

ORIGINAL RESEARCH OPEN ACCESS

# Climate Change-Induced Distribution Shifts of Keratin-Feeding Beetle *Omorgus (Omorgus) suberosus*: Implications for Olive Ridley Sea Turtle *Lepidochelys olivacea* Conservation

Janderson Batista Rodrigues Alencar<sup>1</sup>  | César Murilo de Albuquerque Correa<sup>2</sup>  | Fabrício Beggiano Baccaro<sup>3,4</sup> | Catherine Sole<sup>5</sup>  | Vinícius da Costa-Silva<sup>5,6</sup> 

<sup>1</sup>Pós-graduação em Ecologia, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil | <sup>2</sup>Laboratório de Bioecologia de Scarabaeoidea (Scaralab), Universidade Estadual de Mato Grosso do Sul, Aquidauana, Brazil | <sup>3</sup>Sínteses da Biodiversidade Amazônica – INCT SinBiAm, Universidade Federal do Pará, Belém, Brazil | <sup>4</sup>Departamento de Biologia, Universidade Federal do Amazonas, Manaus, Brazil | <sup>5</sup>Intertebrate Systematics and Conservation Group, Department of Zoology & Entomology, University of Pretoria, Hatfield, South Africa | <sup>6</sup>Laboratório de Scarabaeoidologia, Instituto de Biociências, Universidade Federal de Mato Grosso (UFMT), Cuiabá, Brazil

**Correspondence:** Janderson Batista Rodrigues Alencar ([jandersonrn@gmail.com](mailto:jandersonrn@gmail.com)) | Vinícius da Costa-Silva ([silvavinicius92@gmail.com](mailto:silvavinicius92@gmail.com))

**Received:** 13 July 2024 | **Revised:** 15 February 2025 | **Accepted:** 20 February 2025

**Editor:** Rahel Sollmann | **Associate Editor:** Henry Häkkinen

**Funding:** This research was supported by the Coordination for the Improvement of Higher Education Personnel (CAPES) and CNPq (Grant #312878/2023-0).

**Keywords:** alien species | biodiversity conservation | climate change | climate scenarios | distribution shift | invasive species | predation impact | species distribution modelling

cenários climáticos | conservação da biodiversidade | espécie exótica | espécies invasoras | impacto da predação | modelagem de distribuição de espécies

## ABSTRACT

The sea turtle *Lepidochelys olivacea* (Eschscholtz, 1829) is particularly threatened by egg predation from the invasive beetle *Omorgus (Omorgus) suberosus* (Fabricius, 1775). However, the impact of global climate change on the distribution and overlap of these species is still poorly understood. Our study aimed to predict the global distributions of *O. suberosus* and *L. olivacea* under various climate change scenarios, to examine their distribution overlap and to assess the conservation status of *L. olivacea*. We analysed a dataset of 2896 *O. suberosus* records and 15,329 *L. olivacea* records, using three modelling algorithms: Maximum entropy default (MXD), DOMAIN (DOM) and generalised linear models (GLM) to project their global distributions under the SSP2–4.5 and SSP5–8.5 scenarios. Results revealed shifts in the distribution of *O. suberosus* by 2100. As temperatures increased, the species expanded its range northward into Europe and North America, while substantial habitat losses occurred in tropical and subtropical regions. Under a mild climate change scenario (SSP2–4.5), the suitable habitat for *O. suberosus* decreased globally by 9.5%, whereas under a ‘business-as-usual’ scenario (SSP5–8.5) projected a 20.8% reduction. Our projections indicate that by 2100, *L. olivacea* will experience significant reductions in suitable coastal habitats under the SSP245 (12.11%) and SSP585 (24.63%) scenarios, with particularly severe losses in northern South America and southern Europe under SSP245 (12.11%). The overlap of *O. suberosus* and *L. olivacea* ranges indicates a significant decline. Under the SSP245 scenario for 2081–2100, the overlap area is projected to decrease by 20.66%. The SSP585 scenario forecasts a further reduction of 37.56%. Understanding the interactions between *O. suberosus* and *L. olivacea* is vital for guiding field studies and informing conservation strategies. Although our results suggest a reduction in the overlap of these species, the

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial-NoDerivs](https://creativecommons.org/licenses/by-nc-nd/4.0/) License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2025 The Author(s). *Animal Conservation* published by John Wiley & Sons Ltd on behalf of Zoological Society of London.

decline in the suitable area of *L. olivacea* raises concerns. Our findings emphasise the importance of targeted research and strategic management to mitigate the impacts of invasive species and climate change on vulnerable turtle populations globally.

## RESUMO

A tartaruga-marinha *Lepidochelys olivacea* (Eschscholtz, 1829) está particularmente ameaçada pela predação de ovos causada pelo besouro invasor *Omorgus (Omorgus) suberosus* (Fabricius, 1775). No entanto, o impacto das mudanças climáticas globais na distribuição e sobreposição dessas espécies ainda é pouco compreendido. Nosso estudo teve como objetivo prever as distribuições globais de *O. suberosus* e *L. olivacea* sob vários cenários de mudanças climáticas, examinar a sobreposição de suas distribuições e avaliar o status de conservação de *L. olivacea*. Analisamos um conjunto de dados com 2.896 registros de *O. suberosus* e 15.329 registros de *L. olivacea*, utilizando três algoritmos de modelagem: Máxima Entropia Padrão (MXD), DOMAIN (DOM) e Modelos Lineares Generalizados (GLM) para projetar suas distribuições globais sob os cenários SSP2–4.5 e SSP5–8.5. Os resultados revelaram mudanças na distribuição de *O. suberosus* até 2100. Com o aumento das temperaturas, a espécie expandiu sua distribuição para o norte, atingindo a Europa e a América do Norte, enquanto perdas substanciais de habitat ocorreram em regiões tropicais e subtropicais. Sob um cenário de mudanças climáticas moderadas (SSP2–4.5), o habitat adequado para *O. suberosus* diminuiu globalmente em 9,5%, enquanto o cenário SSP5–8.5 projetou uma redução de 20,8%. As mudanças projetadas no habitat até 2100 indicam reduções significativas nas áreas costeiras para *L. olivacea* nos cenários SSP245 (12,11%) e SSP585 (24,63%), com perdas especialmente severas no norte da América do Sul e no sul da Europa. A sobreposição das distribuições de *O. suberosus* e *L. olivacea* indica um declínio significativo. Sob o cenário SSP245 para 2081–2100, a área de sobreposição deverá diminuir em 20,66%. O cenário SSP585 prevê uma redução adicional de 37,56%. Compreender as interações entre *O. suberosus* e *L. olivacea* é fundamental para orientar estudos de campo e informar estratégias de conservação. Embora nossos resultados sugiram uma redução na sobreposição dessas espécies, a diminuição da área adequada para *L. olivacea* levanta preocupações. Nossos achados destacam a importância de pesquisas direcionadas e gestão estratégica para mitigar os impactos de espécies invasoras e mudanças climáticas em populações vulneráveis de tartarugas marinhas em escala global.

## 1 | Introduction

Global climate change is hastening the introduction and expansion of invasive species, presenting substantial challenges to conservation endeavours (Richardson and Rejmánek 2011; Ahmad et al. 2019). Despite the urgent need to address these impacts, our understanding of the geographic spread of many invasive insects remains limited due to challenges in forecasting invasions (Lomolino 2004; Hortal et al. 2015). Biological invasions disrupt ecosystems and carry significant economic consequences, with the annual global cost estimated at \$26.8 billion (Diagne et al. 2021). According to Seebens et al. (2021), the number of invasive species is projected to increase by 36% across all taxonomic groups by 2050, necessitating prompt identification of non-native species, assessment of their invasiveness and understanding their pathways of entry and spread (Andersen et al. 2004). Defining and managing suitable habitats for these species is crucial to mitigate their impacts on native biodiversity.

Ecological niche modelling (ENM) is an essential tool for predicting species' geographic ranges, providing critical insights into biogeography, conservation and climate change impacts (Peterson et al. 2011; Peterson and Soberón 2012; Zhu et al. 2013). These models traditionally rely on abiotic variables, aligning with the Grinnellian niche framework (Fick and Hijmans 2017). However, neglecting biotic interactions and dispersal limitations, as outlined in the BAM diagram (Biotic, Abiotic, and Movement), can lead to incomplete predictions (Soberón 2007). This issue is compounded by the Wallacean shortfall, which reflects gaps in distribution data for many taxa, particularly underexplored groups such as terrestrial arthropod predators (Mammola et al. 2021). While ENMs can partially address this shortfall, overcoming it fully requires

substantial investments in primary data collection, which remains time-intensive and costly, especially in remote areas (Balmford and Gaston 1999; Aguiar et al. 2020).

Despite these challenges, ENMs provide a robust framework to explore abiotic and biotic interactions, including competition, predation and host–prey dynamics. These factors are often omitted in modelling but, as highlighted in the literature, are primarily addressed through raster grids representing the distribution of other species with potential interactions (González-Salazar et al. 2013; Cosentino et al. 2023; Hill et al. 2024). This can be incorporated directly into ENMs/SDMs as biotic variable representations or during post-processing by overlaying the distributions of target and interacting species (de Araújo et al. 2014; Alencar, Clé Porto, et al. 2024; Alencar, Sampaio, et al. 2024). Integrating such interactions enhances predictive accuracy by recognising the Eltonian niche influence on species distributions. For instance, invasive species often display generalist behaviours, allowing them to outcompete native species across diverse habitats and rapidly adapt to environmental changes (Alexander and Edwards 2010; Li et al. 2014; Petitpierre et al. 2017; Roberts and Stewart 2018). Therefore, assessing environmental factors as drivers of invasive species is crucial for designing effective conservation plans to mitigate their impacts and preserve ecosystem diversity (Bliss et al. 2023).

*Omorgus (Omorgus) suberosus* (Fabricius, 1775) (Coleoptera: Trogidae) is native to the Americas (Huchet and da Costa-Silva 2018; Costa-Silva et al. 2021) but has been introduced to several continents, including Africa, Asia, Europe and Oceania, where it has become a significant predator of the eggs of the sea turtle *Lepidochelys olivacea* (Eschscholtz, 1829) (Testudines:

Cheloniidae), commonly known as the Olive Ridley Sea Turtles. Since the observations by Roffey in 1958, this predation has been confirmed across multiple regions, including Mexico, India, Saudi Arabia and Somalia (Roffey 1958; Baena et al. 2015; Cortez et al. 2017). The larvae consume turtle eggs, often starting at the extremity and leaving no external damage (Roffey 1958; Cortez et al. 2017; Baena et al. 2020). Although *Omorgus* has a plastic diet, feeding on various decomposing materials, it thrives in environments rich in turtle eggs (Roffey 1958; Baena et al. 2015, 2020; Cortez et al. 2017). Nonetheless, this predatory behaviour poses significant risks to *L. olivacea*, which has already suffered a 30% decline due to habitat loss (Abreu-Grobois and Plotkin 2008).

During the 1960s–1980s, extensive industrial exploitation significantly diminished several *L. olivacea* rookeries, notably in Mexico, leading to their classification as endangered on the IUCN Red List (Abreu-Grobois and Plotkin 2008; Patrício et al. 2019; Cáceres-Farias et al. 2022). Olive Ridleys are distinct for their olive green, heart-shaped shells and are famed for their mass nesting events (known as ‘*arribadas*’, in Spanish), occurring exclusively in select locations in Costa Rica, India and Mexico (Owens et al. 2002; Cervantes-Hernández et al. 2017). Information on their populations in other regions, particularly in secluded nesting sites, remains scant, with populations in the western Pacific and Southeast Asia notably depleted due to extensive egg harvesting (Cáceres-Farias et al. 2022).

Climate change poses severe challenges to the survival and distribution of Olive Ridley turtles (Fuentes et al. 2010; Butt et al. 2016; Patrício et al. 2019; Cáceres-Farias et al. 2022). Rising sea levels and higher sand temperatures are expected to adversely affect nesting sites and alter the sex ratios of hatchlings (Fuentes et al. 2010). These environmental changes, coupled with human activities and predation, significantly threaten the preservation of their natural habitats (Butt et al. 2016; Patrício et al. 2019; Baena et al. 2020). The resilience of Olive Ridleys to these changes is crucial, yet their slow growth and reproductive rates compound the risks posed by their declining numbers (Cáceres-Farias et al. 2022). Effective conservation and management strategies are essential to mitigate the impacts of climate change and the predatory behaviour of *O. suberosus*, ensuring the long-term survival of Olive Ridley populations globally (Rosano Hernández and Deloya 2002).

In this study, we assess the effects of climate change on the global distribution of *Omorgus (O.) suberosus* and its implications for the conservation of Olive Ridley Sea Turtles worldwide. More specifically, our objectives were: (1) predict the potential distribution of *O. suberosus* and *L. olivacea* under current and future climate scenarios; (2) identify the environmental factors driving the reduction or expansion of *O. suberosus* populations; and (3) analyse the predicted environmental overlap between *O. suberosus* and *L. olivacea* under both current and future climate scenarios. We hypothesise that climate change will alter the distribution of *O. suberosus*, allowing it to adapt to new regions as temperatures rise. However, significant habitat losses are expected in tropical and subtropical areas, where elevated temperatures and altered precipitation patterns may exceed the

species tolerance (Scholtz and Caveney 1992). Due to climate change also altering the home range of *L. olivacea*, we predict that the overlap area with *O. suberosus* will remain constant in future scenarios. This combination of results may raise concerns, given that the predatory larvae of *O. suberosus* can significantly reduce hatch rates, directly affecting the survival and reproductive success of the already vulnerable Olive Ridley's populations.

## 2 | Materials and Methods

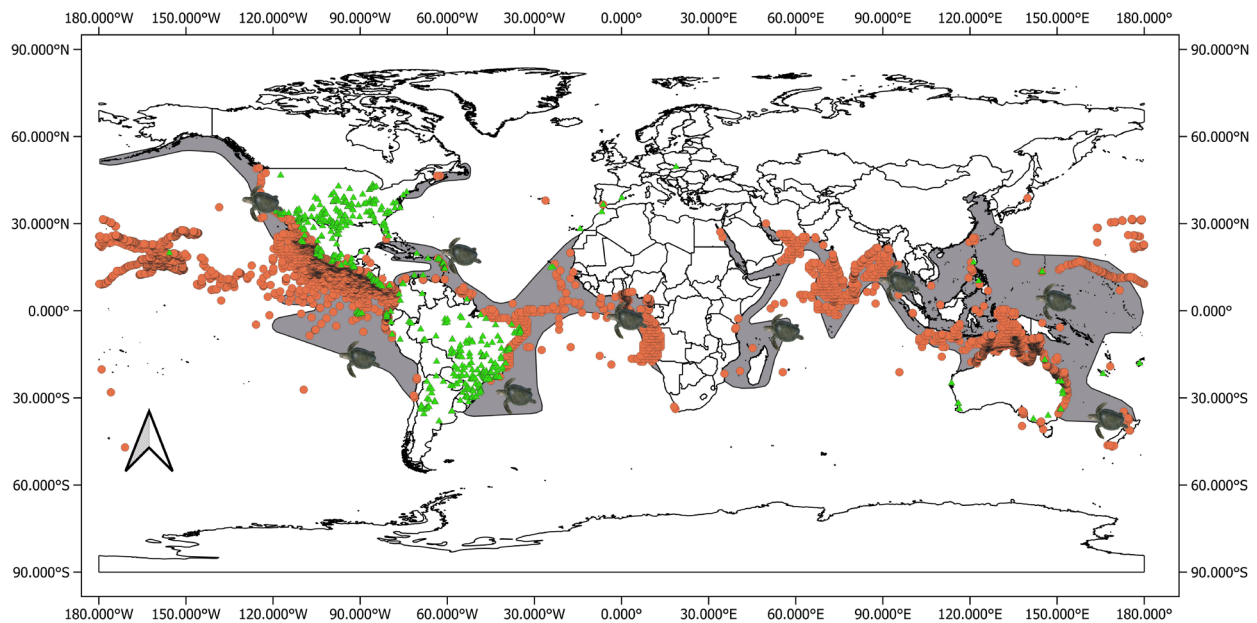
### 2.1 | Occurrence Records and Data Cleaning

Data on the geographical distribution of *Omorgus (O.) suberosus* were collated from three principal sources. Initially, 698 records were compiled from specimens examined in 17 zoological/entomological collections and from reviewed records in specialised literature, such as checklists, catalogues and taxonomic revisions (see File S1). Additionally, 2198 records of *O. suberosus* were obtained from the Global Biodiversity Information Facility (<https://doi.org/10.15468/dl.xcfz9n>) (GBIF 2024b), resulting in a final database of 2896 worldwide raw records, spanning from 1877 to 2024 and covering 147 years of documented records. The geographic range of *L. olivacea* was established using data from the 2008 IUCN Red List, along with 15,329 records from GBIF (<https://doi.org/10.15468/dl.wf8cbm>), the National Museum of Natural History (NMNH), Smithsonian Institution, and reviewed specialised literature. The records span from 1860 to 2024, covering 164 years of documented records (Abreu-Grobois and Plotkin 2008; de Boer 2010; Orrell 2017; GBIF 2024a). Figure 1 illustrates the raw records of *O. suberosus* and *L. olivacea*, with a detailed overview of sources in the File S1.

The records were filtered to remove duplicates, entries with ambiguous coordinates and inaccurately mapped locations (i.e., marine areas for *O. suberosus* and inland records for *L. olivacea*). Furthermore, we applied the CELLSIZE occurrence thinning method (Fourcade et al. 2014) to mitigate sampling bias. It operates by randomly selecting one occurrence per grid cell, where each cell is sized at twice the resolution of the corresponding environmental variables (equivalent to 5 arc-minutes, approximately 9 km at the equator) (Fourcade et al. 2014; Velazco et al. 2019). This method reduced the original 2896 raw records of *O. suberosus* to 551 filtered records and the 15,329 raw records of *L. olivacea* to 1918 filtered records.

### 2.2 | Environmental Data

We considered 20 key variables essential for predicting the distribution of *O. suberosus* and *L. olivacea*, of which 19 are related to climatic conditions (see File S1). These climatic variables, extracted from the WorldClim database (<https://www.worldclim.org/data/bioclim.html>), provide crucial information on temperature and precipitation, drawing from monthly averages to highlight annual trends, seasonality and notable climatic extremes or constraints (Fick and Hijmans 2017). Elevation was also added as a variable, as it indicates mountainous regions and provides essential information on gradients, precipitation patterns and vegetation types, all influencing habitat suitability



**FIGURE 1** | Compilation of known occurrences of *Omorgus* (*O.*) *suberosus* (2896 green dots) superimposed on the geographic range *Lepidochelys olivacea* (15,329 orange dots and grey-shaded areas). The range map for *L. olivacea* has been adapted from the IUCN Red List.

for various species (Fick and Hijmans 2017). It also served as a proxy for coastal positioning, compensating for the lack of detailed topography data, capturing key habitat features like low slopes, shore widths and sand fractions critical for *L. olivacea* nesting (Septiadi et al. 2018). Moreover, these variables impact biological functions like transpiration and insect development (Beirne 1970; Hodkinson 2005; Régnière et al. 2012; Khaliq et al. 2014).

All spatial data were standardised to a 2.5 arc-minute resolution for current and future periods to ensure a controlled spatial assessment of environmental variables. To address multicollinearity and reduce the number of variables, we employed the variance inflation factor ( $VIF > 10$ ) to exclude predictors with solid correlations (Marquardt 1970). The contributions of each variable to the *O. suberosus* model were evaluated using response curves based on the best-performing algorithm, quantified by the average true skill statistic (TSS). This approach helps to determine if the results are stable across the sample of models after 30 simulations, a critical measure given the use of machine learning methods and random allocates background points within the area used to calibrate the models (Phillips et al. 2006; Sillero and Barbosa 2021).

We simulated future geographical distributions of *O. suberosus* and *L. olivacea* using the MIROC6 model from the general circulation models (CMIP6). We projected these distributions under two scenarios: (1) SSP2–4.5, a moderate scenario forecasting a temperature rise of approximately 2.1°C–4.3°C and atmospheric CO<sub>2</sub> levels reaching 26.84 gigatons by 2100, and (2) SSP5–8.5, a ‘business-as-usual’ scenario predicting a temperature increase of about 3.8°C–7.4°C and CO<sub>2</sub> levels escalating to 129.85 gigatons by 2100. These scenarios encompass four distinct periods, extending from the present to 2100, which allows us to project environmental changes over time and evaluate how shifting climatic conditions might affect the distribution of *O. suberosus* and *L. olivacea*.

### 2.3 | Ecological Niche Models

The calibration area for *O. suberosus* was buffered based on the maximum distance between the recorded occurrences of this species, while for *L. olivacea*, the calibration area included a 50 km buffer focusing exclusively on coastal areas (Barve et al. 2011; Peterson et al. 2011), ensuring targeted analysis in regions of ecological significance for the studied organisms. For the generation of pseudoabsences and background data, we maintained a 1:1 ratio to presence data for the generalised linear models (GLM) algorithm. Additionally, for the maximum entropy default (MXD) algorithm, we generated 10,000 random background points. These points were distributed to target predicted low-suitability zones identified by the Bioclim model (Engler et al. 2004).

Predictions of potential distribution were generated using a variety of algorithms, including MXD with presences and background points (Phillips et al. 2006; Phillips 2017), DOMAIN (DOM) using only presences (Hijmans et al. 2017) and GLM with presences and pseudo-absences (McCullagh and Nelder 1989). These algorithms included different theoretical bases for suitability estimations (Pimenta et al. 2022). The ensemble model-averaged predictions from the top-performing algorithms specifically included only those with above-average true skill statistic (TSS) values greater than 0.70 (Allouche et al. 2006; Velazco et al. 2019). TSS, which ranges from –1 to +1, was used to assess predictive accuracy, with values above 0.70 indicating robust performance. The model underwent refinement by applying a threshold-based Sorensen index, with a cut-off for suitability scores set above 0.598 for *O. suberosus* and 0.548 for *L. olivacea*. This adjustment aims to reduce prevalence bias and concurrently bolster the true-positive rates (TPR) and true-negative rates (TNR) (Jiménez-Valverde and Lobo 2007; Leroy et al. 2018). This threshold was established through detailed analysis of distribution maps and expert knowledge of the species, ensuring a

balance between theoretical accuracy and practical applicability. This approach leverages the increased accuracy of ensemble modelling (Araujo and New 2007; Thuiller et al. 2019).

Our models were subjected to k-fold cross-validation using fivefolds (Fielding and Bell 1997). The dataset was divided into five equal parts, with each model iteration being trained on four parts and tested on the remaining one. This cross-validation technique evaluated the models accuracy by systematically alternating the training and testing subsets. Spatial autocorrelation was evaluated using Moran's I to ensure spatial independence, resulting in values of  $0.485 \pm 0.041$  for *O. suberosus* and  $0.521 \pm 0.008$  for *L. olivacea*. Additionally, we assessed environmental similarity within the partitions using multivariate environmental similarity surfaces (MESS) (Elith et al. 2010), with values of  $11.397 \pm 0.938$  for *O. suberosus* and  $8.815 \pm 0.300$  for *L. olivacea*. MESS is a method to evaluate how similar new environments are to the training data used in species distribution models. It quantifies similarity concerning chosen predictor variables, providing positive values for similar environments and negative values for dissimilar ones.

We employed binarised ensemble models to assess the impact of climate change on species distribution, contrasting current conditions with two future scenarios projected for 2100: SSP2-4.5, representing a moderate scenario, and SSP5-8.5, indicative of a high emission scenario. This analysis focused on identifying the relative gains and losses in species range due to climatic change on a global scale. The quantification of coastal areas for *L. olivacea* involved measuring the linear kilometres of current coastal zones that intersect with the turtles projected distribution under two climate change scenarios, SSP2-4.5 and SSP5-8.5. We addressed uncertainties in ENM/SDM projections, particularly concerning model transferability, by applying MOP (mobility-oriented parity) analysis (Owens et al. 2013). This approach identified areas of environmental extrapolation, ensuring that projections remained within regions exhibiting high environmental similarity to the species' native range (see File S2). The MOP analysis revealed that over 98.5% of the projected areas shared an environmental similarity index greater than 0.9 with the native regions, thereby providing a robust ecological foundation for the reliability of our distributional forecasts. To

incorporate a quantitative assessment of uncertainty, we applied the analytic deduction of uncertainty method (Chen et al. 2019). This approach involved compiling 551 cleaned occurrence records, extracting environmental constraints and solving the MXD, GLM and ensemble models to obtain habitat suitability estimates. We then computed the covariance matrix to quantify prediction variability and derived the sensitivity matrix by calculating partial derivatives to account for constraint variations. Finally, we estimated the covariance of output probabilities, providing a comprehensive measure of uncertainty across models. The results are summarised in boxplots of uncertainty and further detailed in Files S3 and S4. The models were developed using the ENMTML R package (v1.0-beta) (de Andrade et al. 2020), facilitating ensemble outputs' integration and binarisation. The resulting distribution maps were visualised using QGIS version 3.22.14.

### 3 | Results

The ensemble models for both species exhibited high accuracy. Regarding model performances for *O. suberosus*, the ensemble model achieved a TSS of  $0.722 \pm 0.038$  and a Sorensen similarity coefficient of  $0.867 \pm 0.016$ , indicating robust model reliability with a TPR of 0.925 and a TNR of 0.861. Similarly, for *L. olivacea*, the ensemble model demonstrated performance with a TSS of  $0.878 \pm 0.009$  and a Sorensen similarity coefficient of  $0.937 \pm 0.004$ . The model reliability for this species was further underscored by a TPR of 0.908 and a TNR of 0.942 (Table 1).

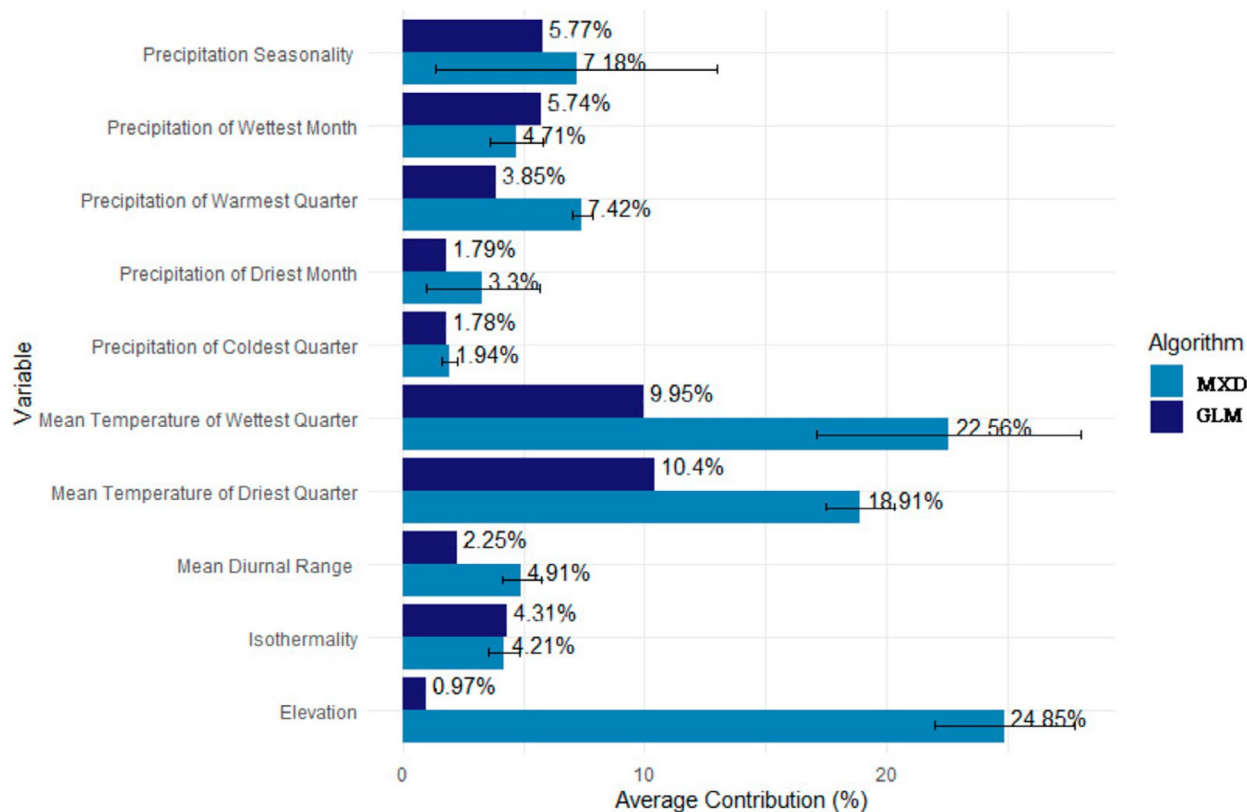
#### 3.1 | Variable Contributions

The GLM and MXD algorithms determined the key environmental variables influencing the habitat preferences of *O. suberosus* (Figure 2). The MXD algorithm highlights the mean temperature of the wettest quarter and the mean temperature of the driest quarter as the most influential factors, with contributions of 22.56% and 18.91%, respectively. Although these variables also play a significant role in the GLM, their impact is less pronounced. The minimum and maximum ranges and means of the registration variables used in both models show that the

**TABLE 1** | Algorithms and ensemble model performance for *Omorgus (O.) suberosus* and *Lepidochelys olivacea*, based on 551 and 1918 presence records, respectively.

Species	Algorithm	TSS ( $\pm$ SD)	Sorensen ( $\pm$ SD)
<i>Omorgus suberosus</i>	MXD	$0.706 \pm 0.058$	$0.859 \pm 0.018$
	DOM	$0.633 \pm 0.099$	$0.835 \pm 0.037$
	GLM	$0.715 \pm 0.040$	$0.864 \pm 0.015$
	Ensemble	$0.722 \pm 0.038$	$0.867 \pm 0.016$
<i>Lepidochelys olivacea</i>	MXD	$0.788 \pm 0.146$	$0.896 \pm 0.054$
	DOM	$0.700 \pm 0.009$	$0.860 \pm 0.004$
	GLM	$0.870 \pm 0.014$	$0.934 \pm 0.007$
	Ensemble	$0.878 \pm 0.009$	$0.937 \pm 0.004$

Abbreviations: DOM, domain; GLM, generalised linear models; MXD, maximum entropy default.



**FIGURE 2** | Comparative contribution of 10 variables to the ecological niche modelling of *Omorgus (O.) suberosus*, based on 551 presence records. Results are shown for maximum entropy default (MXD—light blue) and generalised linear model (GLM—dark blue) algorithms. MXD results vary due to stochastic processes, including random background point selection and iterative entropy optimisation.

mean diurnal temperature range varies from 5.38°C to 20.35°C, averaging 11.85°C. Isothermality ranges from a low of 26.72% to a high of 93.36%, with an average of 57.56%. Temperature fluctuations across different quarters reflect a significant variation, from a low of −7.10°C in the driest quarter to 32.32°C in the wettest, underscoring the importance of thermal factors in ecological modelling for this species.

Precipitation variables also varied in importance across the MXD and GLM algorithms, with MXD showing a generally high emphasis. Specifically, in the MXD, precipitation of the warmest quarter and precipitation seasonality are notably influential, contributing 7.42% and 7.18%, respectively, compared to their lesser yet notable roles in the GLM. Data show that precipitation in the wettest month ranged from 7 mm to 725 mm, averaging 189.73 mm, while in the driest month, it spanned from 0 mm to 367 mm, averaging 36.57 mm. Precipitation seasonality varied broadly, with an index from 5.77 mm to 157.43 mm, averaging 57.84 mm. Additionally, the warmest quarter saw precipitation ranging from 3 mm to 1436 mm, averaging 372.07 mm and the coldest quarter from 0 mm to 1859 mm, averaging 207.05 mm.

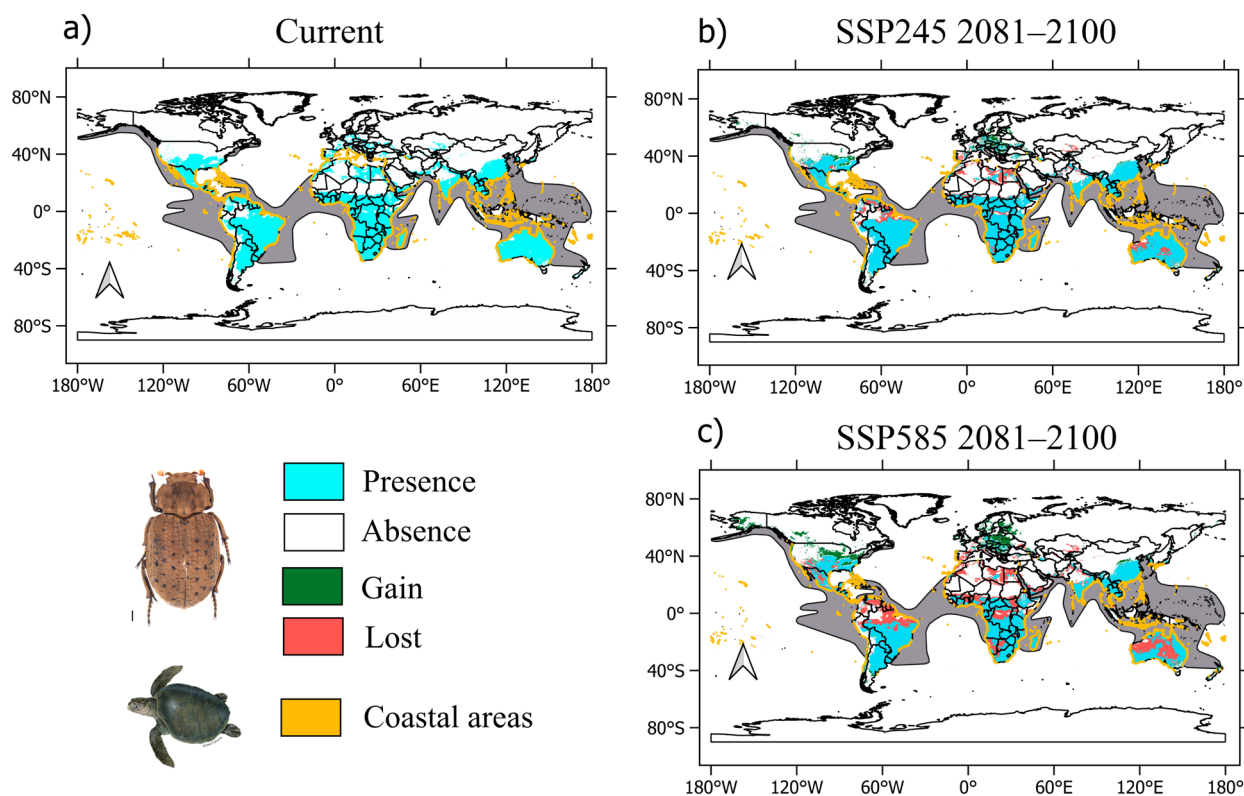
The elevation ranges from −54 m to 3690 m, with an average of 468.36 m above sea level. Within the MXD model, elevation emerged as the most influential factor, contributing significantly at 24.85%, highlighting its critical importance in the model's framework. In stark contrast, the GLM assigned minimal importance to elevation, contributing only 0.97%. This significant discrepancy underscores a clear divergence in how each

model assesses the relevance of elevation to the ecological niche modelling of *O. suberosus* and increases the relevance of assembly models.

### 3.2 | Current and Future Potential Distribution

*Omorgus (O.) suberosus* has been recorded on multiple continents, extending beyond its native range in the Americas (Huchet and da Costa-Silva 2018). The range of this species overlaps  $9.37 \times 10^7$  ha (96%) with the coastal zones inhabited by *L. olivacea* under the current scenario (Table 2), which inhabits tropical and subtropical waters across the Pacific, Indian and Atlantic Oceans, excluding the Gulf of Mexico. The habitat distribution of *L. olivacea* includes a variety of marine zones, such as oceanic (open sea) and neritic (coastal) environments, with its range extending to the coastal waters of over 80 countries, as illustrated in Figure 3.

Projections based on the SSP245 2081–2100 and SSP585 2081–2100 scenarios indicate a potential expansion of the distribution of *O. suberosus* in the Northern Hemisphere. The model projected increased environmental suitability areas across North America, from the United States to Alaska and Canada, and expansion into considerable areas of Eastern Europe. Additionally, there is a projected modest range of extensions into Northern Asia. In the Southern Hemisphere, Argentina and New Zealand are identified as regions of modest range expansion for *O. suberosus* (Figure 3).



**FIGURE 3** | Projected geographic distribution shifts for *Omorgus (O.) suberosus* in response to global warming scenarios, based on 551 presence records: (a) current distribution pattern; (b) predicted distribution change from present to 2100 under the MIROC6: SSP2–4.5 scenario—mild climate change; (c) predicted distribution change from present to 2100 under the MIROC6: SSP5–8.5 scenario—business as usual. The yellow coastal areas represent the linear projections for *Lepidochelys olivacea* in each scenario, based on 1918 presence records. The grey-shaded areas represent the range map for *L. olivacea*, adapted from the IUCN Red List.

**TABLE 2** | Potential changes (losses and gains) in suitability area for *Omorgus (O.) suberosus* under different climate scenarios, based on an ensemble species distribution model fit to 551 presence records.

Continent	current (ha)	ssp245 (ha)	ssp585 (ha)	Gain/Loss SSP245 (ha)	% Change	Gain/Loss SSP585 (ha)	% Change
Africa	$2.0 \times 10^{13}$	$1.7 \times 10^{13}$	$1.3 \times 10^{13}$	$-3.2 \times 10^{12}$	-16%	$-7.1 \times 10^{12}$	-35%
Asia	$1.0 \times 10^{13}$	$9.3 \times 10^{12}$	$8.6 \times 10^{12}$	$-1.1 \times 10^{12}$	-11%	$-1.7 \times 10^{12}$	-17%
Europa	$2.1 \times 10^{12}$	$2.9 \times 10^{12}$	$3.8 \times 10^{12}$	$0.7 \times 10^{12}$	32%	$1.6 \times 10^{12}$	74%
North America	$6.3 \times 10^{12}$	$6.9 \times 10^{12}$	$7.9 \times 10^{12}$	$0.5 \times 10^{12}$	9%	$1.5 \times 10^{12}$	24%
Oceania	$8.3 \times 10^{12}$	$7.4 \times 10^{12}$	$5.2 \times 10^{12}$	$-0.9 \times 10^{12}$	-12%	$-3.1 \times 10^{12}$	-37%
South America	$1.3 \times 10^{13}$	$1.2 \times 10^{13}$	$9.9 \times 10^{12}$	$-1.7 \times 10^{12}$	-13%	$-3.8 \times 10^{12}$	-28%
Global	$6.1 \times 10^{13}$	$5.5 \times 10^{13}$	$4.8 \times 10^{13}$	$-5.8 \times 10^{12}$	-9.50%	$-1.2 \times 10^{13}$	-20.8%

Our projections also indicate substantial losses in environmentally suitable areas for *O. suberosus* across tropical and subtropical regions. Under the mild climate change scenario (SSP245–2081–2100), Africa is projected to lose 16% of its current suitable land area, while Asia will see an 11% reduction. Oceania and South America are expected to lose 12% and 13%, respectively. Europe, however, is predicted to gain 32%, while North America will expand its suitable area by 9%. This scenario predicts an overall global decline of 9.5% (Table 3). Losses are even more substantial in the more extreme SSP585 scenario (2081–2100). Africa will lose 35% of its suitable land area, Asia

17% and South America 28%. Oceania has the most critical decline, losing 37% of its suitable area. Europe and North America, on the other hand, will gain 74% and 24% more suitable land, respectively. Globally, this scenario forecasts a 20.8% reduction in *O. suberosus* habitat suitability (Table 2).

These projections highlight the significant challenges climate change will impose on the global distribution of environmentally suitable areas. Substantial reductions are anticipated in northern South America, particularly in part of the Amazon basin (i.e., Brazil, Venezuela, French Guiana, Colombia and

**TABLE 3** | Potential changes in coastal suitability for overlapping areas of *Lepidochelys olivacea* and *Omorgus (O.) suberosus* under various climate scenarios, based on an ensemble species distribution model fit to 1918 and 551 presence records, respectively.

Scenario	Coastal length (km)	% Lost	Coastal overlap (ha)	% Overlap
	<i>L. olivacea</i>		<i>O. suberosus</i>	
Current	$2.23 \times 10^5$	—	$9.37 \times 10^7$	96.00%
SSP245 scenario (2081–2100)	$1.96 \times 10^5$	–12.11%	$7.43 \times 10^7$	76.16%
SSP585 scenario (2081–2100)	$1.68 \times 10^5$	–24.63%	$5.85 \times 10^7$	59.94%

Peru). Similar patterns of decline are projected for north of Africa, southern Europe, Kazakhstan, northern India, Malaysia and Australia. The trends of contraction and expansion in environmentally suitable areas are consistent across both scenarios, with SSP585 predicting a more intense change by 2100.

The future scenarios project significant habitat loss for *L. olivacea* along the world coastal zones by 2100. According to our data, under the SSP245 scenario (2081–2100), there is an estimated reduction in coastal habitats of 12.11%, with the habitat area decreasing from  $2.23 \times 10^5$  km to  $1.96 \times 10^5$  km. The SSP585 scenario forecasts a more drastic decline of 24.63%, reducing the habitat to  $1.68 \times 10^5$  km. As detailed in Table 3, the coastal overlap area is  $9.37 \times 10^7$  (96%) hectares under the current scenario. This area decreases under the SSP245 scenario (2081–2100) to  $7.43 \times 10^7$  ha, representing a 23.84% reduction. The SSP585 scenario forecasts a more drastic decline to  $5.85 \times 10^7$  ha, marking a 40.06% reduction from the current overlap.

The results in Figure 4 indicate significant reductions in overlapping coastal suitability for *Lepidochelys olivacea* and *Omorgus (O.) suberosus* under SSP245 and SSP585 scenarios for 2081–2100. These reductions are largely due to the habitat contraction of *O. suberosus*, with substantial losses observed in northern South America, including Brazil, Venezuela, Guyana, Suriname, French Guiana and the Caribbean islands, as well as in southern Europe, Asia and Oceania.

## 4 | Discussion

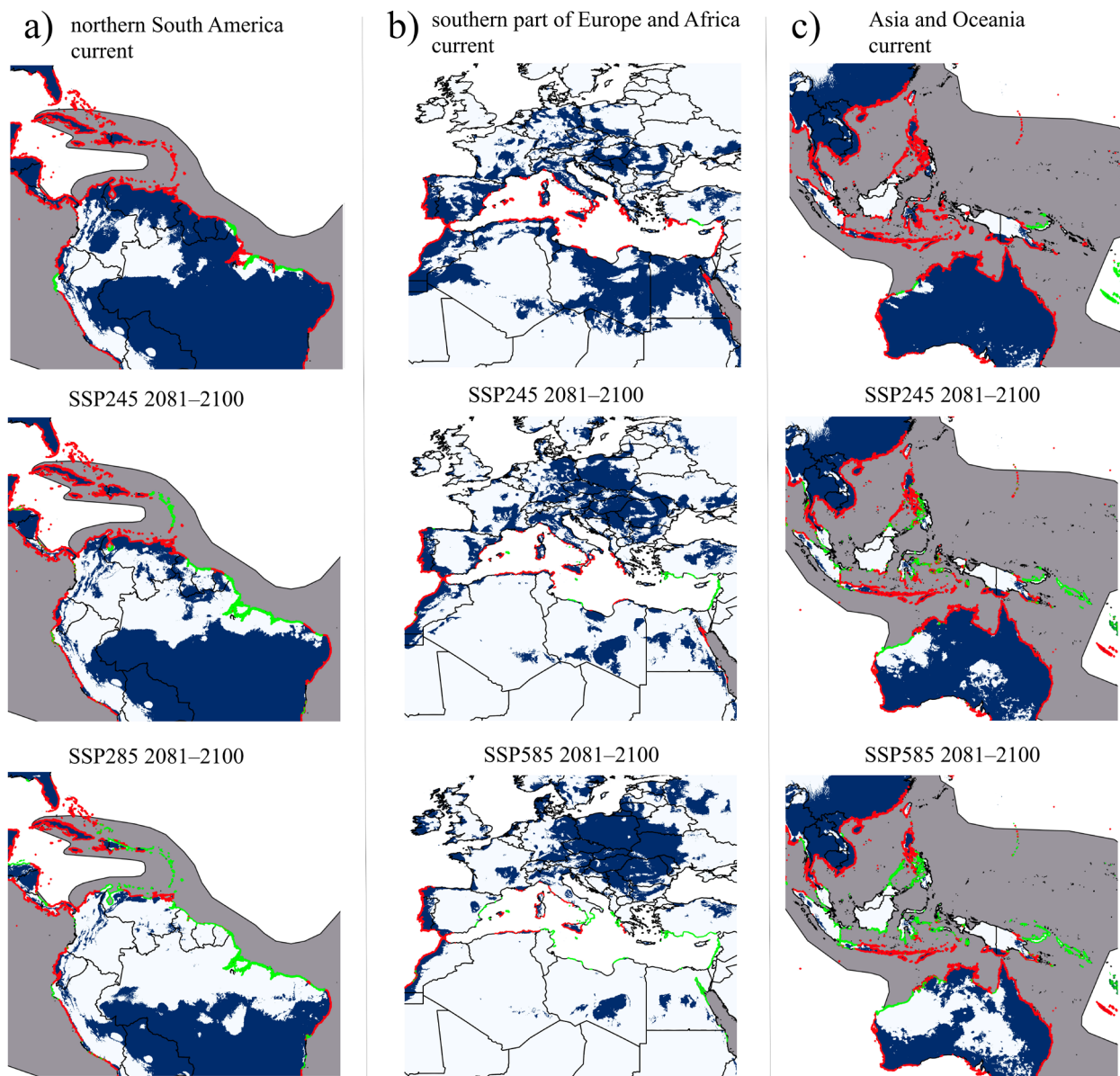
Our findings provide a comprehensive understanding of the interactions between the invasive beetle *Omorgus (O.) suberosus* and the sea turtle *Lepidochelys olivacea* in the context of climate change. We anticipated the contraction of overlapping habitats between these two species under future climate scenarios with a notable decline in suitable coastal areas for *L. olivacea*. This reduction in habitat overlaps, driven by shifts in *O. suberosus* distributions towards higher latitudes and altitudes, alongside significant losses in tropical and subtropical regions, highlights a dual challenge: the necessity to address the impacts of climate change on vulnerable turtle populations and the need for targeted management of invasive species to mitigate predation risks in future overlap areas. By integrating predictive modelling into conservation planning, we demonstrate the potential to optimise resource allocation, thereby improving management strategies for *O. suberosus* across its invasive range. These results underscore the importance of integrating predictive modelling

with conservation strategies to allocate resources and safeguard biodiversity effectively.

### 4.1 | Potential Distribution of *O. suberosus* Under Current and Future Climate Scenarios Worldwide

*Omorgus (O.) suberosus* has established a wide geographical range that spans multiple continents, extending well beyond its native territory in the New World (Costa-Silva et al. 2021). This expansive range can partly be attributed to the thermal tolerance of the species, as *Omorgus* species reach their reproductive optimum near temperatures of 34°C (Scholtz and Caveney 1992). The mean temperature of the wettest quarter and the mean temperature of the driest quarter are identified as primary factors, contributing 22.56% and 18.91%, respectively, indicating that thermal conditions during critical moisture periods are crucial for the distribution of *O. suberosus*. This thermal adaptability could facilitate shifts in their thermal niche in response to climate change scenarios (Roeder et al. 2021). Variations in the impact of precipitation are also noted, with the precipitation of the warmest quarter and precipitation seasonality being especially relevant. Historical data corroborate that temperature and precipitation influence insect distribution, affecting vegetation structure and resource availability, which are particularly critical for ectothermic organisms (Mellanby 1939; Wolda 1978; Kishimoto-Yamada and Itioka 2015; Schowalter 2016). Additionally, the generalist feeding habits of *O. suberosus* (i.e., necrophagous, coprophagous, keratinophagous; see Correa et al. 2013; Baena et al. 2015; Hughes and Vogler 2006) contribute to its success as an invasive species, enhancing its ability to colonise new areas (Antunes-Carvalho and Lopes-Andrade 2013).

The projections suggest a moderate expansion into the northern Hemisphere under both future scenarios. Notably, there is an estimated 2%–4.7% increase in suitable areas, with the most significant gains in North America, extending up to Alaska, Canada and Eastern Europe. Modest expansions are also anticipated into Northern Asia. In the Southern Hemisphere, Argentina and New Zealand show potential for minor range increases. However, these gains are contrasted by considerable losses in tropical and subtropical regions. The SSP2–4.5 scenario predicts a 7.5% decrease in suitable habitats, whereas the SSP5–8.5 scenario projects a more substantial decline of 16.0%. Areas anticipated to experience significant declines include low-altitude regions in northern South America (such as Brazil, Venezuela, French Guiana, Colombia, and Peru), North Africa, Southern Europe, Kazakhstan, Northern India, Malaysia and Australia. These losses primarily occur in the



**FIGURE 4** | Coastal suitability changes and overlapping areas for *Lepidochelys olivacea* and *Omorgus (O.) suberosus* (dark blue) under SSP245 and SSP585 scenarios for 2081–2100. Overlapping areas (red) and non-overlapping areas (green) are shown for (a) part of North America and northern South America, (b) southern Europe and northern Africa and (c) Asia and Oceania. Results are based on an ensemble species distribution model fit to 1918 and 551 presence records, respectively. The grey-shaded areas represent the range map for *L. olivacea*, adapted from the IUCN Red List.

species current range and reflect the impact of increasing temperatures and changing precipitation patterns expected under global warming.

Interestingly, in northern South America, the beetles range shows a potential upward shift to higher altitudes, highlighting its adaptability to environmental changes and its movement away from coastal areas on this continent. This shift suggests that indirect interactions with *L. olivacea* are unlikely. While viable populations at high elevations might theoretically migrate to lower coastal areas where turtles nest, future extreme global warming scenarios (e.g., SSP5–8.5) predict significant declines in overlap areas, further reducing the likelihood of such interactions. Additionally, there is a notable divergence in how models interpret the impact of elevation. The MXD model assigns a high

significance of 24.85%, whereas the GLM model deems it nearly negligible. This variation suggests differing interpretations of how elevation interacts with other environmental predictors and influences the species distribution. A cautious interpretation would be to expect that *O. suberosus* may thrive across a broad range of elevational zones. Such adaptability may serve as a crucial buffer against climate fluctuations, an essential trait given the ongoing changes in global climate conditions.

To ensure a rigorous assessment of predictive uncertainty, we applied the analytic deduction of uncertainty method (Chen et al. 2019), quantifying predictive uncertainty and enabling a more precise selection of the most reliable modelling approach. To mitigate potential biases and predictive uncertainty, we accounted for the geographic and environmental

representativeness of the data and emphasise that both species are sufficiently sampled for robust distribution modelling. For *L. olivacea*, occurrence records demonstrate comprehensive global coverage of coastal areas, with a strong concentration in tropical and subtropical regions. This extensive distribution reflects significant sampling efforts and captures a wide range of environmental heterogeneity, thereby reinforcing the reliability of our model projections. Similarly, *O. suberosus* occurrence records exhibit broad geographic and environmental coverage, spanning various regions and climatic conditions within both its native and potentially invaded ranges. Additionally, our range gain and loss calculations explicitly incorporated uncertainty, facilitating the selection of the least uncertain model and enhancing predictive confidence. The Ensemble model, which integrates the top-performing algorithms (Allouche et al. 2006; Velazco et al. 2019), emerged as the most robust and reliable choice, effectively reducing extreme variations and strengthening confidence in habitat suitability estimations.

Despite rigorous bias controls, uncertainty persists in range estimates, particularly in areas where the distributions of both species overlap. This uncertainty arises from additional factors such as human activity, tourism and sea-level rise, which could not be explicitly included at the scale of this study. While climate models account for environmental conditions and habitat suitability, they do not incorporate spatial projections of sea-level rise or associated changes to coastal habitats as a direct variable in future projections. For instance, coastal areas that are climatically suitable for *L. olivacea* nesting but are heavily impacted by tourism or egg harvesting may no longer serve as viable habitats. Similarly, regions such as southern Europe and northern Africa, despite being environmentally suitable, require less conservation focus due to the absence of *L. olivacea* records, even though *O. suberosus* has been reported. These limitations underscore the need for a cautious interpretation of model outputs, recognising the inherent assumptions and constraints, even when robust bias control measures are applied.

Our methodology adheres to best practices to reduce bias and enhance predictive reliability while identifying critical areas for conservation efforts. Furthermore, the predictive models developed in this study have proven effective across various insect taxa, as evidenced by research on invasive stored-product pests such as *Cryptomorpha desjardinsii* (Guérin-Méneville, 1844) (Coleoptera: Silvanidae) and species of *Microtheca* (Coleoptera: Chrysomelidae) (Alencar et al. 2022; Alencar, Sampaio, et al. 2024), the Asian wood-wasp *Eriotremex formosanus* (Matsumura) (Hymenoptera: Siricidae) (Alencar, Clé Porto, et al. 2024) and the mayfly *Cloeon dipterum* (Linnaeus, 1761) (Ephemeroptera: Baetidae) (Cruz et al. 2023). These models facilitate forecasting global distributions and potential invasions in coastal neritic zones under varying climate scenarios, providing valuable insights for monitoring colonisation dynamics and improving preventative measures against species introductions.

#### 4.2 | Overlap Between the Predicted Distribution of *O. suberosus* and *L. olivacea*

The overlap between the predicted distributions of *Omorgus* (*O.*) *suberosus* and *Lepidochelys olivacea* reveals a dynamic shift

under future climate scenarios. Our analysis indicates a decline in overlap from 76% under SSP2-4.5 to 60% under SSP5-8.5 by 2100. This reduction is primarily attributed to the contraction of *O. suberosus* habitats towards inland and higher elevation zones, particularly in northern South America (e.g., Brazil, Venezuela, Guyana and French Guiana) and overlaps across southern Europe, Asia and Oceania. Future projections reinforce a trend of reduced coastal overlap due to habitat changes for *O. suberosus*, further distancing the distributions of these species.

The ecological relationship between these species predominantly manifests during the hatching period of *L. olivacea* eggs. *Omorgus suberosus* larvae may severely impact hatch rates, with notable predation observed at La Escobilla in Mexico and reported incidences across various Pacific Mexican beaches (Baena et al. 2015, 2020). In their study at La Escobilla, Baena et al. (2015) found 496 nests on the beach, of which 437 had at least one specimen of *O. suberosus* (larvae/adult). They documented significant predation by this beetle, which invaded nests and damaged 9108 out of 14,231 eggs, representing approximately 64% of the eggs. This emphasises the substantial impact of this invasive species on sea turtle reproduction. Furthermore, *O. suberosus* has also invaded nests of *L. olivacea* and other sea turtle species, highlighting a widespread threat (Baena et al. 2015; Cortez et al. 2017).

The temporal availability of turtle eggs significantly influences the abundance and reproductive phenology of *O. suberosus* (Baena et al. 2020). The beetles thrive particularly in areas rich in decomposing turtle eggs, which serve as essential food and nidification sources. The abundance and maturation of female beetles are closely linked to older nests containing decomposing eggs rather than fresh ones (Baena et al. 2020). This suggests that the population dynamics of *O. suberosus* rely more on the availability of decomposing material than on direct predation of fresh eggs, indicating their role as facultative predators. As an opportunistic predator, further research is needed to clarify its role in nest predation. If the beetle predated fresh nests, measures such as off-site incubation and beetle control on beaches are necessary. Conversely, if it targets nests after some eggs decompose, strategies like handling rotten eggs and separating healthy ones, or combined approaches, would be required. Understanding *O. suberosus* behaviour is essential for effectively conserving vulnerable sea turtle populations. This range of interactions highlights the importance of our projections for guiding targeted conservation strategies to manage the influence of *O. suberosus* on vulnerable turtle populations across coastal zones worldwide.

#### 4.3 | Conservation in the Face of Climate Change and Invasive Threats to Olive Ridley

The persistent overlap in habitat and the predatory behaviours of *O. suberosus* necessitate targeted conservation strategies to address habitat preservation and mitigate invasive species threats. Our analysis categorises areas into two groups, each deserving attention for distinct reasons. Non-overlapping areas (green coastal zones in Figure 4): These regions are critical for preserving *L. olivacea* habitats without the added threat of predation by *O. suberosus*, representing key opportunities for conservation

focus. An exception is southern Europe and northern Africa; despite environmentally suitable areas, these regions require less attention regarding potential interactions between the two species due to the lack of current records for *L. olivacea*, although records for the invasive *O. suberosus* already exist.

In contrast, areas of persistent overlap (red coastal zones in Figure 4) demand heightened monitoring to assess potential risks, particularly in high-priority nesting zones. While current evidence suggests that some overlapping regions do not experience predation, future climate scenarios underscore the importance of targeted management to mitigate potential predation risks. This dual approach, which focuses on preserving turtle habitats in non-overlapping areas while mitigating predation risks in overlapping zones, forms the basis for effective conservation strategies under current and future climate scenarios. Therefore, *L. olivacea* conservation strategies must also consider the various invasion pathways and mechanisms of *O. suberosus* spread, including release, escape, contaminant, stowaway, corridor and unaided, which present distinct challenges for management and regulation (Hulme et al. 2008; Hulme 2021; Seebens et al. 2021). Given the significant impact of the beetle on the hatch rates, it is critical to investigate these dynamics through comprehensive field studies to inform conservation efforts better and mitigate the adverse effects on turtle populations in these shared regions.

The observed contraction and expansion trends in habitat suitability of *O. suberosus* across different scenarios suggest a shift towards higher latitudes and altitudes due to climate change. The SSP5–8.5 scenario, with higher greenhouse gas emissions, accentuates these changes, emphasising the significant impact of environmental factors on biodiversity. These findings indicate the ecological flexibility of *O. suberosus* in response to climate change, potentially enabling range expansion and increased survival in certain areas despite the overall habitat contraction. Our model results offer a roadmap to optimise the allocation of management resources, enhancing the efficacy of control measures to manage *O. suberosus* in the invasive range. For example, conservation and management strategies will differ between beaches already colonised by *O. suberosus* and beaches not yet colonised but within the predicted area of *O. suberosus* expansion.

Future studies should also explore the relationship between *O. suberosus* and *L. olivacea* and other potential turtles, exploring ecological dynamics, habitat preferences and interactions in hosts with different geographical and climatic contexts. While there are no records of egg predation on freshwater turtles by *O. suberosus*, its generalist predation behaviour on vertebrate eggs should not be overlooked. This adaptability raises concerns about potentially including other species, such as birds and reptiles, in its predatory range. Thus, management plans should consider the broader ecological implications of *O. suberosus* predation, extending vigilance beyond marine turtles to other taxa that could be at risk. This underscores the need for further research in areas of overlap beyond the Americas, especially in newly invaded continents. Expanding efforts to document interactions in these understudied regions is essential for understanding the ecological dynamics of invasions and developing effective conservation strategies. Such efforts, supported

by additional studies, will strengthen our capacity to prevent the spread of invasive species and advance global initiatives to understand and manage these ecological challenges better.

### Author Contributions

All authors contributed to the study conception and design. Material preparation, software development, data collection and analysis were performed by Janderson Batista Rodrigues Alencar. The first draft of the manuscript was written by Janderson Batista Rodrigues Alencar, César Murilo de Albuquerque Correa and Vinicius da Costa-Silva. All authors commented on previous versions of the manuscript. Validation, review and editing were performed by all authors. Supervision was provided by Fabrício Beggiano Baccaro and Catherine Sole. Data curation was handled by Janderson Batista Rodrigues Alencar and Vinicius da Costa-Silva. All authors read and approved the final manuscript.

### Acknowledgements

J.B.R.A. expresses its gratitude for the support provided by the Programa Institucional de Pós-Doutorado (Edital PIPD-1/2024), a postdoctoral fellowship (process nº 88887.024522/2024-00), and the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brazil (CAPES) (PROEX n. 0742/2020), as well as the Fundação de Amparo à Pesquisa do Estado do Amazonas (FAPEAM) (PAPAC n. 005/2019). This work also received logistical support from the Instituto Nacional de Pesquisas da Amazônia (INPA). V.d.C.-S. thanks the Post-Doctoral Fellowship Programme from the University of Pretoria. F.B.B. is continuously supported by CNPq grant #312878/2023-0.

### Conflicts of Interest

The authors declare no conflicts of interest.

### Data Availability Statement

Data generated or analysed during this study are provided in full within the published article and its [Supporting Information](#).

### References

- Abreu-Grobois, A., and P. Plotkin. 2008. The IUCN Red List of Threatened Species: *Lepidochelys olivacea*. 1–28.
- Aguiar, L. M. S., M. J. R. Pereira, M. Zortéa, and R. B. Machado. 2020. “Where Are the Bats? An Environmental Complementarity Analysis in a Megadiverse Country.” *Diversity and Distributions* 26: 1510–1522.
- Ahmad, R., A. A. Khuroo, B. Charles, M. Hamid, I. Rashid, and N. A. Aravind. 2019. “Global Distribution Modelling, Invasion Risk Assessment and Niche Dynamics of *Leucanthemum vulgare* (Ox-Eye Daisy) Under Climate Change.” *Scientific Reports* 9: 11395.
- Alencar, J. B. R., M. Bento, T. Yoshida, C. R. V. da Fonseca, and F. Beggiano Baccaro. 2022. “Modeling Potential Invasion of Stored-Product Pest *Cryptamorpha desjardinsii* (Guérin-Méneville, 1844) (Coleoptera: Silvanidae) With Emphasis on Newly Recorded Areas.” *Journal of Asia-Pacific Entomology* 25: 101891.
- Alencar, J. B. R., A. Clé Porto, D. Dos Anjos Souza, and D. R. R. Fernandes. 2024. “Global Predictive Invasion Modeling of Asian Wood-Wasp *Eriotremex formosanus* (Matsumura) (Hymenoptera: Siricidae): Insights Gained From *Pinus* L. Occurrences, and the First Record of This Invasive Species in South America.” *Biological Invasions* 26: 3257–3269.
- Alencar, J. B. R., A. Sampaio, and C. R. V. da Fonseca. 2024. “Ecological Niche Modeling of Two *Microthea* Stål, 1860 Species (Coleoptera: Chrysomelidae: Chrysomelinae) in the Americas: Insights From

- Brassicaceae Occurrence." *International Journal of Biometeorology* 68: 891–898.
- Alexander, J. M., and P. J. Edwards. 2010. "Limits to the Niche and Range Margins of Alien Species." *Oikos* 119: 1377–1386.
- Allouche, O., A. Tsoar, and R. Kadmon. 2006. "Assessing the Accuracy of Species Distribution Models: Prevalence, Kappa and the True Skill Statistic (TSS)." *Journal of Applied Ecology* 43: 1223–1232.
- Andersen, M. C., H. Adams, B. Hope, and M. Powell. 2004. "Risk Analysis for Invasive Species: General Framework and Research Needs." *Risk Analysis* 24: 893–900.
- Antunes-Carvalho, C., and C. Lopes-Andrade. 2013. "Two Invaders Instead of One: The True Identity of Species Under the Name *Ceracis cucullatus* (Coleoptera: Ciidae)." *PLoS One* O. Terenius, Ed. 8: e72319.
- Araujo, M., and M. New. 2007. "Ensemble Forecasting of Species Distributions." *Trends in Ecology & Evolution* 22: 42–47.
- Baena, M. L., C. H. Crespo, M. S. Carrillo, and F. Escobar. 2020. "Spatiotemporal Variation in *Lepidochelys olivacea* sea Turtle Nests and Their Influence on the Abundance and Reproductive Phenology of the Sapro-Necrophagous Beetle *Omorgus suberosus*." *Science of Nature* 107: 47.
- Baena, M. L., F. Escobar, G. Halffter, and J. H. García-Chávez. 2015. "Distribution and Feeding Behavior of *Omorgus suberosus* (Coleoptera: Trogidae) in *Lepidochelys olivacea* Turtle Nests." *PLoS One* J. L. Rummer, Ed. 10: e0139538.
- Balmford, A., and K. J. Gaston. 1999. "Why Biodiversity Surveys Are Good Value." *Nature* 398: 204–205.
- Barve, N., V. Barve, A. Jiménez-Valverde, et al. 2011. "The Crucial Role of the Accessible Area in Ecological Niche Modeling and Species Distribution Modeling." *Ecological Modelling* 222: 1810–1819.
- Beirne, B. P. 1970. "Effects of Precipitation on Crop Insects." *Canadian Entomologist* 102: 1360–1373.
- Bliss, C., I. J. Visseren-Hamakers, and D. Liefferink. 2023. "Most (Un) wanted: Explaining Emerging Relationships Between "Invasive Alien" Species and Animal Governance." *Glob Environ Polit* 23: 26–51.
- Butt, N., S. Whiting, and K. Dethmers. 2016. "Identifying Future Sea Turtle Conservation Areas Under Climate Change." *Biological Conservation* 204: 189–196.
- Cáceres-Farias, L., E. Reséndiz, J. Espinoza, H. Fernández-Sanz, and A. Alfaro-Núñez. 2022. "Threats and Vulnerabilities for the Globally Distributed Olive Ridley (*Lepidochelys olivacea*) Sea Turtle: A Historical and Current Status Evaluation." *Animals* 12: 1837.
- Cervantes-Hernández, P., E. Pérez-Vives, and M. A. Gómez-Ponce. 2017. "Arribada y Explotación de la Tortuga Golfina en la Playa Escobilla, Oaxaca, México." *Revista Ciencias Marinas y Costeras* 9: 91.
- Chen, X., N. B. Dimitrov, and L. A. Meyers. 2019. "Uncertainty Analysis of Species Distribution Models." *PLoS One* 14: e0214190.
- Correa, C. M. A., A. Puker, V. Korasaki, and K. R. Ferreira. 2013. "*Omorgus suberosus* and *Polynoncus bifurcatus* (Coleoptera: Scarabaeoidea: Trogidae) in Exotic and Native Environments of Brazil." *Zoologia (Curitiba)* 30: 238–241.
- Cortez, V., J. R. Verdú, A. J. Ortiz, and G. Halffter. 2017. "Identification and Evaluation of Semiochemicals for the Biological Control of the Beetle *Omorgus suberosus* (F.) (Coleoptera: Trogidae), a Facultative Predator of Eggs of the Sea Turtle *Lepidochelys olivacea* (Eschscholtz)." *PLoS One* 12: e0172015.
- Cosentino, F., E. C. J. Seamark, V. Van Cakenberghe, and L. Maiorano. 2023. "Not Only Climate: The Importance of Biotic Interactions in Shaping Species Distributions at Macro Scales." *Ecology and Evolution* 13: e9855.
- Costa-Silva, V., W. P. Strümpher, and F. Z. Vaz-de-Mello. 2021. "Review of the Brazilian Species of *Omorgus* Erichson, 1847 (Coleoptera: Trogidae: Omorginae)." *Journal of Natural History* 54: 1993–2024.
- Cruz, P. V., J. B. R. Alencar, M. N. Cardoso, and F. B. Baccaro. 2023. "Predicting the South American Invasion Pathways of the Mayfly *Cloeon dipterum* Linnaeus 1761 (Ephemeroptera: Baetidae) Using Species Distribution Models." *Insect Conservation and Diversity* 16: 521–530.
- de Andrade, A. F. A., S. J. E. Velazco, and P. De Marco Júnior. 2020. "ENMTML: An R Package for a Straightforward Construction of Complex Ecological Niche Models." *Environmental Modelling & Software* 125: 104615.
- de Araújo, C. B., L. O. Marcondes-Machado, and G. C. Costa. 2014. "The Importance of Biotic Interactions in Species Distribution Models: A Test of the Eltonian Noise Hypothesis Using Parrots." *Journal of Biogeography* 41: 513–523.
- de Boer, M. N. 2010. "Cetacean Distribution and Relative Abundance in Offshore Gabonese Waters." *Journal of the Marine Biological Association of the United Kingdom* 90: 1613–1621.
- Diagne, C., B. Leroy, A.-C. Vaissière, et al. 2021. "Author Correction: High and Rising Economic Costs of Biological Invasions Worldwide." *Nature* 608: E35.
- Elith, J., M. Kearney, and S. Phillips. 2010. "The Art of Modelling Range-Shifting Species." *Methods in Ecology and Evolution* 1: 330–342.
- Engler, R., A. Guisan, and L. Rechsteiner. 2004. "An Improved Approach for Predicting the Distribution of Rare and Endangered Species From Occurrence and Pseudo-Absence Data." *Journal of Applied Ecology* 41: 263–274.
- Fick, S. E., and R. J. Hijmans. 2017. "WorldClim 2: New 1-Km Spatial Resolution Climate Surfaces for Global Land Areas." *International Journal of Climatology* 37: 4302–4315.
- Fielding, A. h., and J. F. Bell. 1997. "A Review of Methods for the Assessment of Prediction Errors in Conservation Presence/Absence Models." *Environmental Conservation* 24: 38–49.
- Fourcade, Y., J. O. Engler, D. Rödder, and J. Secondi. 2014. "Mapping Species Distributions With MAXENT Using a Geographically Biased Sample of Presence Data: A Performance Assessment of Methods for Correcting Sampling Bias." *PLoS One* J. F. Valentine, Ed. 9: e97122.
- Fuentes, M. M. P. B., M. Hamann, and C. J. Limpus. 2010. "Past, Current and Future Thermal Profiles of Green Turtle Nesting Grounds: Implications From Climate Change." *Journal of Experimental Marine Biology and Ecology* 383: 56–64.
- GBIF. 2024a. *Lepidochelys olivacea* (Eschscholtz, 1829) occurrences [WWW Document]. GBIF.org. <https://doi.org/10.15468/dl.wf8cbm>.
- GBIF. 2024b. *Omorgus suberosus* (Fabricius, 1775) occurrences. GBIF.org. <https://doi.org/10.15468/dl.xcfz9n>.
- González-Salazar, C., C. R. Stephens, and P. A. Marquet. 2013. "Comparing the Relative Contributions of Biotic and Abiotic Factors as Mediators of Species' Distributions." *Ecological Modelling* 248: 57–70.
- Hijmans, R. J., S. Phillips, J. Leathwick, et al. 2017. "dismo: Species Distribution Modeling." R Package Version 1.1-4. Cran 55.
- Hill, J. L., M. Grisnik, R. J. Hanscom, J. Sukumaran, T. E. Higham, and R. W. Clark. 2024. "The Past, Present, and Future of Predator–Prey Interactions in a Warming World: Using Species Distribution Modeling to Forecast Ectotherm–Endotherm Niche Overlap." *Ecology and Evolution* 14: e11067.
- Hodkinson, I. D. 2005. "Terrestrial Insects Along Elevation Gradients: Species and Community Responses to Altitude." *Biological Reviews* 80: 489–513.
- Hortal, J., F. de Bello, J. A. F. Diniz-Filho, T. M. Lewinsohn, J. M. Lobo, and R. J. Ladle. 2015. "Seven Shortfalls That Beset Large-Scale Knowledge of Biodiversity." *Annual Review of Ecology, Evolution, and Systematics* 46: 523–549.

- Huchet, J. B., and V. da Costa-Silva. 2018. "A New Species of *Polynoncus* Burmeister, 1876 From Brazil (Coleoptera: Trogidae)." *Zootaxa* 4524: 553–566.
- Hulme, P. E. 2021. "Unwelcome Exchange: International Trade as a Direct and Indirect Driver of Biological Invasions Worldwide." *One Earth* 4: 666–679.
- Hulme, P. E., S. Bacher, M. Kenis, et al. 2008. "Grasping at the Routes of Biological Invasions: A Framework for Integrating Pathways Into Policy." *Journal of Applied Ecology* 45: 403–414.
- Hughes, J., and A. P. Vogler. 2006. "Gene Expression in the Gut of Keratin-Feeding Clothes Moths (*Tineola*) and Keratin Beetles (*Trox*) Revealed by Subtracted cDNA Libraries." *Insect Biochemistry and Molecular Biology* 36: 584–592.
- Jiménez-Valverde, A., and J. M. Lobo. 2007. "Threshold Criteria for Conversion of Probability of Species Presence to Either-or Presence-Absence." *Acta Oecologica* 31: 361–369.
- Khalig, A., M. Javed, M. Sagheer, M. Sohail, M. Sohail, and M. Sagheer. 2014. "Environmental Effects on Insects and Their Population Dynamics." *Journal of Entomology and Zoology Studies* 2: 1–7.
- Kishimoto-Yamada, K., and T. Itioka. 2015. "How Much Have We Learned About Seasonality in Tropical Insect Abundance Since Wolda (1988)?" *Entomological Science* 18: 407–419.
- Leroy, B., R. Delsol, B. Hugué, et al. 2018. "Without Quality Presence-Absence Data, Discrimination Metrics Such as TSS Can Be Misleading Measures of Model Performance." *Journal of Biogeography* 45: 1994–2002.
- Li, Y., X. Liu, X. Li, B. Petitpierre, and A. Guisan. 2014. "Residence Time, Expansion Toward the Equator in the Invaded Range and Native Range Size Matter to Climatic Niche Shifts in Non-Native Species." *Global Ecology and Biogeography* 23: 1094–1104.
- Lomolino, M. V. 2004. "Conservation Biogeography." In *Frontiers of Biogeography: New Directions in the Geography of Nature*, edited by M. V. Lomolino and L. R. Heaney, 293–296. Sinauer Associates.
- Mammola, S., J. Pétilion, A. Hacala, et al. 2021. "Challenges and Opportunities of Species Distribution Modelling of Terrestrial Arthropod Predators." In *Diversity and Distributions*, 2596–2614. John Wiley and Sons Inc.
- Marquardt, D. W. 1970. "Generalized Inverses, Ridge Regression, Biased Linear Estimation, and Nonlinear Estimation." *Technometrics* 12: 591–612.
- McCullagh, P., and J. A. Nelder. 1989. *Generalized Linear Models*. Applied Statistics. Vol. 37. Springer US.
- Mellanby, K. 1939. "Low Temperature and Insect Activity." *Proceedings of the Royal Society of London - Series B: Biological Sciences* 127: 473–487.
- Orrell, T. 2017. *NMNH Extant Specimen Records*. National Museum of Natural History, Smithsonian Institution.
- Owens, D., M. Hamann, and C. Limpus. 2002. "Reproductive Cycles of Males and Females." In *The Biology of Sea Turtles*, vol. 2, 1st ed., 135–161. CRC PRESS.
- Owens, H. L., L. P. Campbell, L. L. Dornak, et al. 2013. "Constraints on Interpretation of Ecological Niche Models by Limited Environmental Ranges on Calibration Areas." *Ecological Modelling* 263: 10–18.
- Patrício, A. R., M. R. Varela, C. Barbosa, et al. 2019. "Climate Change Resilience of a Globally Important Sea Turtle Nesting Population." *Global Change Biology* 25: 522–535.
- Peterson, A. T., J. Soberón, R. G. Pearson, et al. 2011. *Ecological Niches and Geographic Distributions*. Vol. 1. 1st ed. Princeton University Press.
- Peterson, A. T., and J. M. Soberón. 2012. "Species Distribution Modeling and Ecological Niche Modeling: Getting the Concepts Right." *Brazilian Journal of Nature Conservation* 10: 102–107.
- Petitpierre, B., O. Broennimann, C. Kueffer, C. Daehler, and A. Guisan. 2017. "Selecting Predictors to Maximize the Transferability of Species Distribution Models: Lessons From Cross-Continental Plant Invasions." *Global Ecology and Biogeography* 26: 275–287.
- Phillips, S. J. 2017. "maxnet: Fitting 'Maxent' Species Distribution Models With 'glmnet'." R Package: Version 0.1.
- Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. "Maximum Entropy Modeling of Species Geographic Distributions." *Ecological Modelling* 190: 231–259.
- Pimenta, M., A. F. A. de Andrade, F. H. S. Fernandes, et al. 2022. "One Size Does Not Fit all: Priority Areas for Real World Problems." *Ecological Modelling* 470: 110013.
- Régnière, J., J. Powell, B. Bentz, and V. Nealis. 2012. "Effects of Temperature on Development, Survival and Reproduction of Insects: Experimental Design, Data Analysis and Modeling." *Journal of Insect Physiology* 58: 634–647.
- Richardson, D. M., and M. Rejmánek. 2011. "Trees and Shrubs as Invasive Alien Species - a Global Review." *Diversity and Distributions* 17: 788–809.
- Roberts, P., and B. A. Stewart. 2018. "Defining the 'Generalist Specialist' Niche for Pleistocene *Homo sapiens*." *Nature Human Behaviour* 2: 542–550.
- Roeder, K. A., J. Bujan, K. M. de Beurs, M. D. Weiser, and M. Kaspari. 2021. "Thermal Traits Predict the Winners and Losers Under Climate Change: An Example From North American Ant Communities." *Ecosphere* 12: 1–12.
- Roffey, J. 1958. "Observations on the Biology of *Trox procerus* Har. (Coleoptera, Trogidae), a Predator of Eggs of the Desert Locust, *Schistocerca gregaria* (Forsk.)." *Bulletin of Entomological Research* 49: 449–465.
- Rosano Hernández, M. C., and C. Deloya. 2002. "Interacción Entre Trogidos (Coleoptera: Trogidae) y Tortugas Marinas (Reptilia: Cheloniidae) en el Pacífico Mexicano." *Acta Zoologica Mexicana* 87: 29–46.
- Scholtz, C. H., and S. Caveney. 1992. "Daily Biphasic Behaviour in Keratin-Feeding Desert Trogid Beetles in Relation to Climate." *Ecological Entomology* 17: 155–159.
- Schowalter, T. D. 2016. *Insect Ecology: An Ecosystem Approach*. Vol. 1. 4th ed. Elsevier.
- Seebens, H., S. Bacher, T. M. Blackburn, et al. 2021. "Projecting the Continental Accumulation of Alien Species Through to 2050." *Global Change Biology* 27: 970–982.
- Septiadi, R., D. G. Bengen, and N. M. N. Natih. 2018. "Typology of Olive Ridley Turtle (*Lepidochelys olivacea*, Linn 1958) Nesting Habitat in Kuta Beach, Serangan Beach and Saba Beach, Bali Province." *IOP Conference Series: Earth and Environmental Science* 176: 012024.
- Sillero, N., and A. M. Barbosa. 2021. "Common Mistakes in Ecological Niche Models." *International Journal of Geographical Information Science* 35: 213–226.
- Soberón, J. 2007. "Grinnellian and Eltonian Niches and Geographic Distributions of Species." *Ecology Letters* 10: 1115–1123.
- Thuiller, W., M. Guéguen, J. Renaud, D. N. Karger, and N. E. Zimmermann. 2019. "Uncertainty in Ensembles of Global Biodiversity Scenarios." *Nature Communications* 10: 1–9.
- Velasco, S. J. E., F. Villalobos, F. Galvão, and P. De Marco Júnior. 2019. "A Dark Scenario for Cerrado Plant Species: Effects of Future Climate, Land Use and Protected Areas Ineffectiveness." *Diversity and Distributions* 25: 660–673.
- Wolda, H. 1978. "Seasonal Fluctuations in Rainfall, Food and Abundance of Tropical Insects." *Journal of Animal Ecology* 47: 369.

Zhu, G., G. Liu, W. Bu, and Y. Gao. 2013. "Ecological Niche Modeling and Its Applications in Biodiversity Conservation." *Biodiversity Science* 21: 90–98.

### **Supporting Information**

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