



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

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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.

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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 km² for marine and 1 km² 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; Brischox et al. 2012, 2013), while variables such as bathymetry and distance to the shoreline bear consequences on the foraging success of these species (Brischox 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 WorldClim 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 <i>Laticauda</i> species model						
		<i>L. colubrina</i>	<i>L. frontalis</i>	<i>L. guineai</i>	<i>L. latidaudata</i>	<i>L. schistorhynchus</i>	<i>L. semifasciata</i>	<i>L. saintgironsi</i>
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	<i>L. colubrina</i>	rp	0.97	0.10	1.94	0.01	s
	<i>L. frontalis</i>	c	0.99	0.17	–	–	–
	<i>L. guineai</i>	c	0.99	0.12	–	–	–
	<i>L. laticaudata</i>	rp	0.98	0.18	1.95	0.01	s
	<i>L. saintgironsi</i>	rp	0.99	0	2.00	0.00	s
	<i>L. schistrohynchus</i>	c	0.99	0.12	–	–	–
	<i>L. semifasciata</i>	rp	0.99	0.14	2.00	0.00	s
Terrestrial	<i>L. colubrina</i>	rp	0.87	0.13	1.33	0.08	s
	<i>L. frontalis</i>	c	0.99	0.14	–	–	–
	<i>L. guineai</i>	c	0.92	0.13	–	–	–
	<i>L. laticaudata</i>	rp	0.86	0.29	1.20	0.20	ns
	<i>L. saintgironsi</i>	rp	0.99	0.17	1.99	0.00	s
	<i>L. schistrohynchus</i>	c	0.99	0.25	–	–	–
	<i>L. semifasciata</i>	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

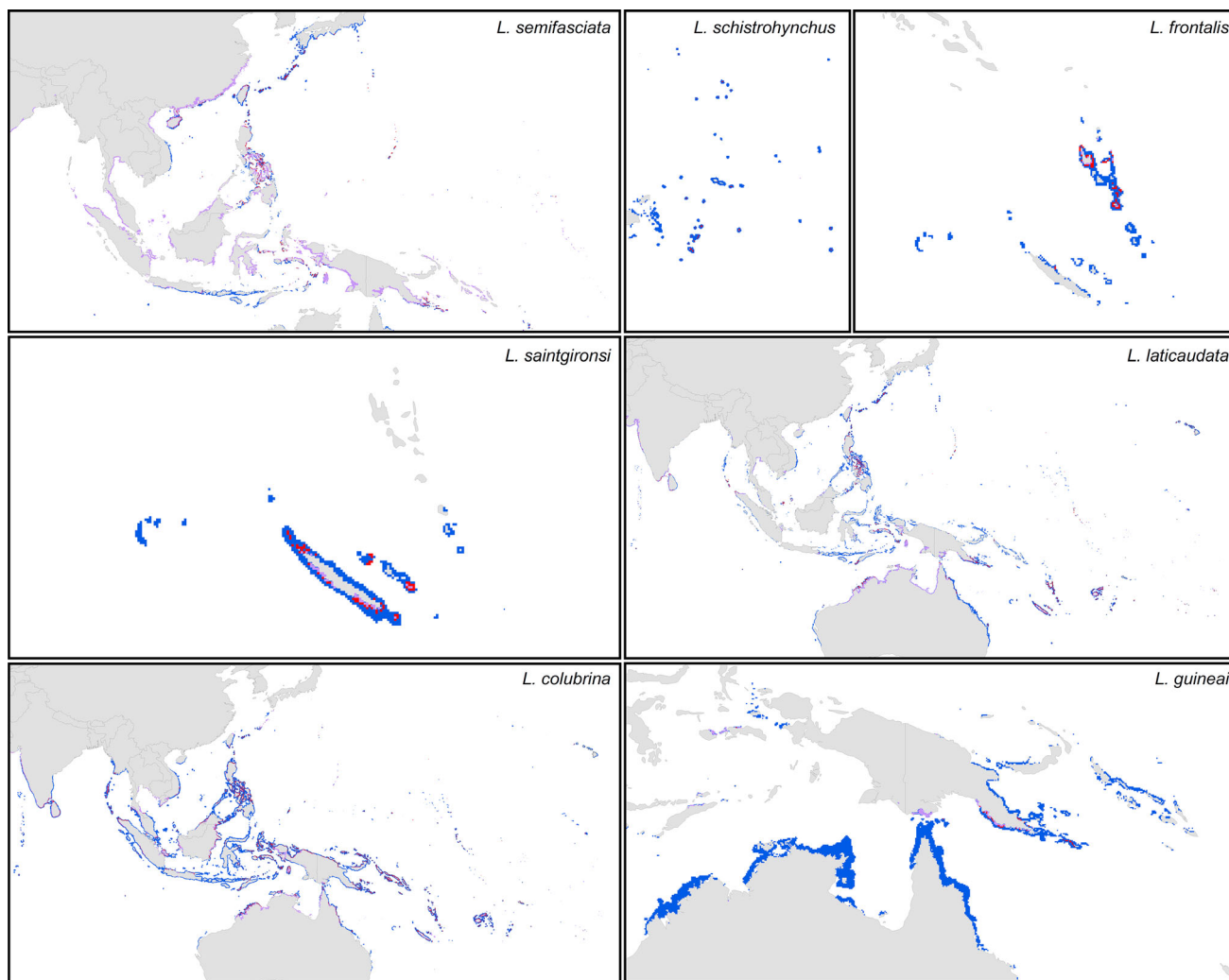


Fig. 1 Potential distribution of sea kraits estimated through dual (marine and terrestrial) ecological niche models. Blue represents areas that are suitable only in the marine environment; violet represents

predicted additional areas as suitable outside species' currently known range, in both marine and terrestrial environmental domains (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

areas that are suitable only in terrestrial environment; and red represents areas that are suitable in both marine and terrestrial environments

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	
<i>L. colubrina</i>	74.28%	22.59%	0.31%	2.82%
<i>L. frontalis</i>	91.87%	7.09%	0.16%	0.88%
<i>L. guineai</i>	67.52%	29.93%	0.00%	2.55%
<i>L. laticaudata</i>	90.30%	8.43%	0.37%	0.90%
<i>L. saintgironsi</i>	79.91%	17.14%	0.68%	2.27%
<i>L. schistrohynchus</i>	81.70%	16.99%	0.00%	1.31%
<i>L. semifasciata</i>	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 multi-state 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.

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