REPORT

A simple framework for estimating potential distributions of amphibious marine species and implications for conservation

Iulian Gherghel[1,2,3] · François Brischoux[4] · Árpád S. Nyári[5] · Monica Papeş[5]

Abstract Due to their complexity, coral reefs are difficult to study especially when considering the role that the interplay between the terrestrial and marine environments has in shaping distribution of marine, terrestrial, and amphibious species. Many organisms live in remote areas of the ocean and inhabit both terrestrial and marine environments. Such amphibious lifestyle poses analytical difficulties due to broad distribution and scale of coral reefs. Ecological niche modeling is a widely used technique that allows to estimate the environmental set of conditions (niche) in which organisms can survive and reproduce. Estimating the distributions of species with complex life histories (i.e., dependent on various natural resources) at broad geographic scales is crucial, as many of these taxa are threatened (i.e., amphibians, aquatic reptiles, birds, and mammals). However, distribution estimates of such species remain challenging; thus, here we propose an approach to account for marine and terrestrial environmental domains to estimate the distribution of amphibious species. We also test whether inclusion of both environments leads to improved estimates of these species' distributions. First we calibrated ecological niche models for marine and terrestrial domains separately, and subsequently we outlined a method to combine the marine–terrestrial potential distributions by integrating estimates of the two ecological niches into a single predictive model. Our ecological niche models produced inaccurate distribution predictions of species with amphibious life histories when only one of the environments was used in model calibration. When both aquatic and terrestrial environments were included, our models predicted narrower and more accurate potential distributions. Accounting for the dual environments involved in shaping the niches of amphibious species and their distributions is essential for studying the ecology and proposing conservation management actions for the species studied here. Models that take into account only a subset of the environmental factors are prone to overestimating species' distributions and should be interpreted with caution.

Keywords Ecological niche models · Large scale · *Laticauda* · Life history · Maxent · Species distribution models

✉ Iulian Gherghel
iulian.gherghel@case.edu

1 Department of Integrative Biology, Oklahoma State University, 501 Life Sciences West, Stillwater, OK 74078, USA

2 Department of Biology, Case Western Reserve University, 2080 Adelbert Road, Cleveland, OH 44106, USA

3 Faculty of Geography and Geology, "Alexandru Ioan Cuza" University of Iaşi, Carol 1 Boulevard, no. 20A, 700505 Iaşi, Romania

4 Centre d'Etudes Biologiques de Chizé, CEBC-CNRS, UMR 7372, 79360 Villiers en Bois, France

5 Department of Ecology and Evolutionary Biology, University of Tennessee, 569 Dabney Hall, Knoxville, TN 37996, USA

Introduction

Ecological niche models (ENMs), or species distribution models (SDMs), correlate species' occurrences with broad environmental (e.g., climate) variables (Guisan and Zimmermann 2000; Elith et al. 2006a; Franklin 2009) to estimate the ecological niche (Hutchinson 1957) and geographic distribution of the species of interest. These

models are used frequently and are considered essential tools for studying species' ecology at various spatial and temporal scales (Guisan and Thuiller 2005). Previously, ENMs have been applied successfully to study a wide range of biogeographical and ecological topics, such as predicting species distributions (e.g., Jimenez-Valverde et al. 2011) and disease spread (e.g., Peterson et al. 2007b; Mueller et al. 2013), invasive species (e.g., Welk et al. 2002; Peterson et al. 2003), conservation (e.g., Peterson et al. 2002; Peterson and Martínez-Meyer 2007; Manzu et al. 2013), and climate change effects (e.g., Siqueira and Peterson 2003; Thomas et al. 2004; Sahlean et al. 2014).

Despite their established utility in ecology, biogeography, and conservation, the process of calibrating ENMs is not always straightforward. This is typically the case for species with complex life histories encompassing disparate environments (e.g., amphibious species or parasites with different hosts). In such situations, estimating the species' niche becomes more challenging due to the fact that the environments occupied by the species can be dramatically different (e.g., marine and terrestrial for amphibious species). Such challenges include, but are not limited to: (1) different sets of environmental variables used to calibrate the niche model in the two environments (marine and terrestrial in our case), for example salinity that is specific to the marine environment, but usually does not apply to the terrestrial environment; (2) creating a single estimate of species' distribution by combining the two niches, in which case a new method is needed; and (3) the lack of environmental datasets with the same spatial, temporal, and accuracy used to calibrate models and estimate the species' distribution. Amphibious animals such as sea turtles, sea kraits, and seals rely on both aquatic and terrestrial environments to complete key stages of their life cycle (e.g., reproduction, growth). Since both environments are central to the ecology of the species, these two ecological facets must be taken into account when estimating niches through ENMs. A few studies of species relying on different habitats estimated potential distributions at a more localized spatial scale, generally appropriate for habitat suitability models (Roever et al. 2014; Frans et al. 2018), and did not account for different proportions of the marine and terrestrial domains; habitat suitability models are sometimes used synonymously to ENMs or SDMs in the literature, but there are fundamental differences between these models (see Peterson and Soberon 2012 for further discussion on this topic). In addition, the relevance and relative contribution of the variables used to calibrate ENMs can vary between multiple environments. For instance, biologically relevant thermal heterogeneity might feature less prominently in aquatic than in terrestrial environments due to the fact that the former is thermally more stable (Folland et al. 1997). Additionally, some variables

may be used to characterize one, but not the other environment (e.g., ocean salinity, soil type). Taken together, these points highlight the need for developing more specific approaches to generate relevant ENMs for species with life cycles that encompass adjacent, but distinct, environments.

Recently, Frans et al. (2018) have presented multistate SDMs as a way to account for species' use of components of the realized niche (different habitats across temporal scales) (sensu Hutchinson 1957) and improve estimates of species' distributions. The aim of our study is complementary to that of Frans et al. (2018). We used an existing modeling algorithm in a new approach to estimate fundamental niches (sensu Hutchinson 1957) by integrating the whole suite of conditions from both aquatic and terrestrial domains, representing two portions of the fundamental niche of an amphibious species that have not been modeled together previously. We selected amphibious sea snakes (sea kraits; *Laticauda* spp.) as our study system for several reasons. Sea kraits are a group of typical amphibious species that rely on two spatially adjacent types of environment: (1) terrestrial, to bask, digest prey, mate, and oviposit, and (2) marine, to forage for prey (Heatwole, 1999). Sea kraits frequently use both environments, typically returning to land once every 2 weeks (Brischoux et al. 2007; Shetty and Shine 2002). Thus, their presence and survival in an area depend on the availability and suitability of both environments. The distribution of sea kraits is well documented in the literature through range maps and occurrence datasets (Elfes et al. 2013; Gherghel et al. 2016), ensuring a multitude of reference comparisons with estimates from ENMs.

Methods

Study species

Sea kraits (genus *Laticauda*) are a clade of amphibious marine snakes that inhabit the warm waters and coastal regions along the eastern Indian Ocean, southeastern Asia, and archipelagoes of the western Pacific Ocean (Heatwole et al. 2005; Gherghel et al. 2016; Heatwole et al. 2016). Overall, the seven species of *Laticauda* have slightly variable amphibious ecologies: Species from the "*L. colubrina* complex" (4 species) are more terrestrial; species from the "*L. semifasciata* complex" (2 species) are more aquatic; and *L. laticaudata* (disregarding the closely related, lake-restricted *Laticauda crockeri*) is intermediate in habitat preference and usage frequency (Greer 1997; Heatwole 1999).

In this study, we used occurrence data for the seven *Laticauda* species compiled by Gherghel et al. (2016), with

the most occurrence records (448) corresponding to *L. colubrina* and the lowest number of records (6) corresponding to *L. schistorhynchus*. The records of this dataset were compiled from the published literature, author's (F.B.) personal records, and online databases (GBIF, HerpNet, iOBIS). Because these amphibious species are known to manifest a high degree of philopatry (Lane and Shine 2011), we converted points in the immediate vicinity of the coasts (within 1 km buffer from the coast) as the presence points for the terrestrial environment. Furthermore, we excluded the occurrence records that did not overlap temporally with the environmental data. The resulting marine and terrestrial occurrence point dataset was reduced to a unique occurrence per pixel at a corresponding resolution of the environmental data (9 km^2 for marine and 1 km^2 for terrestrial domains).

Environmental data

To calibrate our ENMs with marine environmental parameters, we used variables with a 5 arc-minute resolution (9 km) from two databases: Bio-ORACLE (Tyberghein et al. 2012) and Marspec (Sbrocco and Barber 2013). Of the 23 variables available in Bio-ORACLE and 18 in Marspec, we focused on eight environmental variables based on their likely influence on sea krait ecology and distributions (Table 1). Taken broadly, variables such as water temperature and ocean salinity have effects on the physiology of sea kraits and thus are likely to influence their distribution (Heatwole et al. 2012, 2017; Brischoux et al. 2012, 2013), while variables such as bathymetry and distance to the shoreline bear consequences on the foraging success of these species (Brischoux et al. 2007). Previously, these variables have been successfully used to model the distribution of sea kraits in the context of biotic interactions and estimating accessibility areas for the species (Gherghel et al. 2018, in press).

For generating terrestrial ENMs we used the WorldClim database comprising a set of 19 variables (referred to as bioclimatic variables) that represent seasonal, annual, or extreme temperature and precipitation values (Hijmans et al. 2005a, b). These same bioclimatic variables have been used previously for estimating distributions of terrestrial snake species and have produced reliable results (Nix 1986; Hijmans and Graham 2006; Bucklin et al. 2015). To reduce the high dimensionality of WordClim dataset, we ran multiple models to identify and eliminate variables associated with low model performance in a jackknife procedure (see Pearson et al. 2007 for details), after which a final set of 11 variables (Table 1) was used to estimate the terrestrial potential distribution of each *Laticauda* species at a resolution of 30 arc-seconds (1 km, highest available in WorldClim database). We projected

the ENMs to the same subset of 11 WorldClim variables over a wide region of the Indian and West Pacific Ocean coasts, at 2.5 arc-minute resolution (4.5 km), to obtain a broad, coarser-scale estimation of the distribution of sea kraits, overlapped with the marine suitability maps (see Integrating marine and terrestrial species' distribution predictions section of Methods).

Ecological niche modeling methodology

To generate marine and terrestrial ENMs for each sea krait taxon, we selected the maximum entropy algorithm, a widely used machine learning method implemented in Maxent 3.3.3 k (Phillips et al. 2006; Phillips and Dudik 2008; Franklin 2009). Maxent uses species' presence data and randomly selected background data (areas of unknown presence or absence) to create distributional constraints from environmental variables and finally calculate a model of the potential distribution of the studied species (Phillips et al. 2006; Phillips and Dudik 2008; Franklin 2009).

The extent of model calibrating (or training) region has a strong effect on ENMs (Barve et al. 2011) and thus has to be carefully selected; in our study, the extent of training region matched the area accessible for the species, delineated in a recent review of sea krait distributions (Gherghel et al. 2016). Based on the number of presence points available, we grouped the study species in two categories: (1) species with less than 30 points, for which we used *k*-fold cross-validation to generate subsets of model training and testing data and run replicate models, and (2) species with more than 30 points, for which we used a twofold approach where the occurrence data were split into 75% to train the models and 25% to test the models. To obtain binary prediction maps (suitable and unsuitable pixels), we applied a 10% omission threshold (Jimenez-Valverde 2014; Liu et al. 2016) to the model outputs, representing the Maxent suitability value at which 10% of training points are predicted unsuitable. All other Maxent parameters were left as default (10,000 random background points; auto-feature option; default regularization multiplier of 1; maximum 500 iterations; convergence threshold of 0.00001). The final models used in this study represented the average binary suitability across replicate runs, after applying the 10% omission error threshold.

To evaluate the performance of the models, we used the receiver operating characteristic (ROC) method, as well as a modification of the classic ROC, the partial ROC that considers only a section of the ROC curve, corresponding to a user-defined, acceptable omission error threshold (Peterson et al. 2008). We applied the partial ROC method for species with available occurrence points > 30, in addition to the classic ROC, and only the classic ROC for species with low presence samples, < 30. To compute

Table 1 Environmental variables and their contribution to ecological niche models of each species in marine and terrestrial environmental domains. Values represent percent contribution to accuracy of models

Domain	Variable name	Percent contribution of variables for each *Laticauda* species model						
		L. colubrina	*L. frontalis*	*L. guineai*	*L. latidaudata*	*L. schistorhynchus*	*L. semifasciata*	*L. saintgironsi*
Marine	Bathymetry**	5.1	5.5	53.9	1.6	5.1	6.4	16.2
	Distance from the shoreline**	89.3	66.4	19.6	85.1	75.7	75.1	46.5
	Maximum cloud coverage*	0.2	12.6	5.7	1.5	0.1	2.6	14.7
	Water clarity coefficient at 490 nm*	0.5	6.7	1.8	2.6	8.7	1.2	0.2
	Dissolved salt content*	1.1	3.9	16.9	3.2	10.2	4.1	0.6
	Mean sea surface temperature*	0.3	1.2	0.2	2.5	0.2	5.8	7.8
	Minimum sea surface temperature*	2.7	0	0.1	0.3	0	2.7	12.8
	Sea surface temperature range*	0.8	3.4	1.8	3.2	0	2.1	1.4
Terrestrial	Annual mean temperature***	10.1	0	0.3	7.8	0	3.8	18
	Isothermality***	8.7	27.1	0.1	21.9	17.5	1.1	21.7
	Temperature seasonality***	3.3	6.3	17.3	13.2	0	42.6	41.8
	Maximum temperature of warmest month***	8.8	1.5	5	1.7	29.1	0.3	0
	Minimum temperature of coldest month***	26.2	0.3	8	11.9	28.6	1.7	0
	Mean temperature of driest quarter***	6.5	16.8	6.5	1.6	0.1	0.4	2.6
	Mean temperature of coldest quarter***	14.4	10.3	2.9	4.1	8.3	16.7	1.8
	Precipitation of wettest month***	3.6	0.2	54.2	10.4	5.9	4.2	5.5
	Precipitation of driest month***	3.4	17.7	3.2	13.8	1.3	12.7	6.9
	Precipitation seasonality	0.7	0	1.1	12.3	8.3	16.1	1.4
	Precipitation of warmest quarter***	14.3	19.7	1.5	1.2	0.9	0.3	0.2

Asterisks indicate source of environmental data

*Variables from Bio-ORACLE dataset

**Variables from MARSPEC dataset

***Variables from WorldClim dataset

partial ROC scores, we used the *partialAUC* application (developed by Narayani Barve, University of Kansas), with 5% as omission error threshold and 100 bootstrap replicates, as suggested by Peterson et al. (2008). We also calculated the test omission error on the thresholded, binary models. For cross-validation runs (for species with low presence samples), we averaged the omission error values of the model replicates.

Integrating marine and terrestrial species' distribution predictions

We created potential distribution estimates that take into account both marine and terrestrial requirements of each species by integrating the ENMs generated for the two environments separately. We first calculated the overlap

between the predictions for the two environmental domains and applied a "nearest neighbor" interpolation technique to overlap the marine and terrestrial model predictions at a distance of 1 pixel inwards from the shoreline and outwards of the continents. We then produced model agreement maps between thresholded, binary (suitable–unsuitable) terrestrial and marine predictions (see *Ecological niche modeling methodology* section), similarly to the approach used by Gherghel et al. (in press). All geospatial data processing was done in ESRI ArcGIS 10.4 (ESRI 2011). The resulted integrated species' distribution predictions had values of 0 for areas predicted unsuitable in either marine or terrestrial environment, or both; values of 1 representing areas suitable only in one of the environments; and 2 for areas suitable in both marine and terrestrial environments.

Table 2 Ecological niche model design and performance for each species by environmental domain (marine and terrestrial)

Domain	Species	Model evaluation type	ROC AUC	Omission error	Partial ROC		
					$\bar{x}$	σ_x	α
Marine	*L. colubrina*	rp	0.97	0.10	1.94	0.01	s
	L. frontalis	c	0.99	0.17	–	–	–
	L. guineai	c	0.99	0.12	–	–	–
	L. laticaudata	rp	0.98	0.18	1.95	0.01	s
	L. saintgironsi	rp	0.99	0	2.00	0.00	s
	L. schistrohynchus	c	0.99	0.12	–	–	–
	L. semifasciata	rp	0.99	0.14	2.00	0.00	s
Terrestrial	*L. colubrina*	rp	0.87	0.13	1.33	0.08	s
	L. frontalis	c	0.99	0.14	–	–	–
	L. guineai	c	0.92	0.13	–	–	–
	L. laticaudata	rp	0.86	0.29	1.20	0.20	ns
	L. saintgironsi	rp	0.99	0.17	1.99	0.00	s
	L. schistrohynchus	c	0.99	0.25	–	–	–
	L. semifasciata	rp	0.87	0.13	1.55	0.18	s

c = *n*-fold cross-validation

rp = twofold cross-validation, 75% of data for model training, 25% for testing

$\bar{x}$ = mean partial ROC ratios

σ_x = standard deviation of partial ROC ratios

α = statistical significance level of 0.05

s significant, *ns* not significant

The final combined species distribution predictions were contrasted in ArcGIS 10.4 with the IUCN (International Union for Conservation of Nature) range maps for each studied sea krait species to assess the extent to which the range maps were predicted as suitable by our models and to outline other possible suitable areas that could be surveyed in order to find new populations of sea kraits.

Results

Predictor variables and model evaluation

Eight marine and eleven terrestrial predictors were chosen to build the ENMs for seven sea krait species. According to our models, the variables that best explained the distribution of sea kraits in the marine environment were distance from the shoreline, bathymetry, dissolved salt content in ocean, and cloud coverage (Table 1). For the terrestrial environment models, the most important variables were isothermality, temperature seasonality, precipitation of wettest month, minimum temperature of the coldest month, and precipitation of driest month (Table 1). However, interspecific differences in variable contributions were observed, where some variables had low importance for

one species' model and high for another species' model. For example, minimum sea surface temperature had high contribution (12.8%) to the models for *L. saintgironsi*, but did not exceed 2.7% for all other species (Table 1).

All three evaluation methods (classic AUC, omission error, and partial ROC) indicated that the ENMs for both domains (marine and terrestrial) performed well for all species, with the exception of the terrestrial model of *L. laticudata* that omitted 29% of the testing points, almost three times the error threshold of 10% training points (Table 2). The ROC AUC metric showed that all models were better than random model expectation (> 0.5; Table 2) and partial ROC analysis concluded that all models, for both environmental domains, were statistically significant (z test, $P < 0.05$; Table 2).

Species' potential distributions

We found that across all seven species, the terrestrial environment is the portion of the fundamental niche of the sea kraits that limits their distributions most, with the exception of *L. semifasciata* for which the marine environment is restricting its range. In general, our models predicted suitable conditions for sea kraits within the limits of IUCN expert range maps (Fig. 1), although all models
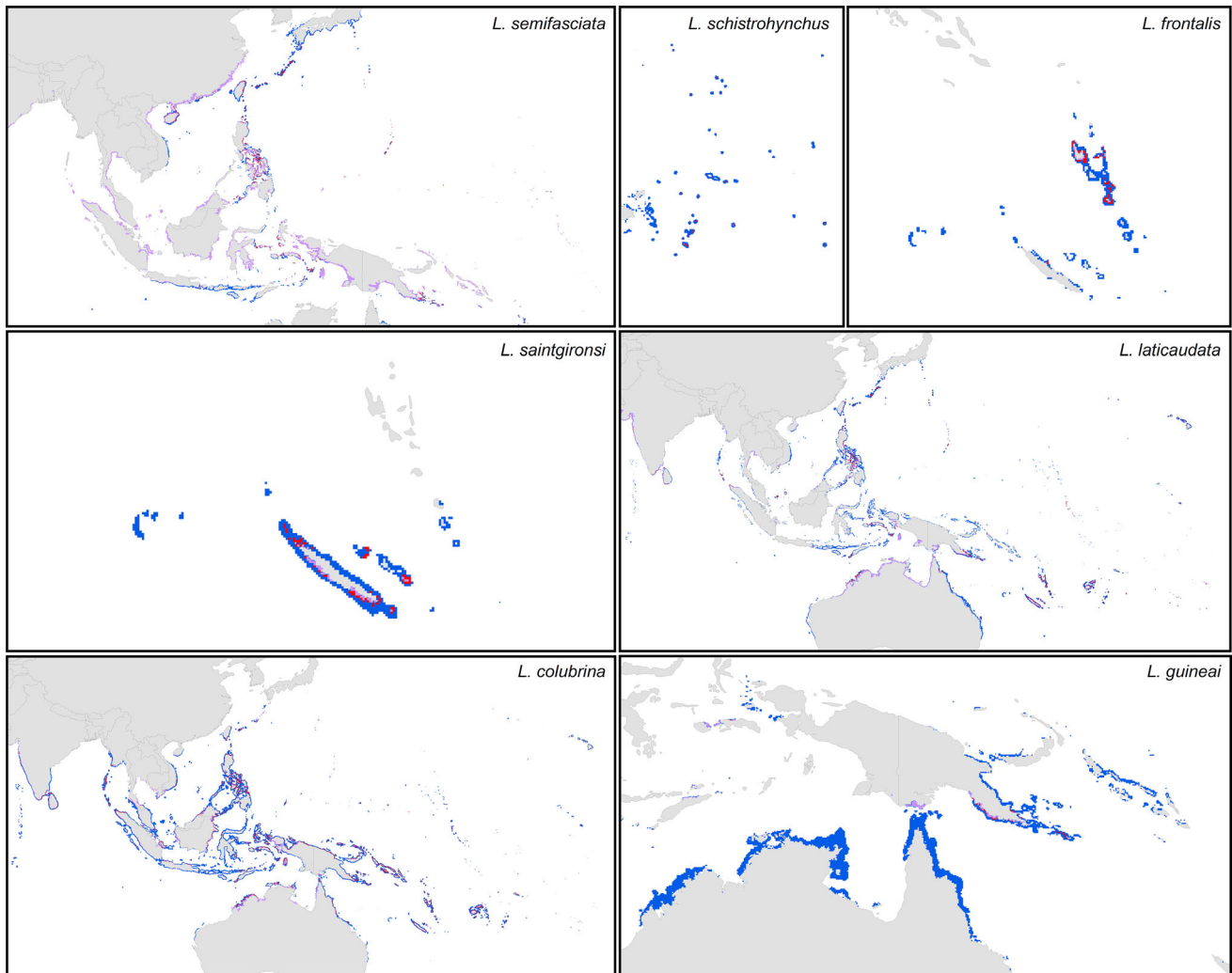
Fig. 1 Potential distribution of sea kraits estimated through dual (marine and terrestrial) ecological niche models. Blue represents areas that are suitable only in the marine environment; violet represents predicted additional areas as suitable outside species' currently known range, in both marine and terrestrial environmental domains; and red represents areas that are suitable in both marine and terrestrial environments

predicted additional areas as suitable outside species' currently known range, in both marine and terrestrial environmental domains (Fig. 1). According to our models, the most widespread species (*L. colubrina*, *L. laticaudata*, and *L. semifasciata*,) also have additional suitable areas outside of their presently documented range: along the coasts of Australia (especially Queensland and Western Australia) and India, and most of the Pacific archipelagoes for *L. laticaudata*; along Western Australian coasts, most of the Pacific archipelagoes, and patchy areas on the Indian subcontinent for *L. colubrina*; and along the coasts of Hong Kong, between Sulawesi and West Papua, and patchy in the rest of the Indonesia and Pacific archipelagoes (especially Vanuatu and Fiji) for *L. semifasciata* (Fig. 1). Moreover, some of the endemic species have potentially suitable areas outside of IUCN range maps: the coasts of Fiji Archipelago for *L. frontalis*; patchy suitable areas in

the Louisiade Archipelago for *L. guineai*; and American Samoa and French Polynesia archipelagoes for *L. schistrohynchus* (Fig. 1). However, our models estimated that *L. saintgironsi* had very limited suitable areas outside of its known range, these areas being restricted only around Norfolk Island and Lord Howe Island (Fig. 1).

Range-wide, our models predicted unsuitable 67.52% (corresponding to *L. guineai*) to 91.87% (corresponding to *L. frontalis*) of the species' IUCN range maps (Table 3). When analyzing suitability in both marine and terrestrial environmental domains, less than 1% of the IUCN range maps were predicted suitable, in case of *L. frontalis* and *L. laticaudata*, to around 2.5% or slightly higher for *L. colubrina*, *L. guineai*, *L. saintgironsi*, and *L. semifasciata* (Table 3). Our results suggest that only very small proportions of the total geographic extent of the IUCN range

Table 3 Comparison of potential distributions estimated with ecological niche models (ENMs) and IUCN range maps

Species	Not suitable	Partially suitable		Suitable
		Marine	Terrestrial	
L. colubrina	74.28%	22.59%	0.31%	2.82%
L. frontalis	91.87%	7.09%	0.16%	0.88%
L. guineai	67.52%	29.93%	0.00%	2.55%
L. laticaudata	90.30%	8.43%	0.37%	0.90%
L. saintgironsi	79.91%	17.14%	0.68%	2.27%
L. schistrohynchus	81.70%	16.99%	0.00%	1.31%
L. semifasciata	85.70%	8.62%	3.19%	2.49%

Percent of IUCN expert range map predicted in the following categories estimated with ENMs: not suitable, partially suitable (suitable in one environmental domain), and suitable (suitable in both marine and terrestrial environmental domains)

maps could meet the sea kraits' life history requirements in both marine and terrestrial environmental domains.

Discussion

Estimating species' geographic distributions is an important and expanding field of study, but remains a challenging task, even though in the past decade much effort and progress have been made to improve methodologies (Elith et al. 2006b; Peterson et al. 2007a, 2008; Warren et al. 2010; Austin and Van Niel 2011). Most of these methodologies are optimized for species limited to single environmental domains, whereas the methodologies for studying amphibious species have been largely overlooked, despite the fact that many of these species are of great conservation concern and difficult to investigate in the field (Gherghel et al. in press). Recently, Rickbeil et al. (2014) showed that incorporating both marine and terrestrial variables into models generated for shorebirds of British Columbia improves species' distributional estimates. Additionally, Frans et al. (2018) introduced a multistate SDM by which the authors aimed to account for the use of different habitats to improve estimates of species' distributions at local geographic scales. Overall, a methodology that integrates different environmental domains (such as marine and terrestrial) for large-scale species' distribution predictions has not been formalized yet, although current work is being done to fill the gap (Gherghel et al. in press). Here, we formally describe and propose an approach to study the potential geographic distribution of species that inhabit two distinct environmental domains (marine and terrestrial) by focusing on analyzing the heterogeneous distributions of sea kraits.

The necessity to develop species' distribution estimates that include both environments of an amphibious species has been discussed in the literature (Dambach and Rödder 2011; Rickbeil et al. 2014). Complementary to the multistate SDM approach by Frans et al. (2018) that combines habitat data for terrestrial species, here we propose to integrate multi-dimensional niche models that span distinct environments (i.e., terrestrial and marine) into a single niche estimate for each species that can be used to further refine a species' potential distribution. The approach that we proposed here is novel in that it considers independently the parameters and factors that affect the species' distribution in the two environmental domains, and then produces a summation of the two models generated for each environment. Because Maxent probability of suitability values are based on different subsets of the environmental space, and thus are not equal in significance, we recommend the use of thresholded, binary (suitable–unsuitable) ENM outputs, corresponding to each environmental domain, for the model summation. The argument supporting our approach of generating models separately for the two environmental domains lies in the reasoning that a species' life history characteristics are generally domain specific (e.g., different physiological requirements, tolerances, and rates of dispersal ability in water compared to land). The summation of the two model outputs improves our ability to estimate the species' distributions because we are considering both environments on which the organisms depend. Our proposed approach does not require modifications of the modeling software or assumptions based on which models are created, thus enabling its use broadly by investigators studying species that inhabit more than one environmental domain. Since the approach we have outlined in this study is relying on ENMs, it will not be immune to the known problems and limitations of ENMs (Peterson 2006; Austin 2007; Franklin 2009; Bedia et al. 2013). Perhaps the most common issues that ENMs are facing are the omission error (known occurrences predicted absent) and commission error (overpredicting the species' distribution) (Franklin 2009). Both error types need to be addressed when creating ENMs in general, but especially when our method for dual-environment species is applied. The main concern is that, when summing the outputs of the two ENMs (marine and terrestrial potential distributions), both omission and commission errors would be reflected in the final distribution estimate which will over- or under-predict the potential distribution of the species. Since omission error can be calculated directly (Phillips et al. 2006), we suggest addressing this problem by reporting the omission error of both ENMs that have been used to create the final potential distribution estimate. On the other hand, commission error is harder to interpret, but in general considered less

problematic than omission error (Anderson et al. 2003), although an extension of the current framework described here allows quantifying for commission error in such complex ENMs (Gherghel et al. in press). The final potential distributions produced using the approach proposed here clearly depend on the performance of individual ENMs that are being summed. Hence, limitations posed by the data quality, spatial bias, variable selection, and omission and commission errors need to be addressed and efforts have to be made to control for them, using knowledge of the species' ecology, distribution, life history, and biogeography. By controlling for as many as possible sources of error in the ENMs, the approach presented here should facilitate estimating potential distributions of amphibious species.

Of the two environmental data categories (marine and terrestrial) used to estimate the potential distribution of sea kraits, the models produced with marine data had, on average, lower omission error than those produced with terrestrial data (Table 1). One possible explanation for the better fit of marine models is that marine environments are more stable and exhibit less variation (Robinson et al. 2011) than the terrestrial environments where atmospheric conditions, topography, and vegetation create a more heterogeneous environment (Hijmans et al. 2005a), hence less uniformity in data translates to an overall lower model fit and predictive ability of distributions of species in question. Moreover, the scale (extent and grain) of the environmental datasets can have a great influence on the modeling process (Seo et al. 2009; Austin and Van Niel 2011), thus careful consideration needs to be given to the selection of scale, especially in light of knowledge of the life history characteristics of the study species (Austin and Van Niel 2011; Anderson 2013). For example, previous studies have shown fundamental differences between employing landscape and seascape modeling in which marine predictors (and thus the scale) generally do not need to be as fine as the terrestrial predictors as long they represent the ecological niche of the target species [i.e., 6 km resolution for whales (Bombosch et al. 2014), 25 m resolution for the New Zealand sea lion (Frans et al. 2018)]. Rickbeil et al. (2014) found a better fit of shorebird occurrences with terrestrial variables than marine variables due to the life history of species studied. Hence, the importance of variables is arguably distinct at different scales and depends on specific ecological requirements and life history characteristics of the studied species. However, our approach departs from these studies in the sense that it aims to model a closer estimate of the fundamental niche (sensu Hutchinson 1957) and can be applied to broad-scale predictions of species' distributions, whereas recently proposed applications (Frans et al. 2018) aim to model components of the fundamental niche of the species (e.g.,

different habitats within a single environmental domain, terrestrial).

How well does this new approach work? A case study of sea kraits

Our models recovered the known distribution of the species and predicted additional suitable areas for each species in both environmental domains considered (Fig. 1). The previous work by Gherghel et al. (in press) used these models to predict sea kraits distributions in the context of species' dispersal over the Pacific and Indian Oceans. In the case of an island system, these results could have implications for field surveys that aim to locate new populations, by narrowing the search to islands that meet the suitability criteria for sea kraits.

Generally, our models predicted as suitable wider areas for sea kraits in the marine environment than the terrestrial one, the latter being most likely the limiting factor for sea krait distribution [Fig. 1, Table 3; see also (Gherghel et al. in press)]. These patterns suggest that the terrestrial portion of the fundamental niche has a stronger effect on the more terrestrial sea krait species (*L. colubrina* complex, four species), whereas the marine portion of the fundamental niche has a stronger effect on the more marine sea krait species (*L. semifasciata* complex, 2 species). Interestingly, the exception is *L. semifasciata*, a sea krait most dependent on the marine environment (Heatwole 1999), for which our models estimated a wider terrestrial potential distribution than the marine one. Overall, the current IUCN range maps for sea kraits are overestimated (Heatwole et al. 2016); however, the magnitude of this overrepresentation is striking. Heatwole et al. (2016) suggested that these range maps are overestimated by 20% to 39%; however, by modeling marine and terrestrial niches we found the overestimation to be even larger. This finding has significance in the context of global warming as the predicted rise of sea level could affect shoreline extent and available habitats (Feagin et al. 2005), and hence the potentially suitable areas, especially for species with the very limited suitable area in the terrestrial environment. Based on our results and other recently published work (i.e., Breiner et al. 2017), we suggest employing IUCN range maps for biodiversity studies with caution, and we highly recommend future improvement of the range maps to include species' environmental preferences.

References

Anderson RP (2013) A framework for using niche models to estimate impacts of climate change on species distributions. Annals of the New York Academy of Sciences 1297:8–28

Anderson RP, Lew D, Peterson AT (2003) Evaluating predictive models of species' distributions: criteria for selecting optimal models. Ecol Model 162:211–232

Austin M (2007) Species distribution models and ecological theory: a critical assessment and some possible new approaches. Ecol Model 200:1–19

Austin MP, Van Niel KP (2011) Improving species distribution models for climate change studies: variable selection and scale. J Biogeogr 38:1–8

Barve N, Barve V, Jimenez-Valverde A, Lira-Noriega A, Maher SP, Peterson AT, Soberon J, Villalobos F (2011) The crucial role of the accessible area in ecological niche modeling and species distribution modeling. Ecol Model 222:1810–1819

Bedia J, Herrera S, Gutiérrez JM (2013) Dangers of using global bioclimatic datasets for ecological niche modeling. Limitations for future climate projections. Global Planet Change 107:1–12

Bombosch A, Zitterbart DP, Van Opzeeland I, Frickenhaus S, Burkhardt E, Wisz MS, Boebel O (2014) Predictive habitat modelling of humpback (Megaptera novaeangliae) and Antarctic minke (Balaenoptera bonaerensis) whales in the Southern Ocean as a planning tool for seismic surveys. Deep Sea Research Part I: Oceanographic Research Papers 91:101–114

Breiner FT, Guisan A, Nobis MP, Bergamini A (2017) Including environmental niche information to improve IUCN Red List assessments. Divers Distrib 23:484–495

Brischoux F, Bonnet X, Shine R (2007) Foraging ecology of sea kraits Laticauda spp. in the Neo-Caledonian Lagoon. Mar Ecol Prog Ser 350:145–151

Brischoux F, Tingley R, Shine R et al (2012) Salinity influences the distribution of marine snakes: implications for evolutionary transitions to marine life. Ecography 35(11):994–1003

Brischoux F, Tingley R, Shine R et al (2013) Behavioral and physiological correlates of the geographic distributions of amphibious sea kraits (Laticauda spp.). Journal of Sea Research 76:1–4

Bucklin DN, Basille M, Benscoter AM, Brandt LA, Mazzotti FJ, Romanach SS, Speroterra C, Watling JI (2015) Comparing species distribution models constructed with different subsets of environmental predictors. Divers Distrib 21:23–35

Dambach J, Rödder D (2011) Applications and future challenges in marine species distribution modeling. Aquatic Conservation: Marine and Freshwater Ecosystems 21:92–100

Elfes CT, Livingstone SR, Lane A, Lukoschek V, Sanders KL, Courtney AJ, Gatus JL, Guinea M, Lobo AS, Milton D (2013) Fascinating and forgotten: the conservation status of the world's sea snakes. Herpetol Conserv Bio 8:37–52

Elith J, Graham CH, Anderson RP, Dudik M, Ferrier S, Guisan A, Hijmans RJ, Huettman F, Leathwick JR, Lehmann A, Li J, Lohmann LG, Loiselle BA, Manion G, Moritz C, Nakamura M, Nakazawa Y, Overton JM, Peterson AT, Phillips SJ, Richardson K, Scachetti-Pereira R, Schapire RE, Soberón J, Williams SE, Wisz MS, Zimmermann NE (2006) Novel methods improve prediction of species' distributions from occurrence data. Ecography 29:129–151

ESRI (2011) ArcGIS desktop: release 10. Environmental Systems Research Institute, Inc., Redlands

Feagin RA, Sherman DJ, Grant WE (2005) Coastal erosion, global sea-level rise, and the loss of sand dune plant habitats. Front Ecol Environ 3:359–364

Folland C, Salinger M, Rayner N (1997) A comparison of annual South Pacific island and ocean surface temperatures. Weather and Climate 17:23–42

Franklin J (2009) Mapping species distributions: spatial inference and prediction. Cambridge University Press, Cambridge

Frans VF, Auge AA, Edelhoff H, Erasmi S, Balkenhol N, Engler JO (2018) Quantifying apart what belongs together: a multi-state species distribution modelling framework for species using distinct habitats. Methods Ecol Evol 9:98–108

Gherghel I, Brischoux F, Papeş M (2018) Using biotic interactions in broad-scale estimates of species' distributions. J Biogeogr 45:2216–2225

Gherghel I, Brischoux F, Papeş M (In Press) Refining model estimates of potential species' distributions to relevant accessible areas. Prog Phys Geog: Earth Envt 1–12

Gherghel I, Papes M, Brischoux F, Sahlean T, Strugariu A (2016) A revision of the distribution of sea kraits (Reptilia, Laticauda) with an updated occurrence dataset for ecological and conservation research. Zookeys 569:135–148

Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. Ecol Model 135:147–186

Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. Ecol Lett 8:993–1009

Greer AE (1997) The biology and evolution of Australian snakes. Surrey Beatty, Sydney

Heatwole H (1999) Sea snakes. Krieger Publishing Company, Malabar

Heatwole H, Busack S, Cogger H (2005) Geographic variation in sea kraits of the Laticauda colubrina complex (Serpentes: Elapidae: Hydrophiinae: Laticaudini). Herpetol Monogr 19:1–136

Heatwole H, Grech A, Monahan JF et al (2012) Thermal biology of sea snakes and sea kraits. Integrative and Comparative Biology 52(2):257–273

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

Heatwole H, Grech A, Marsh H (2017) Paleoclimatology, paleo-geography, and the evolution and distribution of sea kraits (Serpentes; Elapidae; Laticauda). Herpetol Monogr 31:1–17

Hijmans R, Cameron S, Parra J, Jones P, Jarvis A (2005a) Very high resolution interpolated climate surfaces for global land areas. Int J Climatol 25:1965–1978

Hijmans RJ, Graham CH (2006) The ability of climate envelope models to predict the effect of climate change on species distributions. Global Change Biol 12:2272–2281

Hijmans RJ, Cameron S, Parra J (2005b) WorldClim, Version 1.4, http://www.worldclim.org. University of California, Berkeley

Hutchinson GE (1957) Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology 22:415–427

Jimenez-Valverde A (2014) Threshold-dependence as a desirable attribute for discrimination assessment: implications for the evaluation of species distribution models. Biodivers Conserv 23:369–385

Jimenez-Valverde A, Barve N, Lira-Noriega A, Maher SP, Nakazawa Y, Papes M, Soberon J, Sukumaran J, Peterson AT (2011) Dominant climate influences on North American bird distributions. Global Ecol Biogeogr 20:114–118

Lane A, Shine R (2011) Intraspecific variation in the direction and degree of sex-biased dispersal among sea-snake populations. Mol Ecol 20:1870–1876

Liu C, Newell G, White M (2016) On the selection of thresholds for predicting species occurrence with presence-only data. Ecol Evol 6:337–348

Manzu C, Gherghel I, Zamfirescu S, Zamfirescu O, Rosca I, Strugariu A (2013) Current and Future Potential Distribution of Glacial

Relict Ligularia Sibirica (Asteracee) in Romania and Temporal Contribution of Natura 2000 to Protect the Species in Light of Global Change. Carpath J Earth Env 8:77–87

Mueller EK, Baum KA, Papes M, Cohn LA, Cowell AK, Reichard MV (2013) Potential ecological distribution of Cytauxzoon felis in domestic cats in Oklahoma, Missouri, and Arkansas. Vet Parasitol 192:104–110

Nix HA (1986) A biogeographic analysis of Australian elapid snakes. In: Longmore R (ed) Atlas of elapid snakes of Australia. Australian Government Publishing Service, Canberra, pp 4–15

Pearson RG, Raxworthy CJ, Nakamura M, Peterson AT (2007) Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. J Biogeogr 34:102–117

Peterson AT (2006) Uses and requirements of ecological niche models and related distributional models. Biodiversity Informatics 3:59–72

Peterson AT, Martínez-Meyer E (2007) Geographic evaluation of conservation status of African forest squirrels (Sciuridae) considering land use change and climate change: the importance of point data. Biodivers Conserv 16:3939–3950

Peterson AT, Soberon J (2012) Species distribution modeling and ecological niche modeling: getting the concepts right. Nat Conservacao 10:102–107

Peterson AT, Papeş M, Kluza DA (2003) Predicting the potential invasive distributions of four alien plant species in North America. Weed Science 51:863–868

Peterson AT, Papes M, Eaton M (2007a) Transferability and model evaluation in ecological niche modeling: a comparison of GARP and Maxent. Ecography 30:550–560

Peterson AT, Benz BW, Papeş M (2007b) Highly pathogenic H5N1 avian influenza: entry pathways into North America via bird migration. PLoS ONE 2:e261

Peterson AT, Papes M, Soberon J (2008) Rethinking receiver operating characteristic analysis applications in ecological niche modeling. Ecol Model 213:63–72

Peterson AT, Ortega-Huerta MA, Bartley J, Sánchez-Cordero V, Soberón J, Buddemeier RH, Stockwell DRB (2002) Future projections for Mexican faunas under global climate change scenarios. Nature 416:626–629

Phillips SJ, Dudik M (2008) Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31:161–175

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecol Model 190:231–259

Rickbeil GJM, Coops NC, Drever MC, Nelson TA (2014) Assessing coastal species distribution models through the integration of terrestrial, oceanic and atmospheric data. J Biogeogr 41:1614–1625

Robinson LM, Elith J, Hobday AJ, Pearson RG, Kendall BE, Possingham HP, Richardson AJ (2011) Pushing the limits in marine species distribution modelling: lessons from the land present challenges and opportunities. Global Ecol Biogeogr 20:789–802

Roever CL, Beyer HL, Chase MJ, van Aarde RJ (2014) The pitfalls of ignoring behaviour when quantifying habitat selection. Divers Distrib 20:322–333

Sahlean TC, Gherghel I, Papes M, Strugariu A, Zamfirescu SR (2014) Refining climate change projections for organisms with low dispersal abilities: a case study of the Caspian Whip Snake. PLoS ONE 9:e91994

Sbrocco EJ, Barber PH (2013) MARSPEC: ocean climate layers for marine spatial ecology. Ecology 94:979

Seo C, Thorne JH, Hannah L, Thuiller W (2009) Scale effects in species distribution models: implications for conservation planning under climate change. Biol Letters 5:39–43

Shetty S, Shine R (2002) Sexual divergence in diets and morphology in Fijian sea snakes Laticauda colubrina (Laticaudinae). Austral Ecology 27:77–84

Siqueira MFd, Peterson AT (2003) Global climate change consequences for cerrado tree species. Biota Neotropica 3:1–14

Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFN, Ferreira de Siqueira M, Grainger A, Hannah L, Hughes L, Huntley B, Van Jaarsveld AS, Midgely GE, Miles L, Ortega-Huerta MA, Peterson AT, Phillips OL, Williams SE (2004) Extinction risk from climate change. Nature 427:145–148

Tyberghein L, Verbruggen H, Pauly K, Troupin C, Mineur F, De Clerck O (2012) Bio-ORACLE: a global environmental dataset for marine species distribution modelling. Global Ecol Biogeogr 21:272–281

Warren DL, Glor RE, Turelli M (2010) ENMTools: a toolbox for comparative studies of environmental niche models. Ecography 33:607–611

Welk E, Schubert K, Hoffmann MH (2002) Present and potential distribution of invasive garlic mustard (Alliaria petiolata) in North America. Divers Distrib 8:219–233