.1029/2006JC003628.

Jiménez-Valverde, A., Lobo, J.M., 2007. Threshold criteria for conversion of probability of species presence to either–or presence–absence. Acta Oecol. 31, 361–369. https://doi.org/10.1016/j.actao.2007.02.001.

Karvonen, A., Rintamäki, P., Jokela, J., Valtonen, E.T., 2010. Increasing water temperature and disease risks in aquatic systems: climate change increases the risk of some, but not all, diseases. Int. J. Parasitol. 40, 1483–1488. https://doi.org/10.1016/j.ijpara.2010.04.015.

Keith, S.A., Baird, A.H., Hughes, T.P., Madin, J.S., Connolly, S.R., 2013. Faunal breaks and species composition of Indo-Pacific corals: the role of plate tectonics, environment and habitat distribution. Proc. R. Soc. B Biol. Sci. 280, 20130818. https://doi.org/10.1098/rspb.2013.0818.

Kerswell, A.P., 2006. Global biodiversity patterns of benthic marine algae. Ecology 87, 2479–2488. https://doi.org/10.1890/0012-9658(2006)87[2479:GBPOBM]2.0.CO;2.

Kidera, N., Mori, A., Tu, M.C., 2013. Comparison of freshwater discrimination ability in three species of sea kraits (*Laticauda semifasciata*, *L. laticaudata* and *L. colubrina*). J. Comp. Physiol. A. 199, 191–195. https://doi.org/10.1007/s00359-012-0782-6.

Kleisner, K.M., Fogarty, M.J., McGee, S., Hare, J.A., Moret, S., Perretti, C.T., Saba, V.S., 2017. Marine species distribution shifts on the US Northeast Continental Shelf under continued ocean warming. Prog. Oceanogr. 153, 24–36. https://doi.org/10.1016/j.pocean.2017.04.001.

Krause, D.C., 1966. Tectonics, marine geology, and bathymetry of the Celebes Sea-Sulu Sea region. Geol. Soc. Am. Bull. 77, 813–832. https://doi.org/10.1130/0016-7606(1966)77[813:TMGABO]2.0.CO;2.

Lane, A., Shine, R., 2011. Phylogenetic relationships within laticaudine sea snakes (Elapidae). Mol. Phylogenet. Evol. 59, 567–577. https://doi.org/10.1016/j.ympev.2011.03.005.

Leprieur, F., Descombes, P., Gaboriau, T., Cowman, P.F., Parravicini, V., Kulbicki, M., Melián, C.J., de Santana, C.N., Heine, C., Mouillot, D., Bellwood, D.R., Pellissier, L., 2016. Plate tectonics drive tropical reef biodiversity dynamics. Nat. Commun. 7, 11461. https://doi.org/10.1038/ncomms11461.

Lillywhite, H.B., Tu, M.C., 2011. Abundance of sea kraits correlates with precipitation. PLoS One 6, e28556. https://doi.org/10.1371/journal.pone.0028556.

Liu, Y.L., Chen, Y.H., Lillywhite, H.B., Tu, M.C., 2012. Habitat selection by sea kraits (*Laticauda* spp.) at coastal sites of Orchid Island, Taiwan. Integr. Comp. Biol. 52, 274–280. https://doi.org/10.1093/icb/ics085.

Mascle, A., Biscarrat, P.A., 1978. The Sulu Sea: A Marginal Sea in Southeast Asia Tulsa. AAPG Store.

Matsuura, H., Nishida, S., Nishikawa, J., 2010. Species diversity and vertical distribution of the deep-sea copepods of the genus *Euaugaptilus* in the Sulu and Celebes seas. Deep-Sea Res. II Top. Stud. Oceanogr. 57, 2098–2109. https://doi.org/10.1016/j.dsr2.2010.09.013.

Mellin, C., Brown, S., Cantin, N., Klein-Salas, E., Mouillot, D., Heron, S.F., Fordham, D.A., 2024. Cumulative risk of future bleaching for the world's coral reefs. Sci. Adv. 10, eadn9660. https://doi.org/10.1126/sciadv.adn9660.

Mišur, I., Budić, M., Kurečić, T., Korbar, T., 2021. Tectonic influence on Speleogenesis of Sea Caves on Biševo Island (UNESCO Global Geopark Vis Archipelago, Adriatic Sea, Croatia). Geosciences 11, 341. https://doi.org/10.3390/geosciences11080341.

Nakabayashi, A., Yamakita, T., Nakamura, T., Aizawa, H., Kitano, Y.F., Iguchi, A., Yamano, H., Nagai, S., Teshima, K.M., Yasuda, N., 2019. The potential role of temperate Japanese regions as refugia for the coral *Acropora hyacinthus* in the face of climate change. Sci. Rep. 9, 1892. https://doi.org/10.1038/s41598-018-38333-5.

Nishikawa, H., Nishikawa, S., Ishizaki, H., Wakamatsu, T., Ishikawa, Y., 2020. Detection of the Oyashio and Kuroshio fronts under the projected climate change in the 21st century. Prog. Earth Planet. Sci. 7, 1–12. https://doi.org/10.1186/s40645-020-00342-2.

O'Neill, B.C., Kriegler, E., Riahi, K., Ebi, K.L., Hallegatte, S., Carter, T.R., Mathur, R., van Vuuren, D.P., 2014. A new scenario framework for climate change research: the concept of shared socioeconomic pathways. Clim. Chang. 122, 387–400. https://doi.org/10.1007/s10584-013-0905-2.

Park, J., Kim, I.H., Fong, J.J., Koo, K.S., Choi, W.J., Tsai, T.S., Park, D., 2017a. Northward dispersal of sea kraits (*Laticauda semifasciata*) beyond their typical range. PLoS One 12, e0179871. https://doi.org/10.1371/journal.pone.0179871.

Park, J., Koo, K.S., Kim, I.H., Choi, W.J., Park, D., 2017b. First record of the blue-banded sea krait (*Laticauda laticaudata*, Reptilia: Squamata: Elapidae: Laticaudinae) on Jeju Island, South Korea. Asian Herpetol. Res. 8, 131–136. https://doi.org/10.16373/j.cnki.ahr.160066.

Park, D., Jeong, H., Park, J., Park, I.K., 2023. Distribution and habitat assessments of the slender racer, *Orientocoluber spinalis*, for the registration of nationally endangered species in the Republic of Korea. Sci. Rep. 13, 12025. https://doi.org/10.1038/s41598-023-39018-4.

Park, I.K., Shin, Y., Baek, H.J., Kim, J., Kim, D.I., Seok, M., Oh, Y., Park, D., 2024. Establishment potential across South Korea for two gecko species, *Gekko japonicus* and *G. Swinhonis*, adapted to different climates. NeoBiota 93, 39–62. https://doi.org/10.3897/neobiota.93.118085.

Park, I.K., Park, D., Kim, I.H., 2025. Assessment of feeding grounds of loggerhead and green turtles in Korean water through stranding and bycatch data. Biol. Conserv. 302, 110935. https://doi.org/10.1016/j.biocon.2024.110935.

Parmesan, C., Morecroft, M.D., Trisurat, Y., Mezzi, D., 2022. Climate Change 2022: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, New York.

Patrón-Rivero, C., Osorio-Olvera, L., Rojas-Soto, O., Chiappa-Carrara, X., Villalobos, F., Bessesen, B., López-Reyes, K., Yañez-Arenas, C., 2024. Global analysis of the influence of environmental variables to explain ecological niches and realized thermal niche boundaries of sea snakes. PLoS One 19, e0310456. https://doi.org/10.1371/journal.pone.0310456.

Perry, A.L., Low, P.J., Ellis, J.R., Reynolds, J.D., 2005. Climate change and distribution shifts in marine fishes. Science 308, 1912–1915. https://doi.org/10.1126/science.1111322.

Pike, D.A., 2013. Forecasting range expansion into ecological traps: climate-mediated shifts in sea turtle nesting beaches and human development. Glob. Chang. Biol. 19, 3082–3092. https://doi.org/10.1111/gcb.12282.

QGIS.org, 2024. QGIS Geographic Information System. QGIS Association.

R Core Team, 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing.

Ramírez, F., Afán, I., Davis, L.S., Chiaradia, A., 2017. Climate impacts on global hot spots of marine biodiversity. Sci. Adv. 3, e1601198. https://doi.org/10.1126/sciadv.1601198.

Sauro, F., Pozzobon, R., Santagata, T., Tomasi, I., Tonello, M., Martínez-Frías, J., Johannes Smets, L.M., Gómez, G.D.S., Massironi, M., 2019. Volcanic Caves of Lanzarote: A Natural Laboratory for Understanding Volcano-Speleogenetic Processes and Planetary Caves. Springer, Cham, Switzerland.

Shrestha, N., 2021. Factor analysis as a tool for survey analysis. Am. J. Appl. Math. Stat. 9, 4–11. https://doi.org/10.12691/ajams-9-1-2.

Smale, D.A., Wernberg, T., Oliver, E.C.J., Thomsen, M., Harvey, B.P., Straub, S.C., Burrows, M.T., Alexander, L.V., Benthuysen, J.A., Donat, M.G., Feng, M., Hobday, A.J., Holbrook, N.J., Perkins-Kirkpatrick, S.E., Scannell, H.A., Gupta, A.S., Payne, B., Moore, P.J., 2019. Marine heatwaves threaten global biodiversity and the provision of ecosystem services. Nat. Clim. Chang. 9, 306–312. https://doi.org/10.1038/s41558-019-0412-1.

Sobha, T.R., Vibija, C.P., Fahima, P., 2023. Coral reef: a hot spot of marine biodiversity. In: Conservation and Sustainable Utilization of Bioresources. Springer Nature Singapore, pp. 171–194.

Somaweera, R., Udyawer, V., Amarasinghe, A.T., de Fresnes, J., Catherall, J., Molchanova, G., 2023. Apparent coordinated and communal hunting behaviours by Erabu sea krait *Laticauda semifactiata*. Sci. Rep. 13, 21471. https://doi.org/10.1038/s41598-023-48684-3.

Tovar, C., Carril, A.F., Gutiérrez, A.G., Ahrends, A., Fita, L., Zaninelli, P., Flombaum, P., Abarzúa, A.M., Alarcón, D., Aschero, V., Báez, S., Barros, A., Carilla, J., Ferrero, M.E., Flantua, S.G.A., Gonzáles, P., Menéndez, C.G., Pérez-Escobar, O.A., Pauchard, A., Ruscica, R.C., Särkinen, T., Sörensson, A.A., Srur, A., Villalba, R., Hollingsworth, P.M., 2022. Understanding climate change impacts on biome and plant distributions in the Andes: challenges and opportunities. J. Biogeogr. 49, 1420–1442. https://doi.org/10.1111/jpi.14389.

Tu, M.C., Fong, S.C., Lue, K.Y., 1990. Reproductive biology of the sea snake, *Laticauda semifasciata*, in Taiwan. J. Herpetol. 24, 119–126. https://doi.org/10.2307/1564218.

Tyabji, Z., Mohanty, N.P., Young, E., Khan, T., 2018. The terrestrial life of sea kraits: insights from a long-term study on two *Laticauda* species (Reptilia: Squamata: Elapidae) in the Andaman Islands, India. J. Threat. Taxa 10, 12443–12450. https://doi.org/10.11609/jott.4311.10.11.12443-12450.

Uetz, P., Darko, Y.A., Zeliff, D., 2023. Towards digital descriptions of all extant reptile species. Megataxa 10, 27–42. https://doi.org/10.11646/megataxa.10.1.6.

Valavi, R., Guillera-Arroita, G., Lahoz-Monfort, J.J., Elith, J., 2022. Predictive performance of presence-only species distribution models: a benchmark study with reproducible code. Ecol. Monogr. 92, e01486. https://doi.org/10.1002/ecm.1486.

Vieira, C., Keshavmurthy, S., Ju, S.J., Hyeong, K., Seo, I., Kang, C.K., Hong, H.K., Chen, C.A., Choi, K.S., 2015. Population dynamics of a high-latitude coral *Alveopora japonica* Eguchi from Jeju Island, off the southern coast of Korea. Mar. Freshw. Res. 67, 594–604. https://doi.org/10.1071/MF14330.

Waycott, M., Duarte, C.M., Carruthers, T.J., Orth, R.J., Dennison, W.C., Olyarnik, S., Calladine, A., Fourqurean, J.W., Heck Jr., K.L., Hughes, A.R., Kendrick, G.A., Kenworthy, W.J., Short, F.T., Williams, S.L., 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proc. Natl. Acad. Sci. 106, 12377–12381. https://doi.org/10.1073/pnas.0905620106.

Wickham, H., 2016. ggplot2: Elegant Graphics for Data Analysis. Springer, New York. https://ggplot2.tidyverse.org.

Wijffels, S.E., Beggs, H., Griffin, C., Middleton, J.F., Cahill, M., King, E., Jones, E., Feng, M., Benthuysen, J.A., Steinberg, C.R., Sutton, P., 2018. A fine spatial-scale sea surface temperature atlas of the Australian regional seas (SSTAARS): seasonal variability and trends around Australasia and New Zealand revisited. J. Mar. Syst. 187, 156–196. https://doi.org/10.1016/j.jmarsys.2018.07.005.

Zaffos, A., Finnegan, S., Peters, S.E., 2017. Plate tectonic regulation of global marine animal diversity. Proc. Natl. Acad. Sci. 114, 5653–5658. https://doi.org/10.1073/pnas.170229711.

Zurell, D., Franklin, J., König, C., Bouchet, P.J., Dormann, C.F., Elith, J., Fandos, G., Feng, X., Guillera-Arroita, G., Guisan, A., Lahoz-Monfort, J.J., Leitão, P.J., Park, D.S., Peterson, A.T., Rapacciuolo, G., Schmatz, D.R., Schröder, B., Serra-Diaz, J.M., Thuiller, W., Yates, K.L., Zimmermann, N.E., Merow, C., 2020. A standard protocol for reporting species distribution models. Ecography 43, 1261–1277. https://doi.org/10.1111/ecog.04960.