



Global projections of oceanic climate change on marine bioluminescent species distributions: Regional hotspots and climate refugia

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ABSTRACT

Bioluminescent organisms play critical roles in marine ecosystems, contributing to nutrient cycling, predator-prey interactions, and biodiversity maintenance. These species are also sensitive indicators of environmental change, making them valuable for studying climate impacts on ocean health. This study aimed to model the present and future distributions of 17 bioluminescent species under two climate scenarios (SSP1–2.6 and SSP5–8.5) for 2050 and 2100. Using species distribution models (SDMs) and machine learning approaches, we identified key environmental factors influencing species ranges, including light penetration (KDPAR), temperature, and salinity. Results showed heterogeneous responses: some species expanded their distributions, exploiting new habitats, while others contracted or shifted geographically, highlighting vulnerabilities to changing oceanic conditions. Key refugia were identified, specifically highlight regional patterns of management relevance, including regions along the Brazilian coast, the waters between Japan and China, and the Pacific off the USA coast, which offer critical opportunities for conservation. The study also addresses uncertainties in SDMs and emphasizes the importance of filling data gaps through genetic analyses and citizen science initiatives. Identified five regional climate refugia and species-rich biodiversity hotspots provide a spatial framework for future marine conservation, biodiversity monitoring, and adaptive management planning.

1. Introduction

Bioluminescence is the remarkable ability of certain organisms to emit cold light through a biochemical reaction involving a light-emitting molecule, luciferin, and an enzyme, luciferase (Hastings et al., 1995). While some terrestrial organisms exhibit bioluminescent phenomena, it is in the deep-sea (>200 m), sunless ocean regions where bioluminescence is most prevalent, encompassing a wide array of organisms such as bacteria, dinoflagellates, cnidarians, and fish (Haddock et al., 2017). This ability serves essential ecological functions, acting as a defense mechanism, a tool for predation, and a means of communication, vital for survival and interaction within these unique ecosystems (Haddock et al., 2010). Bioluminescent species play crucial ecological roles in marine ecosystems, with light emission involved in intra- and inter-species communication, mate attraction, camouflage (counter-illumination), and predator deterrence. These functions are finely regulated by physiological and environmental cues, making bioluminescence a highly sensitive trait (Haddock et al., 2010; Widder, 2010).

Because light production depends on specific metabolic pathways and ecological interactions, disruptions in environmental conditions, such as temperature changes, oxygen depletion, pollution, or acidification, can directly impact the presence, intensity, or timing of bioluminescent displays (Martini and Haddock, 2017). Therefore, alterations in bioluminescence patterns may serve as visible proxies for underlying ecological imbalances. In this context, the light-producing capabilities of these species position them as natural indicators of environmental health, offering real-time, non-invasive insights into the stability or degradation of oceanic ecosystems (Widder, 2010).

Bioluminescent species offer unique advantages as indicators of environmental change beyond their light-emitting capabilities. Their physiological reliance on highly specific abiotic factors, such as oxygen concentration, temperature, and nutrient availability, makes them particularly sensitive to disturbances in marine ecosystems (Amara et al., 2024; Parmar et al., 2016). Recent reviews have also highlighted the growing range of scientific and monitoring applications of marine bioluminescence, including its use in flow tracers, productivity

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assessments, and fish school estimates (Letendre et al., 2024b). Furthermore, bioluminescence often depends on complex symbiotic relationships with microbial communities or on metabolic processes highly susceptible to environmental stressors (Haddock et al., 2010; Widder 2010). For instance, variations in light production intensity or frequency have been associated with hypoxia, acidification, and temperature anomalies in both pelagic and benthic habitats (Doney et al., 2009; Brierley and Kingsford, 2009). This sensitivity allows bioluminescent organisms to act as early-warning systems for ecological disruptions that may not be immediately evident through traditional biodiversity surveys (Syed and Anderson, 2021). Additionally, because bioluminescent displays are readily detectable through remote sensing and optical surveys, these organisms offer practical advantages for large-scale monitoring efforts (Widder 2010).

In addition to their ecological importance, bioluminescent organisms play crucial roles in the marine food chain, especially in the ocean's deeper regions where sunlight is absent. These organisms, including bioluminescent bacteria and zooplankton, are key contributors to carbon and nitrogen cycles (Brierley and Kingsford, 2009). Their survival and functionality are integral not only to marine biodiversity but also to maintaining global biogeochemical cycles (Haddock et al., 2010; Brierley and Kingsford, 2009). Furthermore, as sensitive bioindicators, their responses to changing environmental conditions could provide valuable data on oceanic health and serve as early warning systems for broader climate impacts on marine life (Widder 2010; Doney et al., 2009), offering insight into the adaptive behaviors of other marine species. Marine bioluminescent organisms also have substantial biotechnological potential; for example, bacterial bioluminescence forms the basis for bio-sensors in ecotoxicology, gene expression studies, and cellular health assays (Syed and Anderson, 2021).

Despite their value, marine bioluminescent species are increasingly threatened by environmental changes driven by climate change, such as rising ocean temperatures, acidification, and oxygen depletion (Brierley and Kingsford, 2009; Doney et al., 2009). These conditions, often with irreversible consequences, disrupt marine habitats and impact bioluminescent organisms directly, altering their geographic distribution and affecting critical behaviors like mating and predation (Brierley and Kingsford, 2009; Oschlies, 2019). As climate change reshapes ocean ecosystems, bioluminescent organisms' roles as indicators of ocean health and their interactions with other marine species may also shift, potentially reducing their resilience and survival and affecting ecosystem stability.

To anticipate changes and support conservation and management strategies, predictive modeling offers a powerful tool to project future scenarios and assess species distributions under climate change. Species distribution modeling (SDM) has proven to be an important tool for identifying regions that are at risk for vulnerable marine organisms and for guiding the development of effective conservation strategies (Danovaro et al., 2017; Melo-Merino et al., 2020). By modeling the impacts of climate change on the distribution of bioluminescent species, conservation strategies can be better informed to guide targeted actions, including the establishment of marine protected areas and the regulation of human activities in critical regions (Hattab et al., 2014; Karp et al., 2025). Species distribution models are increasingly recognized as key tools for supporting fisheries management, conservation planning, and marine spatial planning under climate change scenarios (Karp et al., 2025).

To face these challenges, this study aims to evaluate the potential of marine bioluminescent species as indicators of regional climate refugia, climate impacts, and to explore their role in ocean conservation efforts. This work addresses the following research question: (1) How will climate change impact the distribution of marine bioluminescent species? and (2) Can marine bioluminescent species provide critical insights for climate change monitoring and regional ecosystem management and preservation? To answer this, we modeled the present and future distribution of seventeen bioluminescent marine species, from distinct

phyla, under projected oceanic climate changes. We hypothesize that these species will experience significant range shifts due to climate-induced changes in ocean conditions, potentially compromising their ecological functions and survival in affected regions. Here, we define 'future periods' as the mid-century (2050) and end-century (2100) projections under two Shared Socioeconomic Pathways (SSP1–2.6 and SSP5–8.5) following CMIP6 climate trajectories. These scenarios encompass moderate and extreme greenhouse gas emission pathways, respectively, providing a comparative framework for assessing species vulnerability and potential refugia.

2. Material and methods

2.1. Occurrence data

Using data from the GBIF (Global Biodiversity Information Facility) and OBIS (Ocean Biogeographic Information System) databases, occurrence points were identified for 17 selected bioluminescent species. Occurrence records were not temporally filtered to match the environmental baseline period (2000–2014), in order to maximize spatial coverage and represent the full known distribution of each species. The 17 selected species represent a broad taxonomic and ecological diversity (Table 1), including both planktonic and benthic organisms, with distributions across pelagic, epipelagic, and deep-sea environments. These species encompass a range of ecological strategies: from sessile filter feeders (e.g., *Clytia hemisphaerica*), to active predators (e.g., *Etmopterus lucifer*), gelatinous zooplankton with opportunistic traits (e.g., *Mnemiopsis leidyi*), and symbiotic light-emitting organisms (e.g., *Vampyroteuthis infernalis*). Many of them are mobile and capable of wide dispersal, while others are associated with specific substrates or depth zones. This heterogeneity reflects the functional diversity of marine bioluminescent organisms and supports the ecological relevance of modeling their projected distributions under climate change scenarios. A detailed summary of ecological traits for all species is provided in Table 1.

2.2. Georeferenced occurrence data and environmental layers

The selection of these species for the SDM study was based on the inclusion of organisms from different phyla, ensuring the presence of a minimum number of occurrence points required for this analysis, and having baseline knowledge of their habitat, behavior, and ecology of these organisms. To eliminate records from impossible/improbable regions and duplicates within the datasets, we employed the R packages *scrubr* (Chamberlain, 2016), *CoordinateCleaner* (Zizka et al., 2019), and *spThin* (Aiello-Lammens et al., 2015). Then, to minimize spatial autocorrelation, we (i) enforced one record per native 5' grid cell (5 arc-minutes) and (ii) performed spatial thinning with *spThin* using a 10 km minimum distance (matching the grid scale at low latitudes). We verified that no grid cell retained > 1 occurrence per species after thinning.

Bioclimatic variables, from surface and benthic layers, at a 5 arc-minute resolution were obtained from the Bio-ORACLE v3 database (Assis et al., 2024), ensuring methodological compatibility (offers stable and reliable environmental layers) and facilitating comparison with previous studies (integrates more easily with established modeling pipelines). These variables represent climatic conditions for the period between 2000 and 2014. The extent of accessible area ('M') was constrained to oceanic regions where occurrences were recorded within 10° latitudinal and longitudinal buffers around known points, preventing model extrapolation into unoccupied ocean basins. All maps were generated at a 5' resolution, with predictions cropped to these biologically accessible extents. To address multicollinearity, which can compromise the reliability and generalizability of species distribution models (SDMs), we conducted a variance inflation factor (VIF) analysis using the *olsrr* package (Heballi and Heballi, 2017) in R. Predictors with

Table 1

Number of occurrence records for the 17 bioluminescent marine species analyzed in this study and their habitat, categorized by their respective phyla. These records were compiled from global biodiversity databases to model present and future species distributions under different climate scenarios.

Phylum	Species	number of occurrences recorded	Habitat	Depth Zone	Mobility	Ecological Role
Annelida	<i>Alitta virens</i> M Sars, 1935	1566	Benthic	Intertidal to shallow subtidal	Mobile	Burrowing detritivore
Myzozoa	<i>Karenia brevis</i> , C.C.Davis) G.Hansen & Ø.Moestrup, 2000	44,514	Pelagic	Epipelagic zone	Planktonic	Primary producer
Arthropoda	<i>Euphausia superba</i> Dana, 1850	85,518	Pelagic	Epipelagic to mesopelagic	Mobile	Primary consumer
Arthropoda	<i>Oplophorus gracilirostris</i> A Milnes-Edwards, 1881	474	Pelagic	Mesopelagic to bathypelagic	Mobile	Planktivore
Chordata	<i>Etmopterus lucifer</i> Jordan & Snyder, 1902	5771	Demersal	Deep sea	Mobile	Mesopredator
Chordata	<i>Etmopterus spinax</i> Linnaeus, 1758	1455	Demersal	Bathyal	Mobile	Predator
Chordata	<i>Pyrosoma atlanticum</i> Péron, 1804	3474	Pelagic	Epipelagic to mesopelagic	Colonial/mobile/planktonic	Filter feeder
Cnidaria	<i>Clytia hemisphaerica</i> Linnaeus, 1767	2194	Pelagic	Coastal/epipelagic	Planktonic	Predator
Cnidaria	<i>Obelia bidentata</i> Clark, 1875	2658	Benthic/Pelagic	Shallow coastal	Sessile (polyp), planktonic (medusa)	Planktivore
Ctenophora	<i>Pleurobrachia pileus</i> O. F. Müller, 1776	3045	Pelagic	Epipelagic	Mobile	Predator of zooplankton
Ctenophora	<i>Mnemiopsis leidyi</i> A. Agassiz, 1865	2943	Pelagic	Epipelagic	Mobile	Opportunistic predator
Echinodermata	<i>Pseudocolochirus violaceus</i> Théel, 1886	358	Benthic	Shallow subtidal	Sessile to low mobility	Planktivore
Echinodermata	<i>Synapta maculata</i> Chamisso & Eysenhardt, 1821	442	Benthic	Shallow coral reefs	Mobile	Detritivore
Mollusca	<i>Octopoteuthis deletron</i> R.E. Young, 1972	235	Pelagic	Mesopelagic to bathypelagic	Mobile	Predator
Mollusca	<i>Vampyroteuthis infernalis</i> Chun, 1903	706	Pelagic	Bathypelagic	Mobile	Detritivore
Myzozoa	<i>Gymnodinium lunula</i> F. Schütt 1895	1222	Planktonic	Epipelagic	Motile	Photosynthetic/mixotroph
Myzozoa	<i>Tripos furcatus</i> (Ehrenberg) F. Gómez, 2013	97,721	Planktonic	Epipelagic	Motile	Primary producer

high collinearity were excluded, retaining nine variables (Table 2).

Environmental variables used in present-day (2000–2014) modeling were also employed to forecast future climate scenarios for 2050 and 2100. After refining the variables, we modeled five scenarios for each species: i) current, ii) 2050 SSP1–2.6 ("Shared Socioeconomic Pathways"), iii) 2050 SSP5–8.5, iv) 2100 SSP1–2.6, and v) 2100 SSP5–8.5. These pathways enable assessing potential climate change impacts based on varying levels of atmospheric greenhouse gas concentrations and associated radiative forcing (Van Vuuren et al., 2011). We selected SSP1–2.6 and SSP5–8.5 as low- and high-emission scenarios to capture the range of potential future climate conditions. This approach is commonly used in species distribution modeling to assess ecological responses under contrasting climate trajectories (Melo-Merino et al., 2020). Although intermediate scenarios may represent more likely pathways, using extreme scenarios provides a robust envelope of potential outcomes, particularly relevant for identifying conservation priorities and climate refugia. Future environmental projections (SSP1–2.6 and SSP5–8.5) were obtained from the Bio-ORACLE v3 database, which is based on an ensemble of CMIP6 global climate models (GCMs). These ensemble layers represent averaged projections across multiple models,

Table 2

Environmental predictors used in this study, including Bio-ORACLE variable names and descriptions.

Variable code	Description	Layer
curvelltmax_ss	Maximum current velocity (sea surface)	Surface
curvelrange_bdmax	Range of current velocity (benthic)	Benthic
salinityrange_bdmin	Range of salinity (benthic)	Benthic
curvelmin_bdmean	Mean minimum current velocity (benthic)	Benthic
curvelrange_ss	Range of current velocity (sea surface)	Surface
salinityrange_ss	Range of salinity (sea surface)	Surface
curvelmin_ss	Minimum current velocity (sea surface)	Surface
salinitymean_bdmax	Maximum mean salinity (benthic)	Benthic
temprange_ss	Temperature range (sea surface)	Surface

reducing uncertainty associated with individual GCMs and providing robust estimates of future oceanographic conditions.

The occurrence data retrieved from GBIF and OBIS span records from 1950 to 2023, encompassing both fishery-dependent and independent observations, scientific expeditions, and environmental monitoring programs. These records represent the global distribution of species presence, with higher sampling effort in coastal and continental shelf regions compared to open-ocean and deep-sea environments. This uneven coverage was accounted for by spatial thinning procedures, ensuring balanced representation across ocean basins.

Although occurrence records span a broader temporal range (1950–2023), we used environmental data representing the period 2000–2014 as a proxy for present-day conditions. This approach is commonly adopted in large-scale SDM studies due to the limited availability of temporally matched environmental datasets. It assumes that species–environment relationships are relatively stable over time (niche conservatism), particularly for marine species with broad distributions (Peterson et al., 2011; Araújo and Peterson, 2012).

2.3. Species distribution modeling

We performed species distribution modeling (SDM) analyses for both present and future global scenarios to predict the potential distributions of bioluminescent species over time. To achieve this, we applied five modeling algorithms using presence and pseudo-absence data: generalized linear models (GLM; Nelder and Wedderburn, 1972), support vector machines (SVM; Cortes and Vapnik 1995), random forests (Breiman 2001), Bioclim (Nix 1986), and maximum entropy (MaxEnt; Phillips and Dudík, 2008), implemented through the *dismo* (Hijmans et al., 2017) and *caret* (Kuhn et al. 2020) packages in R. Species occurrence data were randomly split into two subsets, with 70% used for training and 30% for testing. For each species, models were calibrated using environmental variables for current conditions and projected to

future scenarios. Each model was replicated ten times to account for variation in training data partitioning. Model evaluation was performed using repeated random partitioning (70/30 split, 10 replicates), and overall robustness was further assessed using fivefold cross-validation. Continuous model outputs were converted to binary maps using species-specific thresholds that maximize the sum of sensitivity and specificity (Liu et al., 2013), and model performance was assessed using Area Under the Curve (AUC) and True Skill Statistic (TSS). Background points were randomly sampled within each species' accessible area ('M'), defined based on buffered occurrence records, following Barbet-Massin et al. (2012). For presence-absence algorithms (GLM, SVM, Random Forest, Bioclim), these points were randomly subsampled and treated as pseudo-absences, maintaining a 1:1 ratio with presence records to ensure balanced model calibration. For the presence-only algorithm (MaxEnt), the same set of sampled points was used as background, representing environmental availability within the accessible area. We acknowledge that, particularly in deep-sea environments, absence data may reflect limited sampling effort rather than true absence. To mitigate this, sampling was restricted to ecologically accessible areas and combined with spatial thinning procedures to reduce sampling bias. This combined strategy, restricting sampling to accessible areas, applying spatial thinning, and balancing pseudo-absences for presence-absence models, reduces sampling bias while improving model calibration. Model robustness was further evaluated using fivefold cross-validation. No manual hyperparameter tuning was performed, and default algorithm settings were used to ensure consistency and reproducibility across species. Rather than optimizing each model individually, which can increase the risk of overfitting in presence-only datasets, model robustness was addressed through cross-validation, ensemble modeling, and strict performance filtering (AUC \geq 0.8 and TSS \geq 0.7). This approach prioritizes generalizable patterns over model-specific optimization and is commonly adopted in large-scale comparative SDM frameworks. The ensemble modeling functionality provided by the *sdm* package (Naimi and Araújo, 2016) was employed to integrate the outputs from individual models into a unified projection. Binary maps for areal calculations and stacking used a species-specific threshold chosen by the maximum sensitivity + specificity (maxSSS) criterion (Liu et al., 2013). This avoids arbitrary cutoffs and reflects species-level detection/omission trade-offs. Final species distribution projections were generated using an ensemble approach that combined the results from the five models through a consensus method.

We used QGIS software v.3.2.3 (QGIS Development Team, 2018) to delineate suitable habitat areas in square kilometers (km²) and estimate changes in area extent across different scenarios and timeframes. Displacement of the centroid of each raster was also measured to assess spatial shifts over time, enabling quantification of changes in habitat size and geographic location of suitable areas.

2.4. Evaluation of changes in SDM across different scenarios

The rasters generated by the modeling were loaded into the R environment, and the species distribution scenarios (present and future) were analyzed. Binary maps used for model evaluation and general distribution estimates were derived using the maximum sensitivity plus specificity (maxSSS) threshold, following Liu et al. (2013). For spatial analyses focused on conservation prioritization and identification of stable refugia, we applied a more conservative threshold (\geq 0.95) to delineate core high-suitability areas. This approach intentionally emphasizes areas of highest model agreement and reduces the influence of marginal predictions, and therefore should not be interpreted as representing the full extent of species' potential distributions. The area of these pixels was calculated in square kilometers, converting degree measurements based on the raster resolution. With the areas for the present and future scenarios calculated, the change in area was determined, allowing for a comparison of species distribution expansion or

contraction. Additionally, the displacement of high-probability pixels between the present and future scenarios was calculated, identifying the predominant direction of shift.

2.5. Predictive occurrence analysis based on abiotic features

Species occurrence data for current and future scenarios were processed, along with the associated environmental variables. For the construction of the SDMs, only the nine environmental variables selected after the variance inflation factor analysis were used, ensuring the removal of multicollinearity effects. However, we employed the full set of available environmental predictors from the Bio-ORACLE database for the predictive analysis of variable importance, without prior VIF filtering (mean dissolved oxygen concentration, pH at the sea surface, chlorophyll-a concentration, nitrate concentration, phosphate concentration, and photosynthetically available radiation (PARmean)). These were included solely to assess the relative influence of additional abiotic factors on predictive performance and were not used for final SDM projections. This broader approach aimed to comprehensively assess the potential abiotic drivers influencing the presence of marine bioluminescent species, beyond those strictly retained for the SDM projections.

While SDMs were calibrated using the reduced set of nine predictors to minimize multicollinearity and improve model stability, the variable importance analysis was conducted using the full set of available environmental variables from the Bio-ORACLE database. This approach was adopted to provide a broader ecological interpretation of potential abiotic drivers influencing species occurrence, rather than to directly explain the fitted SDMs. Therefore, the variable importance results should be interpreted as complementary exploratory analyses, not as a direct reflection of the predictors used in the final SDM projections.

The occurrence values and the abiotic variables were normalized to the same length, removing incomplete cases with missing values. Class imbalance was handled implicitly by using continuous suitability and, where applicable, by case weights proportional to prevalence. Models were cross-validated with spatial blocking (5 folds, ~300–500 km blocks) to reduce over-optimism under spatial autocorrelation. Machine learning models were then trained and evaluated for each scenario (present, future at 50 years, and future at 100 years) using the Random Forest algorithm with cross-validation. Model performance was assessed, and the most important variables for predicting occurrence were identified and analyzed for each time scenario.

2.6. Spatial analysis of species conservation and vulnerability

We employed the *randomForest* algorithm in R to identify critical pixels for species conservation under current and future climate scenarios (SSP1.26 and SSP5–8.5). Species distribution rasters were aggregated, normalized, and combined for analysis. A subset of samples was used to train the model and determine pixel importance. The most relevant pixels, accounting for 80% of cumulative importance, were selected and highlighted in a final raster to indicate conservation priorities.

Additionally, we analyzed the ecological niche and vulnerability of marine species across historical and future climate scenarios using the *CENFA* (Climatic and Ecological Niche Factor Analysis; Rinnan and Lawler, 2019) package in R. Bioclimatic data, provided in raster format, were loaded for both historical and future conditions (year 2100, SSP5–8.5 scenario to evaluate upper-bound vulnerability under the most severe CMIP6 trajectory, which best discriminates species-specific sensitivities), standardized to the WGS84 coordinate reference system, and stacked to improve computational efficiency. Species occurrence data were converted into spatial objects to define their historical ranges using convex hull polygons. Marginality measures the deviation of the species' optimum environmental conditions from the mean conditions available in the study area, sensitivity quantifies the species' response to environmental variability, and vulnerability

integrates both metrics to assess potential exposure to climate change (Rinnan and Lawler, 2019).

For each species, CENFA modeling was performed to assess their climatic niche based on historical climate variables and range maps. Departure analysis was conducted to evaluate differences between historical and future climate conditions within each species' range, while vulnerability assessments integrated the CENFA results with the departure analysis to identify potential impacts of climatic changes. This approach provides valuable insights into the spatial and temporal dynamics of species' ecological niches and informs conservation strategies in the face of future climate scenarios.

In this study, climate refugia were identified using an operational definition based on areas that consistently showed high suitability and high importance across present and future scenarios, consistent with approaches used to identify climate refugia based on ecological stability and persistence (Balantic et al., 2021). Specifically, we defined refugia as regions encompassing the top 80% of cumulative importance values derived from the Random Forest analysis, representing areas with persistent environmental suitability and species overlap. This approach focuses on identifying stable and ecologically relevant regions under climate change, rather than strictly applying predefined global refugia frameworks.

3. Results

3.1. SDM

The analysis of species distribution areas (Table 3) reveals distinct

patterns of change under different climate scenarios (SSP1.26 and SSP5–8.5) and future timeframes (2050 and 2100). All models exhibited high predictive accuracy (mean AUC = 0.86 ± 0.05; mean TSS = 0.74 ± 0.06 across species), indicating robust model performance and reliable projections under both present and future scenarios. Spatial predictions of current and future distributions are presented in the Supplementary Figures (S1–S2), where range expansions and contractions under both SSP1–2.6 and SSP5–8.5 scenarios are illustrated. For clarity, Fig. 2 summarizes key regions showing the most pronounced changes in species overlap and displacement, serving as a representative synthesis of modeled projections.

Several species exhibit significant expansions in their distribution areas, particularly under the more extreme SSP–8.5 scenario. For instance, *V. infernalis* shows an expansion of 143.21% by 2100 in SSP5–8.5. Similarly, *P. pileus* and *A. virens* demonstrate notable increases in their ranges, with expansion percentages exceeding 100% in certain scenarios. Moderate expansions are also observed for species like *E. superba*, depending on the scenario. The ensemble models demonstrated high predictive performance across species (Table 3).

In contrast, several species are projected to experience significant reductions in their distribution areas, particularly under the SSP5–8.5 scenario. *T. furca*, for example, shows a drastic reduction of 81.75% by 2100. Similarly, *K. brevis*, *E. spinax*, and *G. lunula* exhibit substantial area losses, highlighting their vulnerability to climate change. Distribution shifts are also evident, with several species showing spatial movements toward the "North" or "South." For instance, *O. bidentata* and *M. leidy* shift northward, whereas *O. gracilirostris* moves southward, emphasizing the importance of regional conservation strategies tailored to these

Table 3

Present and projected future distribution areas (in km²) of 17 marine bioluminescent species under climate scenarios SPP1-2.6 and SSP5-8.5 for 2050 and 2100. The table includes percentage changes in distribution area, displacement direction of the species' geographic range, and highlights variations between the northern and southern hemispheres.

Species	Area in km ²					SSP1-2.6 area change 2050	SSP5-8.5 area change 2050	Displacement 2100-SSP1-2.6	Displacement 2100-SSP5-8.5
	Present	Future 2050-SSP1-2.6	Future 2050-SSP5-8.5	Future 2100-SSP1-2.6	Future 2100-SSP5-8.5				
<i>A. virens</i>	6571713,37	5275527,06	11471877,75	7224640,81	11471877,75	expansion - 9,93%	expansion - 74,56%	North	North
<i>E. spinax</i>	4781489,18	2524949,37	3683294,5	3925265,25	3683294,5	reduction - 17,90%	reduction - 22,96%	South	South
<i>K. brevis</i>	431235	415234,81	258741	415405,93	258741	reduction - 3,67%	reduction - 40%	North	North
<i>O. gracilirostris</i>	6273185,81	1500509,56	11065455,87	10852405,25	11065455,87	expansion - 72,99%	expansion - 76,39%	South	South
<i>P. atlanticum</i>	4596845,31	1849433,43	3315461,31	4111192,56	3315461,31	reduction - 10,56%	reduction - 27,87%	North	North
<i>M. leidy</i>	3769113,68	5024657,81	7931387,06	4328778	7931387,06	expansion - 14,85%	expansion - 110,43%	North	North
<i>P. pileus</i>	5610846,5	4093652,25	12314925,06	7717737,5	12314925,06	expansion - 37,55%	expansion - 119,48%	North	North
<i>S. maculata</i>	5577733,81	6658131,5	5849565,87	5752965,81	5849565,87	expansion - 3,14%	expansion - 4,87%	South	South
<i>C. hemisphaerica</i>	9631342,81	7136511,43	10122813,81	9314504,87	10122813,81	reduction - 3,29%	expansion - 5,10%	North	North
<i>E. superba</i>	10997177	9454485,12	10990845,37	14017362,12	10990845,37	expansion - 27,46%	reduction - 0,06%	North	North
<i>O. bidentata</i>	5484984,06	4288306,93	8856488,81	7632517,25	8856488,81	expansion - 39,15%	expansion - 61,46%	North	North
<i>P. violaceus</i>	2909039,43	3383397,93	2994687,5	3061682,93	2994687,5	expansion - 5,24%	expansion - 2,94%	South	South
<i>T. furca</i>	10682649,25	1977777,18	1949199,31	4786451,81	1949199,31	reduction - 55,19%	reduction - 81,75%	South	South
<i>E. lucifer</i>	2798492,68	1998740	2021756,31	2269288,62	2021756,31	reduction - 18,91%	reduction - 27,75%	North	North
<i>G. lunula</i>	6008968,81	3648727,25	3319397,18	3493688	3319397,18	reduction - 41,86%	reduction - 44,76%	North	North
<i>O. deletron</i>	1965798,43	63401,81	1516424,18	1272827,75	1516424,18	reduction - 35,25%	reduction - 22,86%	South	South
<i>V. infernalis</i>	2113821,56	224173,75	5141193,93	4883137,43	5141193,93	expansion - 131,00%	expansion - 143,21%	South	South

anticipated dynamics.

The SSP5–8.5 scenario results in more pronounced changes, including both expansions and reductions of distribution areas, underscoring the greater impact of severe climate conditions. This demonstrates the critical role of mitigating climate change to reduce biodiversity loss. Some species, such as *S. maculata* and *P. violaceus*, show relatively minor changes in their distribution areas, suggesting a degree of stability under the modeled scenarios. The results highlighted differences in species sensitivity to climatic variables, particularly salinity and temperature. The greater impact observed in the SSP5–8.5 scenario indicating a stronger impact under the SSP5–8.5 scenario (Table 3).

3.2. Predictive variable for the occurrence of marine bioluminescent species

KDPAR (Light Attenuation Coefficient in PAR) was identified as the most significant variable for predicting species distribution over time (Fig. 1). While KDPAR emerged as the most important predictor on average across all species, its influence was not uniform. For example, *E. lucifer* and *E. superba* showed a stronger response to mean sea surface temperature (SST_{mean}), while *V. infernalis* was more affected by deep-sea oxygen concentration. *O. bidentata*, on the other hand, responded predominantly to salinity gradients, indicating variation in species responses to different abiotic factors. Besides, this predictors is equally described for benthic and deep-sea taxa, its influence should be interpreted as an indirect proxy of surface-driven processes. KDPAR reflects light attenuation in the upper ocean, which is closely linked to primary productivity and phytoplankton dynamics, ultimately influencing the export of organic matter to deeper layers.

3.3. Impacts of environmental variables on species vulnerability

The analyses conducted using the GENFA method revealed the effects of environmental variables, such as salinity and temperature, on

the distribution and vulnerability of various species (Table 4). Salinity emerged as a critical variable, significantly influencing the sensitivity and vulnerability of species such as *P. violaceus* and *E. lucifer*. Species with high thermal marginality, like *O. deletron*, showed dependency on specific conditions, emphasizing the importance of temperature for these groups. Additionally, some species demonstrated dependency on multiple variables. Species like *E. lucifer*, *E. superba*, and *P. violaceus* were identified as highly vulnerable, suggesting they should be prioritized in conservation strategies. Conversely, more resilient species, such as *G. lunula*, exhibited lower sensitivity, although they may occupy specific ecological niches. These results underscore how climatic variables specifically shape the ecological vulnerability, persistence, and future redistribution of marine bioluminescent taxa across diverse oceanic systems.

3.4. Key conservation areas

The predictive analysis of important conservation areas identified five key regions of significance and species overlap in both present and future scenarios, associating them with the vulnerability map. These areas include the Brazilian coast in the southeast region, stretching from São Paulo to Espírito Santo states; the Pacific region off the U.S. coast; the sea between England and mainland Europe; the Australian coastline; and the waters between Japan and China (Fig. 2; for more details, see Fig. S2). These regions showed a high concentration of pixels, representing 80% of the cumulative importance for species distribution as determined by the RF model.

4. Discussion

4.1. Climate impacts on species distribution

The results of this study reveal a complex interplay of ecological and physiological factors driving the future distribution of bioluminescent species under changing climate conditions. While some species are

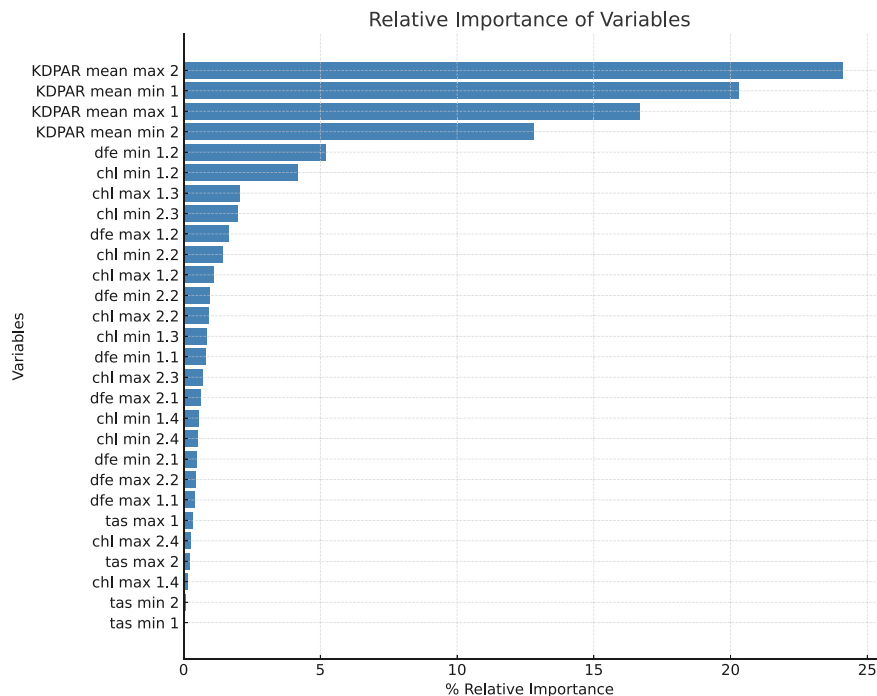


Fig. 1. Barchart illustrating the most relevant abiotic variables for predicting the distribution of marine bioluminescent species. Mean importance scores of environmental variables for predicting the presence of marine bioluminescent species, based on Random Forest analysis across abiotic predictors (see Methods). The values represent the average relative importance of each variable across all species. Note that variable importance was calculated using the full set of environmental predictors and is intended to provide a broader ecological context, rather than directly reflect the reduced predictor set used in SDMs.

Table 4
 Relationship between environmental variables and the metrics of marginality, sensitivity, and vulnerability of species analyzed using the CENFA method. The values in parentheses reflect the intensity of the association for each metric.

Species	Overall Marginality	Overall Sensitivity	Overall vulnerability
<i>A. virens</i>	BO22_temprange_ss (0.75)	BO22_curvellmax_ss (1.45)	BO22_curvellmax_ss (1.183)
<i>E. spinax</i>	BO22_curvelmin_ss (0.36)	BO22_salinityrange_bdmn (1.514)	BO22_salinityrange_bdmn (1.258)
<i>K. brevis</i>	BO22_curvelmin_ss (0.47)	BO22_salinityrange_ss (1.259)	BO22_salinityrange_ss (1.112)
<i>O. gracilirostris</i>	BO22_curvelmin_ss (0.539)	BO22_salinitymean_bdmx (1.534)	BO22_salinitymean_bdmx (1.233)
<i>P. atlanticum</i>	BO22_curvelmin_ss (0.444)	BO22_salinityrange_bdmn (1.299)	BO22_salinityrange_bdmn (1.118)
<i>P. pileus</i>	BO22_curvelmin_ss (0.363)	BO22_curvellmax_ss (1.191)	BO22_curvellmax_ss (1.087)
<i>S. maculata</i>	BO22_curvelmin_ss (0.576)	BO22_salinityrange_bdmn (1.573)	BO22_salinityrange_bdmn (1.237)
<i>C. hemisphaerica</i>	BO22_curvelmin_ss (0.353)	BO22_salinityrange_ss (1.203)	BO22_salinityrange_ss (1.092)
<i>E. superba</i>	BO22_curvellmax_ss (0.336)	BO22_salinitymean_bdmx (1.975)	BO22_salinityrange_ss (1.095)
<i>O. bidentata</i>	BO22_curvellmax_ss/BO22_curvelmin_ss (0.323)	BO22_salinityrange_bdmn (1.255)	BO22_salinityrange_bdmn (1.133)
<i>P. violaceus</i>	BO22_curvelmin_ss (1.174)	BO22_salinitymean_bdmx (2.284)	BO22_salinitymean_bdmx (1.407)
<i>T. furcatus</i>	BO22_curvelmin_ss (0.404)	BO22_salinityrange_bdmn (1)	BO22_salinityrange_bdmn (0.993)
<i>E. lucifer</i>	BO22_curvellmax_ss/BO22_curvelmin_ss (0.741)	BO22_salinitymean_bdmx (2.268)	BO22_salinitymean_bdmx (1.384)
<i>G. lunula</i>	BO22_curvelmin_ss (0.436)	BO22_salinityrange_bdmn (0.993)	BO22_salinityrange_bdmn (0.984)
<i>O. deletron</i>	BO22_temprange_ss (0.764)	BO22_curvellmax_ss (1.843)	BO22_curvellmax_ss (1.334)
<i>V. infernalis</i>	BO22_curvelmin_ss (0.388)	BO22_salinityrange_bdmn (1.427)	BO22_salinityrange_bdmn (1.179)
<i>M. leidy</i>	BO22_temprange_ss (0.396)	BO22_salinityrange_bdmn (1.225)	BO22_salinityrange_bdmn/BO22_salinityrange_ss (1.098)
<i>P. militaris</i>	BO22_temprange_ss (0.327)	BO22_curvellmax_ss/BO22_curvelmin_ss (1.167)	BO22_curvellmax_ss/BO22_curvelmin_ss (1.078)

projected to expand their ranges under more extreme climate scenarios, others are likely to contract or maintain their current distribution. These contrasting responses highlight the nuanced ways in which species interact with their environments and adapt, or fail to adapt, to new conditions.

A key factor for species that show range expansions is their physiological tolerance to a broader range of environmental conditions, such as temperature and nutrient availability (Franco et al., 2018; Mannocci et al., 2017; Martínez et al., 2018). For instance, species with high dispersal capacity and opportunistic ecological strategies among marine bioluminescent taxa may exploit newly suitable habitats created by warming waters, contributing to projected regional expansions (Fiedler et al., 2023). Species like *A. virens* and *O. gracilirostris* showed significant expansion, likely due to their adaptability and ability to exploit newly available niches created by climate change (Monteiro et al., 2024). Deep-adapted organisms such as *V. infernalis* demonstrate remarkable expansion, indicating resilience to environmental changes. This pattern could be linked to the relatively stable physicochemical conditions of deep-sea environments, where variability in temperature and other environmental factors is typically lower than in surface layers, potentially buffering these species against rapid climate-driven shifts. Similarly, species capable of thriving in areas with increased primary productivity may benefit from climate-driven shifts in oceanographic features, such as upwelling zones or nutrient plumes. Opportunistic species such as *M. leidy* and *P. pileus* also expand, possibly benefiting from eutrophic, varying salinity and temperature conditions and high dispersal potential (Schroeder et al., 2017).

In contrast, species experiencing range contractions may be constrained by narrow ecological niches or specific habitat requirements (Bulleri et al., 2016; Scheele et al., 2017). For instance, species that rely on highly stable and localized environmental conditions, such as deep-sea organisms adapted to oxygen-poor habitats, are particularly vulnerable to even small shifts in temperature or oxygen levels (Gowri et al., 2025; Rogers, 2000). Conversely, specialized species like *E. spinax* and *K. brevis* face reductions, likely due to their reliance on specific habitats and sensitivity to changes in temperature and oxygen levels (Verberk et al., 2021). Similarly, *G. lunula* and *O. deletron* experience contractions, reflecting habitat constraints. This pattern aligns with studies on coral reefs, where thermal stress events have led to significant habitat losses, particularly in regions with low genetic connectivity (Cacciopaglia and van Woesik, 2018).

Some species are expected to maintain their current distributions, due to their ability to buffer against environmental fluctuations through physiological and/or behavioral adaptations (Somero et al., 1983; Somero, 2022). Some species, e.g., *E. aphroditois*, maintain or slightly expand their ranges, demonstrating moderate adaptability to shifting conditions. For example, benthic species that inhabit highly variable environments, such as intertidal zones, may already be adapted to tolerate a range of conditions. These species could act as ecological stabilizers, maintaining their role in the ecosystem even as surrounding species shift (Narayan et al., 2022).

In all these cases, the varied responses of bioluminescent species to climate change reflect the diversity of ecological and physiological strategies within this group. While some species may capitalize on new opportunities, others are at significant risk of decline. Recognizing the factors driving these patterns is essential for interpreting the future redistribution and vulnerability of marine bioluminescent species. It is also important to note that the observed range shifts in our models should not be interpreted as direct evidence of evolutionary or physiological adaptation. Rather, they reflect changes in the environmental suitability of habitats under future oceanic conditions. Adaptive potential, including acclimation or genetic responses, cannot be inferred from correlative SDMs and remains a topic for experimental or genomic approaches.

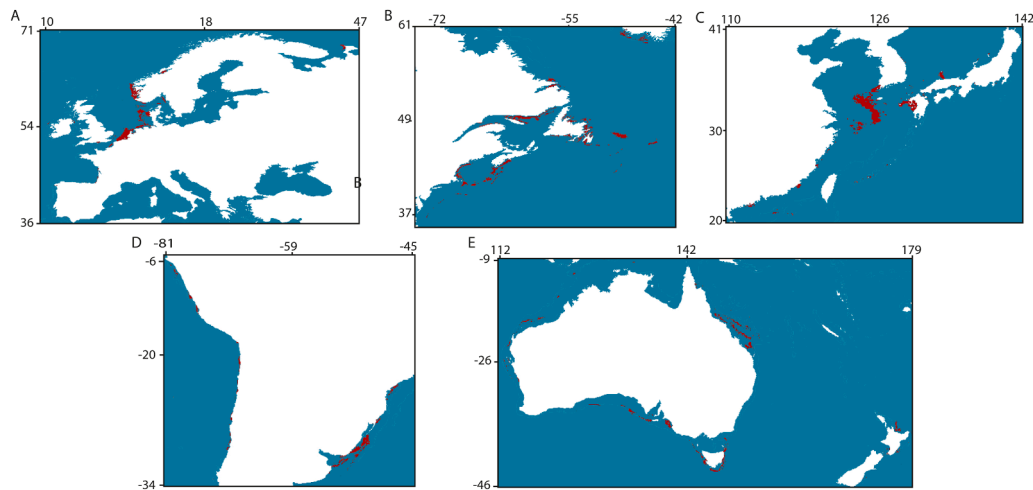


Fig. 2. Overlap areas of marine bioluminescent species, illustrating the main regions identified as critical for conservation based on future species distribution modeling. The common regions observed across studied species are showed in red. The oceans boarder are in light blue. Map values are referenced to geographic coordinates in degrees of latitude and longitude. These areas include: (A) the sea between England and mainland Europe; (B) part of the Pacific Ocean off the United States coast; (C) the waters between Japan and China; (D) the Atatlntic and Pacific coast extending from South America; and (E). the Australian coastline.

4.2. Regional conservation and management implications

Here, we highlight the role of certain regions as climate refugia for bioluminescent species and, consequently, for other species. These regional hotspots, characterized by stable environmental conditions such as moderate temperatures, sufficient nutrient availability, and consistent oceanographic features, provide a sanctuary for species that are less capable of adapting to rapid environmental changes (Fig. 2). For instance, regions where species were commonly observed along the time show persistence or expansion could serve as priority zones for conservation. These refugia represent spatially explicit areas where projected suitability persists across scenarios, supporting their use as model-derived conservation priorities.

For instance, the Brazilian coast showcases a concentration of species that rely on a combination of stable salinity and light penetration conditions, particularly in areas influenced by nutrient inputs from coastal upwellings. These conditions make it a key refuge for species that display resilience under shifting environmental parameters. Similarly, the waters between Japan and China, influenced by complex ocean currents and varying salinity gradients, are critical for supporting both resident and migratory bioluminescent organisms, which depend on these dynamic ecological interactions for survival. These areas have already been described as critical marine biodiversity hotspots (Claudet et al., 2020; Harzhauser et al., 2024; Jefferson and Costello, 2020; Ogawa and Mitani, 2024; Ruthrof et al., 2021; Santos et al., 2022).

From a regional management perspective, these refugia intersect with areas already recognized for their ecological and socio-economic relevance, including important fishing grounds, coastal development zones, and existing MPAs. For example, along the southeastern Brazilian shelf and the North-East Atlantic shelf, our projections can support regional marine spatial planning by refining MPA boundaries, identifying candidate areas for new protections, and anticipating future conflicts between conservation and coastal development. The significant displacement trends of marine bioluminescent species toward these regions under progressing climate scenarios, particularly SSP5–8.5, further suggest that these areas may function not only as current refuges but also as future strongholds for species responding to warming waters and altered oceanic conditions (Balantic et al., 2021). Consequently, our findings identify spatially explicit refugia and biodiversity hotspots that may inform conservation gap assessments, adaptive management priorities, and dynamic planning strategies that evolve alongside projected species redistribution. Regular monitoring and the integration of

predictive modeling into management frameworks will be essential to preserve the ecological roles of marine bioluminescent species while strengthening broader marine ecosystem resilience under ongoing climate change (Balantic et al., 2021; Friesen et al., 2021; Hodapp et al., 2023).

4.3. Determinants of distribution

The analysis showed the critical role of abiotic factors, such as light penetration (KDPAR), salinity, and temperature, in shaping the distribution of marine bioluminescent species under the climate change scenarios. KDPAR emerged as the most predictive variable, underlining the importance of photosynthetically active radiation in sustaining the primary productivity that underpins marine food webs (Castant et al., 2024). This dependency on light penetration suggests that species distributions are intrinsically tied to regions where adequate levels of sunlight penetrate the water column, supporting phytoplankton growth and, consequently, higher trophic levels. Temperature also played a pivotal role, particularly for species with narrow thermal tolerances, such as *E. superba* and *O. gracilirostris*. These organisms rely on stable cold-water conditions, and their projected contractions highlight their vulnerability to rising ocean temperatures (Du Pontavice et al., 2020).

Salinity also emerged as an important predictor for several species, particularly those associated with coastal and shelf environments, where strong environmental gradients are common. In these regions, salinity is influenced by freshwater inputs, evaporation, and ocean circulation, shaping species' physiological tolerances and distribution limits (Bal et al., 2022). Additionally, salinity often co-varies with broader oceanographic processes, including nutrient availability and carbonate chemistry, which can indirectly influence species distributions (Doney et al., 2009; Mostofa et al., 2016). Acidification, in turn, is a direct consequence of climate change, as the oceans absorb excess CO₂ from the atmosphere. This not only lowers the pH of seawater but also reduces the carbonate ions that many marine organisms, like corals and shellfish, need to build their structures (Doney et al., 2009; Findlay and Turley, 2021). Thus, the importance of salinity in our models likely reflects both direct physiological constraints and indirect ecological processes.

These climate-driven changes threaten not only species with specific salinity requirements, such as *P. violaceus* and *E. lucifer*, but also broader marine ecosystem stability. In contrast, species displaying lower sensitivity values in CENFA, such as *G. lunula*, likely possess broader environmental tolerances or greater phenotypic plasticity, indicating that

ecological versatility may be a stronger determinant of climatic sensitivity among marine bioluminescent taxa than phylogenetic relatedness alone. Although KDPAR does not directly affect deep-sea environments where sunlight is absent, its strong predictive importance likely reflects its function as an indirect proxy for upper-ocean productivity, which governs particulate organic carbon export to deeper layers and sustains deep-sea food webs (Burd and Thomson, 2022; Danovaro et al., 2017; Brierley and Kingsford, 2009). Therefore, KDPAR in this context likely captures broader ecosystem-level productivity processes rather than direct light exposure. However, vertical carbon flux and particle export were not explicitly modeled, representing an important limitation of the current framework and a priority for future research.

4.4. Functional and Ecological Implications

The projected SDM shifts for marine bioluminescent species under future climate scenarios are likely to have profound ecological, functional, and scientific implications for marine ecosystems. Bioluminescent organisms play essential roles as predators, prey, symbionts, and ecological indicators, contributing to trophic interactions, biodiversity maintenance, and biogeochemical cycles (Amaral et al., 2024). Consequently, projected distributional shifts may alter marine food webs, nutrient cycling, and broader ecosystem processes. Beyond ecological consequences, changes in the distribution of bioluminescent organisms may also affect their scientific and technological applications. Bioluminescence is increasingly used as a natural biosensor for environmental monitoring, genetic expression systems, and oceanographic studies, where light emission characteristics support in situ species detection and biomass estimation (Letendre et al., 2024a). Climate-driven changes in temperature, pH, and oxygen availability may therefore influence not only species distributions but also luciferin-luciferase efficiency, signal stability, and the long-term reliability of these organisms in applied biological systems, particularly under progressive ocean acidification.

Species projected to expand may alter community composition through intensified competition, trophic restructuring, and shifts in nutrient recycling, particularly in deep-sea ecosystems where bioluminescent taxa often occupy important ecological roles as predators or scavengers. Conversely, contractions in key taxa such as *E. superba* may destabilize specialized food webs and reduce ecosystem resilience in vulnerable systems such as Antarctic marine environments (Braun et al., 2022; Burd and Thomson, 2022). Similarly, shifts in dinoflagellate distributions may influence regional primary productivity, nutrient cycling, and the potential emergence of harmful bloom dynamics (Monteiro et al., 2024).

These projected changes may also affect predator-prey dynamics and broader ecosystem stability, as opportunistic species such as *M. leidy* expand into newly suitable habitats. Overall, shifts in marine bioluminescent species distributions may alter ecological monitoring capacity, trophic interactions, and the functional stability of bioluminescence-dependent marine systems (Braun et al., 2022). Monitoring marine bioluminescent taxa under future climate scenarios will therefore be critical for understanding ecosystem restructuring, preserving biodiversity, and maintaining the scientific and ecological value of these uniquely informative marine organisms.

4.5. Uncertainties and model limitations

Our findings, while providing valuable information in the context of the future distribution of bioluminescent species, are not without uncertainties. These uncertainties stem primarily from areas of environmental extrapolation and non-analog conditions, where models predict species distributions based on environmental variables outside the range of current observations (Melo-Merino et al., 2020; Ploton et al., 2020). Such extrapolations can lead to over- or underestimations of suitable habitats, particularly under extreme climate scenarios. For instance, changes in temperature, salinity, and light penetration in regions with

sparse historical data may result in model outputs that lack robustness, underscoring the need for caution when interpreting predictions for these areas (Ploton et al., 2020). Another critical limitation is the presence of data gaps in both environmental variables and occurrence datasets. The reliability of SDMs heavily depends on the quality and comprehensiveness of input data. However, many marine regions, particularly those in the deep sea or remote coastal zones, remain under-sampled, leading to biases in model calibration. Additionally, inconsistencies in the temporal and spatial resolution of environmental data, such as those for salinity or ocean currents, further complicate efforts to generate accurate projections (Feldman et al., 2021). Addressing these gaps will require expanded monitoring efforts, particularly in poorly studied areas, and the standardization of data collection protocols.

An important source of uncertainty not explicitly addressed in this study is model transferability. SDMs calibrated under present-day environmental conditions may not fully capture species responses under future climate scenarios, particularly if novel environmental combinations arise (Melo-Merino et al., 2020). This limitation can affect the ecological realism of projections, as species–environment relationships may shift beyond the conditions represented in the training data. Therefore, model transferability and extrapolation risk should be considered when interpreting future projections. Occurrence data derived from GBIF and OBIS are subject to well-documented spatial and taxonomic sampling biases, particularly the overrepresentation of coastal and well-sampled regions relative to deep-sea and remote oceanic environments (Coro et al., 2016; Yiu Cheung and Helfer, 2025). These biases may affect model calibration by disproportionately reflecting accessible or historically surveyed habitats, while under-representing less-sampled offshore systems. Additionally, pseudo-absence data may not necessarily represent true absences, especially in deep-sea or under-sampled regions where absence may instead reflect limited sampling effort rather than biological exclusion (Barbet-Massin et al., 2012; Phillips et al., 2009). Although we mitigated these limitations through rigorous data cleaning, spatial thinning (Aiello-Lammens et al., 2015), and by constraining pseudo-absence generation within species-specific accessible areas, these uncertainties remain inherent to large-scale marine SDM frameworks and should be carefully considered when interpreting projected distributions (Andrella et al., 2023; Melo-Merino et al., 2020).

Another important source of uncertainty is the temporal mismatch between occurrence records (1950–2023) and environmental predictor layers representing present-day conditions (2000–2014). While this approach is widely adopted in broad-scale marine SDM studies due to limitations in globally standardized environmental datasets (Melo-Merino et al., 2020; Assis et al., 2024), it inherently assumes relative stability in species–environment relationships over time (niche conservatism; Peterson et al., 2011; Araújo and Peterson, 2012). Consequently, this framework may underestimate or fail to fully capture recent climate-driven distributional shifts, particularly for highly mobile or environmentally sensitive taxa (Randin et al., 2020; Innoci et al., 2017). Although this assumption remains acceptable for global-scale projections, it reinforces the need for cautious interpretation, especially when inferring recent or rapidly emerging ecological responses.

As with all species distribution modeling approaches, our results are subject to multiple sources of uncertainty that may affect interpretation and application. These include spatial and taxonomic biases in the occurrence records from GBIF, assumptions made when generating pseudo-absence data, and limitations in the resolution and completeness of environmental layers. Model-based uncertainties also arise from the specific algorithms used, as different methods (GLM, ANN, MaxEnt) may capture different response curves, although the ensemble approach was used to mitigate this effect. Furthermore, climate projection uncertainty, arising from variation across global climate models (GCMs) and emission scenarios (e.g., SSP1–2.6 vs SSP5–8.5), adds layer of variability. Finally, the models do not explicitly incorporate biotic interactions,

dispersal limitations, or local adaptation, which are known to influence species responses to climate change. Following the guidelines of Brodie et al. (2022), we recommend that future work aim to quantify these uncertainty sources and integrate them into scenario planning and conservation decision-making.

4.5.1. Future perspectives

This study highlights the relationships between bioluminescent species and their dynamic oceanic environments, emphasizing the profound impacts of climate change on their distribution. By modeling present and future scenarios, we revealed significant shifts in geographic ranges, with some species expanding into new habitats, others contracting, and a few maintaining stable distributions. These patterns show the importance of key environmental drivers, such as light penetration (KDPAR), temperature, and salinity, in shaping marine biodiversity. Our findings also emphasize the critical role of climate refugia as stable havens for vulnerable species, underscoring their conservation value in mitigating biodiversity loss.

Moving forward, a more integrated approach is essential to address the complexities of species distribution under future climate scenarios. Incorporating genetic analyses to assess population connectivity and resilience could refine predictions and support targeted conservation strategies. Stakeholders and scientific initiatives should work together to offer an untapped potential for expanding occurrence data, especially in under-sampled regions, thereby improving the robustness of species distribution models. Additionally, adaptive management strategies, including the establishment and dynamic adjustment of marine protected areas, will be vital to ensure the preservation of bioluminescent species (and others) and the ecological networks they sustain.

By framing these projections in terms of regional hotspots and climate refugia, our work offers a practical baseline for regional agencies, MPA networks and coastal planners seeking to align local management decisions with global climate projections and the targets of SDG 14.

CRedit authorship contribution statement

Thaís Kaori Enoki Takishita: Conceptualization, Methodology, Formal Analysis, Investigation, Data Curation, Visualization, Writing. **Rodrigo O. Castro:** Methodology, Formal Analysis, Investigation, Data Curation, Writing—Review and Editing. **Isabel A.S. Bonatelli:** Writing—Review and Editing. **Danilo T. Amaral:** Conceptualization, Methodology, Formal Analysis, Investigation, Writing—Original Draft Preparation, Writing—Review and Editing, Supervision, Project Administration.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the authors used ChatGPT 4.0 to improve the text grammar. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

Submission declaration

The present article has not been published previously except in the form of a preprint, an abstract, a published lecture, an academic thesis, or a registered report. It is not under consideration for publication elsewhere; the article's publication is approved by all authors and tacitly or explicitly by the responsible authorities where the work was carried out.

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Declaration of Competing Interest

The authors declare no conflicts of interest.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.rsma.2026.105066](https://doi.org/10.1016/j.rsma.2026.105066).

Data availability

Data will be made available on request.

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