

Global analysis of the influence of environmental variables to explain distributions and realized thermal niche boundaries of sea snakes

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Abstract

Understanding the factors that affect species' distributions is a central topic of ecology and biogeography. However, the majority of research about this topic has focused on species inhabiting terrestrial environments. At broad scales, abiotic variables consistently serve as the primary determinants of species' distributions. In this study, we investigate the explanatory power of different abiotic variables in determining the distributional patterns of sea snakes on a global scale. Additionally, as the boundaries of realized thermal niches have significant implications for the ecology of the species and their geographic distributions, we also evaluated the asymmetry of realized thermal limits (i.e., differences in variances between upper and lower limits of the realized thermal niche). We obtained global environmental variables and occurrence data for each species across their entire known geographic range. Using this data, we employed a correlative ecological niche modeling procedure to analyze the influence of individual variables in explaining species' distributions. To estimate the realized thermal limits of each species, we extracted the mean, minimum, and maximum values of temperature at four depths (superficial, mean benthic, minimum benthic, and maximum benthic) for each occurrence record of the species. We then evaluated the asymmetry of the realized thermal niche by measuring and comparing the variances of the upper and lower limits. Both analyses (the importance of variables and realized thermal limit asymmetry) were performed at three taxonomic levels (sea snakes as a lineage of marine-adapted elapids [true sea snakes + sea kraits], subfamily, and genus) and at two spatial resolutions. Overall, we found that temperature, phosphate, nitrate, salinity and silicate concentrations were the most influential factors in explaining the spatial distribution patterns of sea snakes, regardless of the taxonomic level or spatial resolution. Similarly, we observed that the realized thermal limits were asymmetric with higher variance in the lower limits, and that this asymmetry decreases as the taxonomic level and spatial resolution increased. Finally, our results align with previous findings regarding patterns of asymmetry in realized thermal limits and the significant influence of abiotic variables in explaining the distribution of marine species.

1 INTRODUCTION

Anthropogenic activities have led to rapid global changes that are creating unprecedented climatic conditions, which could compromise the viability of many species (Walther et al. 2002; Walther et al. 2009). Understanding how environmental conditions affect the survival of species' populations and shape their distributions is fundamental for establishing conservation strategies (Bosch et al. 2018). However, estimating the relationships between species and their environment is a complex task, as it involves multiple factors (Gaston and Fuller 2009; Sexton et al. 2009; Wiens 2011). These factors can be summarized into three

categories: 1) limiting or regulatory, which control the ecophysiological responses of the species, 2) disturbance factors, which describe the historical modifications in the occupation of habitats by both natural and anthropogenic processes, and 3) resource factors, which represent the supplies necessary for the survival of organisms (Guisan and Thuiller 2005). Some causal relationships between these factors and species' attributes, such as abundance and distribution, have been demonstrated through physiological experiments in laboratories and wildlife demographic studies (Gause 1931; Hutchings and Myers 1994; Kordas et al. 2011). However, carrying out laboratory experiments or fieldwork to obtain demographic data has some drawbacks. First, both are generally costly and time-consuming. Secondly, implementing physiological experiments is not ethically feasible for many organisms (Fraser 1999). Finally, some environmental variables are more relevant at broad spatial scales (>200 km). For instance, limiting or regulating factors associated with climate are considered to be the most relevant in explaining the distribution of species across their entire range (Contreras-Díaz et al. 2022; Gillespie et al. 2008; Pearson and Dawson 2003).

An alternative approach to studying species-environment relationships in a spatial context is the use of correlative methods, known generically as ecological niche modeling (ENM) and species distribution modeling (SDM) (Bentlage et al. 2013; Pearson and Dawson 2003; Peterson and Soberón 2012). The inputs required by correlative methods are easier to acquire since they are generally available in online repositories. These inputs are sets of georeferenced localities where the presence of the species in question has been observed (some methods also require points that represent absence) and spatial surfaces that describe the environmental conditions of the area of interest (Randin et al. 2009). Thus, correlative methods are extensively used to model species-environment relationships and estimate their actual and potential distributions, both in terrestrial (Colwell and Rangel 2010; Eme et al. 2014) and marine ecosystems (Bosch et al. 2018; Bradie and Leung 2017). Although correlative methods have certain limitations (e.g., it can be difficult to discern whether their results are mere statistical associations or causal relationships; see Wiens et al. 2009), they allow us to recognize diverse ecological patterns (Ashcroft et al. 2011). As a result, these methods have become popular for analyzing the importance of environmental variables as limiting factors of distribution ranges and various ecological aspects across multiple taxa (Bosch et al. 2018; Bradie and Leung 2017; Lee-Yaw et al. 2016).

One of the most studied limiting factors is temperature, as it has a key relevance for many physiological and ecological processes (Bicego et al. 2007; Clarke 2003; Kordas et al. 2011). Thus, studying the thermal niche (TN) and realized thermal niche (TNR) of species has been a major focus of ecological research (Gvoždík 2018; Lee-Yaw et al. 2016; Magnuson et al. 1979; Stuart-Smith et al. 2017). According to Gvoždík (2018), TN refers to the range of body temperature that individuals of a species require for the population to experience positive growth, while TNR refers to the environmental range of temperatures that individuals of a species are exposed to (Collin et al. 2021; Stuart-Smith et al. 2017). Based on the concepts of TN and TNR, two hypotheses have been proposed to explain patterns of temperature tolerance and organismal response to global warming. The first hypothesis suggests that tropical and polar terrestrial species have lower TN than those from temperate climates (Pörtner 2001; Pörtner and Farrell 2008). The second hypothesis is the realized thermal limit asymmetry, which refers to significant differences in the variation of upper limits in a species or taxon compared to the variation of lower limits within the same taxon, with the variation being greater in the lower limits. This means that under climate change scenarios, high rates of global warming can severely impact the conservation of most species (Collin et al. 2021; Stuart-Smith et al. 2017). Ideally, evaluating these hypotheses requires direct estimation of the species' TN in question through physiological population growth-mortality experiments (Dong and Somero 2009; Helmuth et al. 2006; Sánchez-Fernández et al. 2012; Stillman and Somero 2000). However, despite the high cost, time and ethical constraints, there are global initiatives to analyze this patterns (Bennett et al. 2018). Nonetheless, characterization of the TN for most taxa is still lacking.

Therefore, through the use of correlative methods, it is possible to characterize a portion of the TN called TNR, which represents the range of temperatures associated with the presence of a species (Descombes et al. 2015; Gaüzère et al. 2015; Quintero and Wiens 2013). Since correlative methods do not require experimentation and management of organisms, they are a more feasible option for studying species TNs. As a result, they have been commonly applied to many taxonomic groups (Huff et al. 2005; Kuo and Sanford

2009; Sánchez-Fernández et al. 2012; Sánchez-Fernández et al. 2016). Moreover, most TNs analysis have been focused on species from terrestrial environments (Bennett et al. 2018), leaving no information on many important marine groups, such as sea snakes.

Sea snakes are an ecologically diverse and marine-adapted lineage of elapids that includes two subfamilies, Hydrophiinae (true sea snakes) and Laticaudinae (sea kraits). The group comprises >60 species widely distributed in the tropical and subtropical regions of the Indian and Pacific Oceans (Sanders et al. 2013; Wallach et al. 2014). Sea snakes' lineage has evolved with unique physiological adaptations to survive in marine environments, being their ability to thermoregulate a critical adaptation to adjust their metabolic rate and behavior in response to water changes in temperature (Heatwole et al. 2012). Recent research has also shown that temperature plays a critical role in the diving behavior and metabolism of sea snakes, as individuals exhibit different diving behaviors and metabolic rates in response to changes in water temperature (Dabruzzi et al. 2012; Udyawer et al. 2016). These findings highlight the complex ways in which temperature influences the behavior and physiology of sea snakes and underscore the importance of understanding the thermal biology of these reptiles for conservation and management efforts. Nevertheless, most sea snake research has focused on their toxicity, and their phylogenetic and evolutionary relationships (Udyawer et al. 2018). However, to date, there is no information on the factors that determine sea snakes' distribution, nor the asymmetry of their realized thermal limits. In this study, we used correlative ecological niche modeling (ENM) to evaluate the relative importance of environmental variables in explaining the distribution of almost all sea snake species on a global scale. We also analyzed whether there is an asymmetry in the dispersion of their lower and upper realized thermal limits. The results of our research provide a better understanding of the biogeographical phenomena that determine the distribution patterns in this group and will allow us to infer their vulnerability to future ocean warming scenarios.

2 MATERIALS AND METHODS

2.1 Presence records

We searched presence records with geographic coordinates for all sea snakes in public online repositories. These platforms were the Global Biodiversity Information Facility (gbif.org; DOI information associated with data are available in Table SM1), VertNet (vertnet.org), the Ocean Biogeographic Information System (obis.org), the Atlas of Living Australia (ala.org.au), the Online Zoological Collections of Australian Museums (ozcam.org.au) and the UNAM open data portal (datosabiertos.unam.mx). We integrated the presence records obtained from the different platforms into a single database per species. Then, we eliminated duplicate records, uncertain data (e.g., taxonomic mistakes, records outside the known distribution of the group), and obvious errors (e.g., records in terrestrial environments). Next, we eliminated occurrences that might represent sink populations through an environmental outliers' analysis. In this process, we considered environmental variables previously identified in the literature as important to the group (see below). For this, we used the *outliers* function of the "biogeo" package (Robertson et al. 2016) in R (R Core Team 2013), which searches for presence records that are located at a distance above 1.5 times the interquartile range of the data. Additionally, we employed the *gridSample* function of the "dismo" package (Hijmans et al. 2017) to minimize data bias towards more intensely sampled environments. These processed records comprised the complete database for each species.

2.2 Environmental data

We downloaded environmental variables in raster format, commonly used in spatial modeling of marine environments from the global repositories Bio-Oracle (Assis et al. 2018) and MARSPEC (Sbrocco and Barber 2013) at four depths (superficial, benthic maximum, benthic mean and benthic minimum). Then, we classified the variables into five groups: Bsurf (superficial Bio-Oracle; $n = 10$), Bma (maximum benthic Bio-Oracle; $n = 8$), Bme (mean benthic Bio-Oracle; $n = 8$), Bmi (minimum benthic Bio-Oracle $n = 8$), and Msurf (superficial MARSPEC; $n = 6$). This protocol was used to select the combination repository/depth that maximizes the explanatory capacity of predictors (Table 1). To standardize the spatial resolution of the variables, we resampled the MARSPEC variables to match the 5 arc-minutes cell resolution of Bio-Oracle. Subsequently,

we resampled both repositories at a resolution of 10 arc-minutes with the same method, to assess the effect of spatial resolution on our results (Connor et al. 2019).

For each species, we defined a polygon representing a hypothesis of its historical accessibility (area **M** ; sensu Soberon and Peterson 2005) based on the marine biogeographical provinces of the world (Spalding et al. 2007) and ocean current information (earth.nullschool.net/#current/ocean/surface/currents/patterson). We first selected as area **M** all the provinces with at least one presence record of the species in question. Then, based on the natural history of the species and the geographical configuration of its occurrences, we limiting or expanding it depending on whether we consider that the currents could serve as physical barriers or dispersal channels. Then, we also defined a calibration area and masked the variables by selecting only the areas within the intersection between the presence records of the species in question and the marine eco-regions; a finer sub-regionalization than the provinces. Finally, to reduce collinearity and dimensionality of predictors, we eliminated individually for each species, variables in each of the five groups that had a pairwise Pearson correlation >0.8 with the function *correlation_finder* in “ntbox” package (Feng et al. 2019; Mateo et al. 2013; Osorio-Olvera et al. 2020).

2.3 Modeling ecological niches

We use the Jackknife cross-validation procedure for improving the accuracy and to minimize the variability of the models in taxa with fewer than 25 localities. In this method, one presence record is excluded randomly from modeling and the procedure is repeated as many times as the data allow; all records are excluded just once. In each iteration, the $n - 1$ data are used as model training information and the excluded record is used for model evaluation (Shcheglovitova and Anderson 2013). Finally, in species with more than 25 occurrence records, we applied the *get.checkerboard1* function in the “ENMeval” package (Muscarella et al. 2014). In this method, the database is divided into two sets using a checkerboard pattern across the extent of the study area. Occurrences are separated according to their position on the board. Finally, we defined the set with more records as training data and the set with less information as evaluation data (Brown 2014).

To characterize the ecological niches of sea snakes we used the MaxEnt 3.4.1 algorithm (Phillips et al. 2006). A series of candidate models were calibrated with the training database of each species via the “kuenm” package (Cobos et al. 2019). This package allows varying parameter combinations of the MaxEnt algorithm. We tested combinations of seven feature classes in MaxEnt (“l”, “q”, “p”, “lq”, “lqp”, “lp”, and “qp”, where “l” is linear, “q” is quadratic, and “p” is product), eight regularization multipliers (0.10, 0.25, 0.50, 0.75, 1, 2, 3 and 4), and the five groups of environmental variables described above (thus, the maximum possible number of variables used to build any model is full set of “repository/depth” if no correlation between all variables were found). This results in 560 candidate models per species (spp x 2 resolutions x 7 Fs x 8 RMs x 5 groups of variables). Then we selected using the test database the best subset of models that met the following criteria hierarchically: 1) statistical significance, where we retained those models that were better than expected by chance, depending on the proportion of bootstrap replicates with ratios of the partial area >1 (Peterson et al. 2008), 2) predictive capacity, where we selected those models with statistical significance, which were also able to predict at least 90% of the evaluation records (i.e., models with an omission rate –OR– [?] 0.10), and 3) complexity, through the Akaike information criterion corrected for small samples ($\Delta AICc$) we selected as best combinations those [?] 2 units, that are also the models that present a better fit and fewer parameters (Radosavljevic and Anderson 2014; Warren and Seifert 2011). Based on the best parameter combinations (full set of best combinations are available in Table SM2), we built a final set of models using the whole database (training and evaluation data) with the bootstrap functionality of MaxEnt performing 10 replicates. In each iteration, we divided presence records randomly into 80% for training and 20% for evaluation; we define Cloglog as output format and 10,000 background points (masked by our calibration area). Finally, we calculated the median and the range of the predicted values across the total replicates (10 replicates $\times$ final parameter combination) to represent the consistency and variation in predictions.

2.4 Importance of variables

To analyze the relative importance of environmental variables in explaining sea snakes’ distributions, we first

classified the variables into ten groups based on their identity. For example, the group “Temperature (Tem)” included seven variables that represent the median of the mean, maximum and minimum values of the sea surface and benthic temperature (Table 1).

We used two measures to assess the relative importance of environmental variables: the percentage of contribution (PC) and the permutation of importance (PI) estimated by MaxEnt. PC measures the gain of a model built with a single specific variable divided by the total gain of a model built with all the variables. PI is obtained from randomizing the values of each variable so that this variable is not informative and then measures the resulting drop in the area under the curve (Phillips 2011). To identify the consistency or variability in our results, we performed this procedure at three levels: “lineage”, when we analyzed the variables for all species independently of subfamily; “subfamily”, where we divided the results into the Hydrophiinae and Laticaudinae subfamilies; and “genus”, where we repeated the same analysis for each of the six genera. We performed this analysis at both resolutions (5 and 10 arc-minutes).

We also separated the identity variables into two groups (high relative importance and low relative importance) based on their relative importance using the natural Jenks thresholds calculated with the *getJenksBreaks* function of the “BAMMtools” package (Rabosky et al. 2014).

To determine if the results depended on spatial resolution, we evaluated the consistency of the importance of each variable between the two spatial resolutions for the two MaxEnt metrics (PC and PI) through a non-parametric Mann-Whitney-Wilcoxon test through the *wilcoxon.test* function in “stats” package (R Core Team, 2013). Overall, our approach allowed us to identify the most important environmental variables driving the distributions of sea snakes and to assess the consistency of these results across different metrics of importance, taxonomic levels and spatial resolutions.

2.5 Asymmetry of the realized thermal niche

We extracted the mean, maximum, and minimum temperature values for the five groups depending on the repository and depth (Bsurf, Bma, Bme, Bmi, and Msurf) associated with each post processed presence record (see above in “2.1 Presence records”) of each species at 5 and 10 arc-minutes of spatial resolution. For Bio-Oracle, we used directly the mean, maximum, and minimum temperature variables in each depth. In the case of MARSPEC, we used the surface temperature of the warmest month to represent the maximum temperature and the surface temperature of the coldest month to represent the minimum temperature. With those values, we conserved and grouped the minimum and maximum value from each species for characterized the lower and upper TN_R limits respectively.

Finally, we tested the asymmetry in TN_R limits hypothesis (asymmetry in the variances with more variance in lower limit) by testing the homogeneity of variances between the lower and upper realized thermal limits. This process was repeated for each variable group on each temperature measurement at the three taxonomic levels and two spatial resolution by applying a non-parametric Fligner-Killeen test (Fligner and Killeen 1976) ($5 \text{ groups} \times 3 \text{ temperatures} \times 3 \text{ taxonomic levels} \times 2 \text{ resolutions}$). Particularly, in genus level, we excluded the genus *Laticauda* due to represent the same result at the Laticaudinae subfamily, and *Ephalophis* and *Microcephalophis* as a result of only have data for one species.

3 RESULTS

We obtained 5,020 spatially unique presence records of 50 of the >60 recognized sea snakes. Most of the records of the species were distributed in the Indo-Pacific Ocean and *Hydrophis platurus* being the only species with representation in the Pacific of the new world (density map by genus is available in Fig_SM1. Additionally, an interactive map can be performed with “3_Density_plot.r” code in <https://github.com/PatronRiveroC/Ssnakes>).

Regarding model evaluation, we obtained a median partial AUC ratio >1 for all species (i.e., all our models were better than expected by chance). The ORs in the final models were [?] 0.10, but three species when we used the variables at 5 minutes resolution and seven species at 10 minutes and six for 10 minutes (Table 2). We show species’ environmental suitability maps for each species in Fig_SM2-SM51.

3.1 Importance of variables

All results of relative importance for each taxonomic level (lineage, subfamily and genus) are shown in Figure 1 (results by each species are in Fig_SM52). Summary of the relatively high important variables are presented in Figure 2 for the PC and PI estimated by MaxEnt at 5 and 10 arc-minutes of spatial resolution.

3.1.1 Lineage

At a resolution of 5 arc-minutes, the most important variables for the sea snakes' lineage were phosphates (Pho), salinity (Sal), and temperature (Tem), which together accounted for the highest PC. However, when the importance of variables was permuted (PI), nitrates (Nit), silicates (Sil), and Tem emerged as the most important factors. At 10 arc-minutes for PC and PI, Sil and Tem were important variables, while Nit was also important in PI. Finally, we only found differences between the median of Sil when comparing both resolutions in PC (Table SM3).

3.1.2 Subfamily

At the subfamily level, the patterns were different. For the Hydrophiinae subfamily, Sal and Tem were the most important variables at 5 arc-minutes for PC, while Nit, Sil and Tem were the most important for PI. At 10 arc-minutes, Sil and Tem were the most important variables for PC and Nit and Sil for PI. For the Laticaudinae subfamily, the variables with highest PC at 5 arc-minutes were Nit, Pho and Sal, while the variables with highest PI included in addition the Tem. At 10 arc-minutes, Sil and Tem were the most important variables for both PC and PI. Finally, we did not find differences between each pair of the same variable when comparing resolutions for both subfamilies in PC and PI (Table SM3).

3.1.3 Genus

At the genus level, for *Aipysurus* at 5 arc-minutes, calcites (Cal), dissolved molecular oxygen (Doxy), iron (Iro), Pho, Sal and Tem were the most important variables for PC, while Doxy, Iro, Pho and Tem were the most important for PI. At 10 arc-minutes, Sil was the most important variable for PC and Doxy, Pho and Sil for PI. In *Emydocephalus* at 5 arc-minutes for PC, Doxy, Sal, Sil and Tem were the most important variables, while Sil and Tem were the most important for PI. At 10 arc-minutes, currents Velocity (Cvel), Sal, Sil and Tem were the most important variables for PC and the same variables omitting Sal for PI. For *Ephalophis* at the 5 arc-minutes for both PC and PI, Iro, Sal and Tem were the most important variables. While at 10 arc-minutes, Nit and Sal were important for PC and only Nit for PI.

For *Hydrophis* and *Laticauda*, the results at the genus level were similar to those obtained at the subfamily level due to contain same all species in case of Laticaudinae (the reason for we are not presented the same results here) and almost all for Hydrophiinae. Specifically, for *Hydrophis* at 5 arc-minutes for PC, Nit, Pho, Sal and Tem were the most important variables, while Nit and Tem were the most important for PI. At 10 arc-minutes, Nit, Sil and Tem were the most important variables for both PC and PI, and additionally, Pho was important only in PC.

Finally, *Microcephalophis* was influenced by Sal and Tem at 5 arc-minutes for PC, while Tem was the only important variable for PI. At 10 arc-minutes, Tem was the most important variable for both PC and PI. We also did not find any statistical difference between comparison same variable in both resolutions, importance metric in any genus (Table S3).

3.2 Variation in the TN_R limits

At the lineage level, our results reveal significant differences in the variance of the realized lower thermal limit compared to the realized upper thermal limit across all temperature measurements (mean, maximum, and minimum), regardless of the group of variables used (Bma, Bme, Bmi, Bsurf, and Msurf) or cell resolution (Fig 3A-B; Table SM4). The same pattern was observed in the Hydrophiinae subfamily (Fig 3C-D; Table SM4), whereas for the Laticaudinae subfamily, we found this pattern only in the minimum temperature measure at both resolutions (Fig 3E-F; Table SM4).

At the genus level, we observed higher variances in the lower limits than the upper limits for *Aipysurus* and *Hydrophis* and all temperature measures, repository and depth, and spatial resolution (Figure 3G-H; Table SM4). However, we did not find significant differences between the lower and upper limits in any temperature, repository and depth, and spatial resolution for the *Emydocephalus* genus (Figure 3I-J; Table SM4).

4 DISCUSSION

4.1 Environmental variables

Our study confirms the importance of environmental variables in shaping the distribution of sea snakes, which is consistent with previous studies (Bessesen et al. 2023; Udyawer et al. 2014). Environmental variables play a crucial role in determining the habitat suitability and area of occupancy of marine species, including sea snakes, and prioritizing search efforts based on habitat suitability models can help locate previously unknown populations of endangered marine reptiles (Udyawer et al. 2020). This aligns with our findings and emphasizes the importance of our research in generating crucial information that could guide future conservation and management strategies for protecting a highly vulnerable and ecologically important group, which is sea snakes.

Our findings are consistent with a meta-analysis on the importance of variables used in MaxEnt species distribution models, which found that the most important factors in determining the distribution of marine organisms were temperature, bathymetry, and precipitation (Bradie and Leung 2017). Additionally, our study highlights the importance of nutrient availability in shaping the distribution of marine species. Those environmental variables were not important in the meta-analysis. The study by Bosch et al. (2018) found that temperature, bathymetry, and distance to shore were the most important predictors for marine species distribution, while salinity and nutrients had less influence. Although our study's results on the importance of salinity and nutrients in determining sea snakes' distribution appear to conflict with previous analysis, it is worth noting that our study specifically focused on sea snakes, which may have different environmental preferences than other marine species. Our study's results on the importance of phosphates, salinity, and temperature in determining the habitat suitability and area of occupancy of sea snakes are consistent with the findings of Bessesen et al. (2023) on *H. platurus* and Udyawer et al. (2014) on sea snakes in the Great Barrier Reef Marine Park.

The combination of climate and nutrient variables are known to have implications for the morphology, diving behavior, feeding habits of sea snakes and also coral reefs health (Brischoux et al. 2012; Gherghel et al. 2018; Heatwole et al. 2012; Sherratt et al. 2018; Veron 2000, 2008). Temperature, along with salinity, plays a crucial role in the physiology of sea snakes, affecting their metabolic rates, oxygen uptake, and blood chemistry (Heatwole et al. 2012; Udyawer et al. 2016). Studies have also demonstrated that metabolic thermal sensitivity optimizes sea krait amphibious physiology, enabling them to tolerate fluctuations in temperature (Dabruzzi et al. 2012; Heatwole et al. 2012). Furthermore, trophic specialization drives morphological evolution in sea snakes, while the dependence of dive behaviors and metabolism on temperature has also been observed (Dabruzzi et al. 2012; Sherratt et al. 2018; Udyawer et al. 2016). However, plasticity in thermal tolerance has limited potential to buffer ectotherms from global warming, which may lead to mosaic patterns of thermal stress with implications for climate change (Gunderson and Stillman 2015; Helmuth et al. 2006). Phosphates play a significant role in the distribution of sea snakes as they are essential for the growth and development of the coral reefs where sea snakes are commonly found (Veron 2000). Although the importance of nitrogen and silicates in the distribution of sea snakes is less clear, they are likely to play a role in the availability of prey species that sea snakes feed on (Gherghel et al. 2018). Nitrogen is an essential nutrient for many marine organisms, and its availability can influence the abundance and distribution of prey species (Brischoux et al. 2012). Silicates are important in the growth of diatoms, which are a primary food source for many marine organisms, including some species of sea snakes (Sherratt et al. 2018).

The sea snakes' distribution may have influenced their diet and feeding behavior, as species that occur in areas with higher nutrient availability may have evolved to specialize on prey that require higher energy

requirements, such as fish, while species occurring in areas with lower nutrient availability may have evolved to specialize on prey that require less energy, such as crustaceans (Gherghel et al. 2018; Sherratt et al. 2018).

Our study utilized correlative models to determine the relationships between sea snakes and environmental variables, but caution must be exercised in interpreting the results since correlative models cannot establish causality. Some correlations may reflect direct effects of environmental variables, while others may represent indirect relationships. We used MaxEnt, which can handle collinearity among explanatory variables; however, collinearity may still pose challenges when estimating the importance of explanatory variables (Smith and Santos 2020). The programmers of MaxEnt incorporated two different metrics (PC and PI) to evaluate the contribution of predictors to the model (Phillips 2011), although there is no consensus in the literature on which is more informative. Most studies use the PC, possibly because it appears first in the algorithm's results. Halvorsen (2013) concluded that the PC is most informative, whereas (Searcy and Shaffer 2016) suggested that the PI is better for describing the biological properties of species. Our study provides insights into the environmental factors important for the distribution of sea snakes, but further research is necessary to establish causal relationships between these factors and the distribution of sea snakes, as well as to gain a better understanding of their ecology and behavior.

In summary, our results on the relative importance of environmental variables in shaping the distribution and potentially the abundance of sea snakes, are consistent with previous research on marine organisms and provide a valuable framework for developing effective conservation management plans for sea snakes.

4.1.1 Subfamily level

Previous research has identified important variables for the Laticaudinae subfamily, which can provide context for our results. Gherghel et al. (2018) found that the most relevant variables for predicting the presence of the Laticaudinae subfamily were distal variables such as distance to the coast and bathymetry. We excluded these distal variables from our analysis because they may not directly reflect the ecological and physiological requirements of sea snake species. The inclusion of distal variables is not recommended when an interpretation of a species' biology is desired (Merow et al. 2014). Instead, we focused on environmental variables directly related to physical and resource factors. On the other hand, as there are no definitive conclusions in the literature regarding the Hydrophiinae subfamily, which comprises the vast majority of species within the lineage, a specific discussion of this subfamily would entail repeating information already covered above. Therefore, we have not included a dedicated discussion of this subfamily.

Overall, it appears that important variables for the Hydrophiinae and Laticaudinae subfamilies may vary depending on the particular group of snakes being studied, as well as the specific methods used for analysis. Our results add to the growing body of literature on the ecology and distribution of sea snakes, and provide further insights into the factors that may influence their distribution patterns.

4.1.2 Genus level

Environmental variables play a significant role in shaping the abundance and distribution of prey species, influencing the availability of suitable habitat for sea snakes. Studies on *Aipysurus* indicate that environmental factors play crucial roles in shaping their distribution and abundance. (Lynch et al. 2023) reported that environmental factors are important in shaping the behavior and distribution of *A. laevis*, while (Borczyk et al. 2021) found sexual dimorphism in skull size and shape for *A. eydouxi*, which may affect feeding and ecological niche differentiation between males and females.

Previous studies have also highlighted the importance of environmental variables in the distribution and population dynamics of *Emydocephalus*. (Lukoschek et al. 2007) found that *E. annulatus* exhibited metapopulation dynamics influenced by prey abundance, habitat quality, and complex reef habitats, while (Goiran and Shine 2013) reported a decline in *E. annulatus* abundance on a protected coral reef system in the New Caledonian Lagoon, attributed to changes in the physical environment resulting from anthropogenic modification to the system. Our study found that Sal, Sil, and Tem are significant variables for both PC and PI

at different resolutions, consistent with (Brischoux et al. 2012) finding that oceanic salinity influences body condition. However, we found a discrepancy in our results regarding the importance of T_{em} compared to a previous study on *E. annulatus*, which reported no significant effects of annual thermal variation on population densities. Further research is necessary to clarify these discrepancies and enhance our understanding of the importance of environmental variables, such as salinity and other nutrient variables, in the distribution and population dynamics of *Emydocephalus*.

For *Ephalophis*, our findings align with the idea of a rapid radiation of sea snakes, driven by adaptations to environmental factors. The importance of adaptation to the marine environment is highlighted by the variable importance of environmental factors observed in *Ephalophis*. This is supported by previous studies on sea snakes in Australian waters (Sanders et al. 2013), molecular phylogeny of sea snakes (Lukoschek and Keogh 2006), association between habitat type and skin thickness in snakes (Shine et al. 2019), presence of paddle-shaped tails in viviparous sea snakes (Sanders et al. 2012), and the feeding strategies and foraging ecology of the Hydrophiinae sea snakes, as analyzed in previous studies (Hampton 2019).

The *Hydrophis* genus is found to have almost identical results to the whole lineage analyzed, indicating a similar influence of environmental variables on their distribution and abundance. Meanwhile, discussing the *Laticauda* genus alone may be redundant as it represents the whole Laticaudinae subfamily. Further diverse ecological research is needed to support the findings and test the relative importance of variables for the *Microcephalophis* genus. Overall, the importance of environmental factors in shaping the ecology and evolution of sea snakes is reinforced by the results obtained from our analysis. We also emphasize the importance of further diverse ecological research to support the findings and test the relative importance of variables for this genus.

4.2 TN_R limits

Sea snakes demonstrate a greater consistency in their upper thermal limits compared to their lower thermal limits, according to our research findings. This aligns with previous studies on some terrestrial (Araujo et al. 2013; Sunday et al. 2011, 2012) and marine ectothermic species (Grady et al. 2019; Nishizaki et al. 2015; Stuart-Smith et al. 2017). The results imply that cold tolerance evolves more quickly than heat tolerance in both endothermic and ectothermic organisms (Bennett et al. 2018). Sea snakes may have developed greater plasticity in their lower thermal limits through an evolutionary process (Gunderson and Stillman 2015; Verberk et al. 2018), resulting in less variation in their upper thermal limits. However, if sea temperatures continue to rise due to climate change, the reduced variability in upper thermal limits could have significant consequences for sea snakes (Araujo et al. 2013; Udyawer et al. 2020).

Marine ectotherms have a low physiological acclimatization rate, making them particularly susceptible to the effects of climate change (Deutsch et al. 2008; Sunday et al. 2011). Previous studies have indicated that sea snakes exist near their upper thermal limits (Heatwole et al. 2012), and that tropical species generally do not surpass the maximum temperatures of the organisms that have been collected (Deutsch et al. 2008; Huey et al. 2009). Although our study observed this pattern at the lineage level, we obtained mixed results at the subfamily and genus level, potentially owing to our limited sample size. Other factors, including biotic interactions, geographic barriers, and dispersal processes, may restrict species distribution and impact the capacity to measure complete thermal niches (Bennett et al. 2018; Sunday et al. 2011, 2012).

The consequences of the observed asymmetric realized thermal limits for sea snakes' physiological performance and their ecological interactions with other species in their habitat are significant. Sea snakes are critical predators in their marine ecosystems, and alterations in their distribution or abundance could have cascading effects on the food webs they inhabit (Lukoschek et al. 2013). Thus, the observed thermal limits of sea snakes have implications not only for their own survival but also for the health and functioning of marine ecosystems.

To address the conservation implications of our findings, it is crucial to consider the potential impact of climate change on sea snakes and the measures needed to protect them. Management and conservation efforts must recognize the susceptibility of many marine species, including sea snakes, to climate change

(Somaweera et al. 2021). Our research highlights the importance of conservation efforts that consider the potential vulnerability of sea snakes to changes in sea temperature, including identifying areas that provide thermal refugia for sea snakes, monitoring populations for changes in distribution or abundance, and implementing adaptive management strategies that can respond to changing conditions (Udyawer et al. 2020).

While our study offers valuable insights into the realized thermal limits of sea snakes, there are limitations and gaps in knowledge that future research could address. For example, our sample size for some subfamilies and genera was relatively small, which may have affected our results. Increasing the sample size may enhance the robustness of our findings. Moreover, future research could explore the potential for sea snakes to acclimate or adapt to warming temperatures and investigate the mechanisms underlying the observed pattern of asymmetric realized thermal limits. Integrating physiological and genetic data could provide a more comprehensive understanding of the thermal ecology of sea snakes and their ability to adapt in the face of climate change.

5 CONCLUSIONS

Our study reveals the significant role of temperature, salinity, and some nutrients (such as nitrates, phosphates and silicates) in shaping the distribution of sea snakes. These variables are known to have implications for the morphology, diving behavior, coral reefs health, and feeding habits of sea snakes. Moreover, our findings offer valuable insights for conservation management strategies.

Furthermore, our study demonstrates the asymmetric realized thermal limits of sea snakes, with less variation in their upper thermal limits compared to their lower thermal limits. This pattern is consistent with previous research on other endothermic and ectothermic species and has critical implications for sea snakes under scenarios of sea warming. Suggesting that sea snakes have accumulated greater plasticity in their lower thermal limits through an evolutionary process.

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7 TABLE LEGENDS

Table 1. Variable groups with description of each individual variable by repository and depth. VCode = variable code. Bma = Bio-Oracle benthic maximum, Bme = Bio-Oracle benthic mean, Bmi = Bio-Oracle benthic minimum, Bsurf = Bio-Oracle surface, Msurf = MARSPEC surface.

Table 2. Summary of inputs and evaluations from ecological niche modeling. Scode = species code, Tocc = total occurrences, Focc = final post-processed occurrences, M5 = number of final models at 5 arc-minutes, M10 = number of final models at 10 arc-minutes, AUCR5 = median of AUC ratios at 5 arc-minutes, AUCR10 = median of AUC ratios at 10 arc-minutes, OR5 = median of omission rate at 5 arc-minutes, OR10 = median of omission rate at 10 arc-minutes, * = omission rate > 10%.

8 FIGURE LEGENDS

Figure 1. All variable contribution estimated by MaxEnt percentage of contribution (PC) and permutation of importance (PI) for each taxonomic level at both spatial resolutions. A) = 5 arc-minutes, B) = 10 arc-minutes. Warmer colors denoted higher contribution while lighter colors less contribution.

Figure 2. Chord diagram for the relative important variables under the percentage of contribution (PC) and permutation of importance (PI) estimated by MaxEnt and their representation in different taxonomic and spatial resolution levels. More connected variables represent that are relatively important variables in more taxonomic and spatial resolution levels comparing to variables less connected. A) = PC at 5 arc-minutes, B) = PI at 5 arc-minutes, C) = PC at 10 arc-minutes, D) = PI at 10 arc-minutes, Nit = nitrates, Pho = phosphates, Sal = salinity, Sil = silicates, Tem = temperature.

Figure 3. Lower and upper thermal limits of sea snakes at three taxonomic levels, three temperatures measures, five variable groups and two spatial resolutions. A) = Sea snakes' lineage at 5 arc-minutes, B) = Sea snakes' lineage at 10 arc-minutes, C) = Hydrophiinae subfamily at 5 arc-minutes, D) = Hydrophiinae

subfamily at 10 arc-minutes, E) = Laticaudinae subfamily at 5 arc-minutes, F) = Laticaudinae subfamily at 10 arc-minutes, G) = *Aipysurus* genus at 5 arc-minutes, H) = *Aipysurus* genus at 10 arc-minutes, I) = *Emydocephalus* genus at 5 arc-minutes, H) = *Emydocephalus* genus at 10 arc-minutes, Max = maximum temperature, Mean = mean temperature, Min = minimum temperature, Bma = maximum benthic Bio-Oracle, Bme = mean benthic Bio-Oracle, Bmi = minimum benthic Bio-Oracle, Bsurf = superficial Bio-Oracle, Msurf = superficial MARSPEC. All *p* values are in Table SM4.

9 SUPPORTING INFORMATION

Table SM1. List of dataset keys (DOIs) and occurrence count for all GBIF data used.

Table SM2. List of final configuration models by species.

Table SM3. Non-parametric Wilcoxon Test comparison between medians of variables at 5 and 10 arc-minutes of spatial resolution and at relative importance metric estimated by MaxEnt for lineage, family and genus level.

Table SM4. Summary of *p* values for homogeneity of variances by non-parametric Fligner-Killeen test.

Figure SM1. Density map of Sea snakes' lineage by genus. Bigger points represent more density of presence records and smaller points less presence records.

Figure SM2-51 . Suitability and range of variability maps at 5 and 10 arc-minutes for each species.

Figure SM52. All variable contribution estimated by MaxEnt percentage of contribution (PC) and permutation of importance (PI) for each species at both spatial resolutions.

A)

PC

Sea snakes lineage

10.253.35.636.2715.033.822.2326.864.4440.26

Hydrophiinae

10.252.945.636.2713.063.819.3726.824.4441.53

Laticaudinae

04.026.658.2177.31067.3541.8631.4520.12

Aipysurus

17.165.2315.217.815.90.2130.6716.6015.59

Emydocephalus

05.439.813.2600047.5823.3538.39

Ephalophis

00024.3800036.28039.34

Hydrophis

6.632.622.327.3527.034.3819.3725.363.1542.14

Laticauda

04.026.658.2177.31067.3541.8631.4520.12

Microcephalophis

00.310.77000048.82049.7

CalCvelDoxyIroNitpHpHoSalSilTem

PI

Sea snakes lineage

2.662.885.727.6243.945.7912.623.6756.1539.81

Hydrophiinae

2.663.095.917.5636.925.798.753.3529.6549.26

Laticaudinae

01.684.978.5669.59033.017.3657.9830.41

Aipysurus

1.972.6225.825.065.53031.080.84019.8

Emydocephalus

04.432.232.680000.0979.1154.38

Ephalophis

00032.8400028.35038.81

Hydrophis

3.083.095.917.5946.455.798.753.6721.2363.22

Laticauda

01.684.978.5669.59033.017.3657.9830.41

Microcephalophis

01.562.5400004.59087.93

CalCvelDoxyIroNitpHpHoSalSilTem

B)

PC

Sea snakes lineage

5.423.756.7210.7816.386.0824.6715.952.9538.06

Hydrophiinae

5.423.536.728.916.386.0824.6715.950.332.42

Laticaudinae

05.7913.2114.8700026.4672.0171.01

Aipysurus

4.569.9227.4819.4411.7625.3829.4411.9193.6211.38

Emydocephalus

4.2728.7904.9600033.652.9520.93

Ephalophis

0001.6233.340051.13013.91

Hydrophis

8.413.485.526.6425.036.0824.6716.4826.7740.87

Laticauda

05.7913.2114.8700026.4672.0171.01

Microcephalophis

01.680700015.41074.44

CalCvelDoxyIroNitpHpHoSalSilTem

PI

Sea snakes lineage

2.462.8510.266.6449.536.189.614.5865.8134.3

Hydrophiinae

2.462.8910.266.6449.536.189.614.5865.1623.14

Laticaudinae

02.5613.0815.220008.8565.8187.07

Aipysurus

0.43.4333.0618.258.2914.5334.923.4163.718.08

Emydocephalus

10.8626.8804.580004.5866.6330.81

Ephalophis

0006.770.130022.0101.25

Hydrophis

3.122.898.175.6556.236.188.193.2463.1132.58

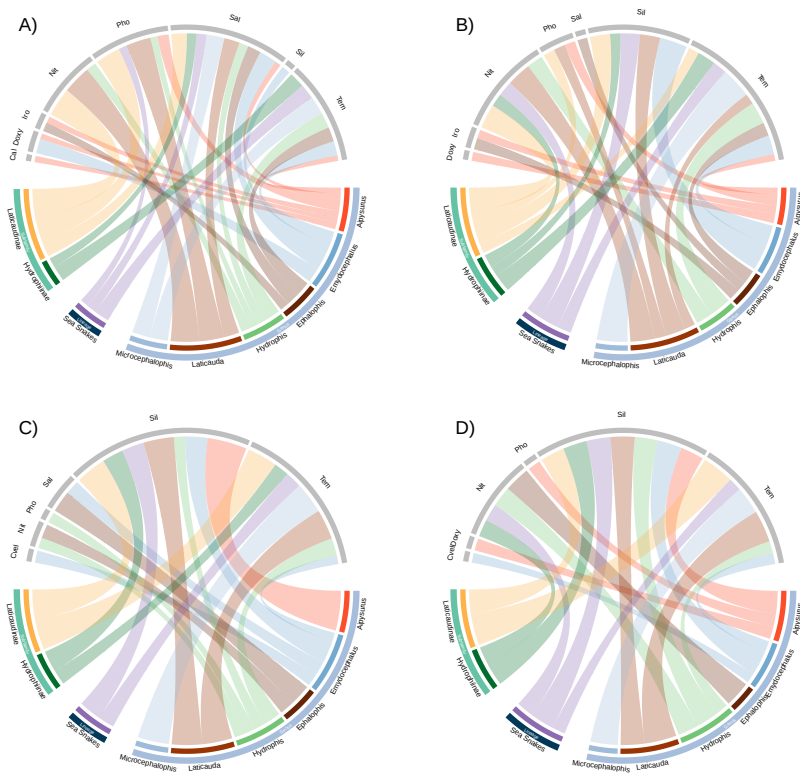
Laticauda

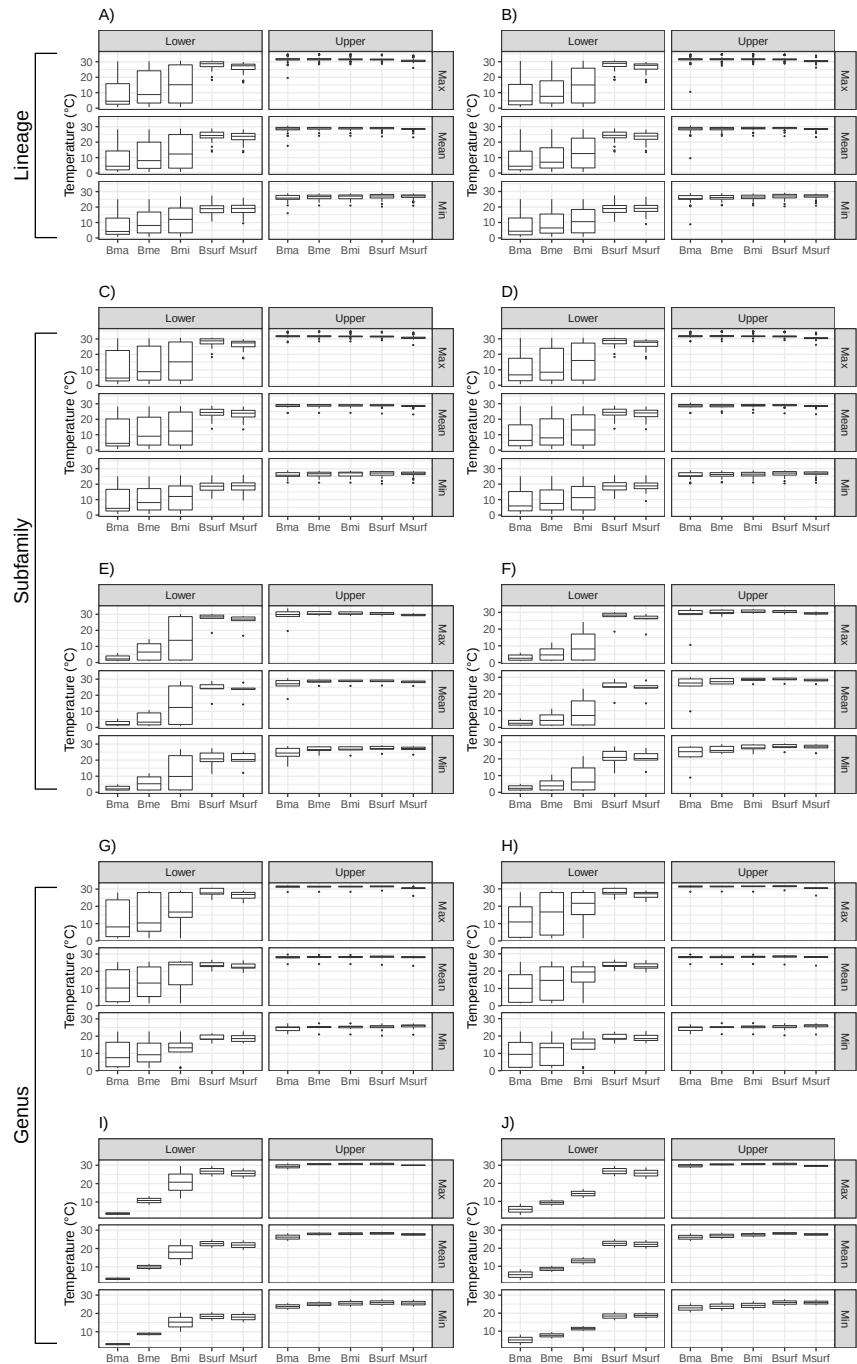
02.5613.0815.220008.8565.8187.07

Microcephalophis

02.31011.50009.16075.03

CalCvelDoxyIroNitpHpHoSalSilTem





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Table_2.docx available at <https://authorea.com/users/627538/articles/708286-global-analysis-of-the-influence-of-environmental-variables-to-explain-distributions-and-realized-thermal-niche-boundaries-of-sea-snakes>