



Using biotic interactions in broad-scale estimates of species' distributions

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Abstract

Aim: To examine the combined effect of abiotic and biotic factors on species distributions in a marine environment. Specifically, we aim to account for the effects of trophic interactions at broad scales in ecological niche models (ENMs) of sea kraits (*Laticauda*: Reptilia) by including the potential distribution of food resources as predictor variables.

Location: Oceania and Southeast Asia.

Methods: First, we outline a simple method to generate biotic interaction variables for ENMs. We then test whether ENMs that include biotic interactions perform better than ENMs based on abiotic variables only.

Results: The models based on biotic interactions (i.e. trophic interactions) and abiotic variables slightly outperformed the models informed only by abiotic variables. We found a strong relationship between prey species richness and probability of distribution of predator (sea kraits). The models that included potential distributions of prey species as predictor variables showed an increase in proportion of pixels predicted present and a decrease in omission error, compared with models based only on abiotic variables.

Main conclusions: Distribution estimates of predator species at broad scales are more accurate if calibration of ENMs includes relevant biotic variables (prey species richness, in this study). Hence, when data are available, biotic variables should be included in ENMs.

KEYWORDS

ecological niche modelling, Maxent, resource availability, sea kraits, species distribution modelling, species' interactions

1 | INTRODUCTION

The ecological niche of a species comprises all abiotic and biotic requirements that allow individuals to survive, develop and reproduce (Hutchinson, 1957). This totality of requirements has been coined by Hutchinson (1957) as the n -dimensional niche and has been debated in the expanding field of ecological niche modelling or species distribution modelling. The focus of this field is to estimate species' distributions by examining the relationship between known species' occurrences and environmental variables (Peterson et al., 2011). Soberón and Peterson (2005) and, later, Soberón and

Nakamura (2009) and Soberón (2010) incorporated the Hutchinson (1957) niche concept into the BAM diagram consisting of three components: the Biotic (B) and Abiotic (A) conditions necessary for the species' survival, and Mobility (M), the species' ability to disperse to suitable areas. Although this framework includes biotic interactions and species' dispersal abilities, ecological niche modelling has been centred on abiotic requirements of species. Generally, abiotic, climate-based factors influence species' distributions at broad scales, as species have physiological limits (e.g. freeze tolerance, humidity preference, see Araújo et al., 2013; Eme et al., 2014; Gouveia et al., 2014; Sunday, Bates, & Dulvy, 2011). While the role of abiotic

factors on species' distribution estimates has been the subject of many studies in the past couple of decades (e.g. Jimenez-Valverde et al., 2011; Lee, Papeş, & Van den Bussche, 2012; Peterson et al., 2002; Raxworthy et al., 2003), few studies have investigated the effects of biotic interactions on species' distribution estimates (see Anderson, 2017; Trainor & Schmitz, 2014; Wisz et al., 2013).

The role of one type of biotic interaction, namely trophic relationships, on population persistence has attracted much interest in ecological research, having a fundamental influence on our understanding of a wide range of topics in ecology, including community structure, speciation and species' distributions (Estes et al., 2011; Holt & Barfield, 2009; Trainor, Schmitz, Ivan, & Shenk, 2014). Trophic interactions (food webs) connect ecological communities in networks, whereby direct pathways of energy transfer link nodes (species) in a hierarchical organizational system (Estes et al., 2011; Scotti, Bondavalli, Bodini, & Allesina, 2009). One major weakness in our understanding of the role of biotic interactions, such as trophic interactions, is scalability (McGill, 2010; Whittaker, Willis, & Field, 2001). While these interactions are highly dynamic in time and can strongly affect population demographics and community structure, our understanding of how trophic interactions affect species' distributions at broad scales (e.g. continental) is limited (Araújo & Rozenfeld, 2014; Wisz et al., 2013). This has resulted in a debate on whether the geographical patterns of species are determined by abiotic characteristics or by interactions among species. Gotelli, Graves, and Rahbek (2010) found that at extents of few hundred kilometres some biotic interactions (competition) are still noticeable. However, at extents of biomes these interactions are greatly diluted (Russell, Wood, Allison, & Menge, 2006). While the effects of trophic interactions on broad-scale distributions of species have rarely been investigated (see Araújo & Rozenfeld, 2014; Wisz et al., 2013 for recent reviews), broad-scale species' distributions are likely to be influenced by a combination of abiotic and biotic factors (Peterson et al., 2011; Soberón, 2007, 2010).

Currently, many efforts to investigate species' distributions at broad scales involve ecological niche modelling that estimates species distributions using correlations between species' occurrences and environmental variables (Elith et al., 2006; Peterson et al., 2011). Ideally, if the goal is to estimate occupied distributions, the ecological niche models (ENMs) would be calibrated with both abiotic and biotic factors that might influence the distribution of species (Peterson et al., 2011; Soberón, 2007, 2010). Recent studies have shown that availability and abundance of prey strongly influence the presence and abundance of consumer species (Araújo, Marcondes-Machado, & Costa, 2014; Womble, Sigler, & Willson, 2009). Yet, the inclusion of biotic interactions along with abiotic (generally climatic) variables in ENMs has received little attention in the literature (Araújo & Rozenfeld, 2014; Peterson et al., 2011; Wisz et al., 2013). Inclusion of biotic interactions in ENMs is difficult due to their temporally and spatially dynamic nature (Peterson et al., 2011; Soberón, 2007, 2010; Soberón & Nakamura, 2009). Moreover, Soberón and Nakamura (2009) suggested that, at broad scales, biotic interactions are highly diluted and represent noise, referred to as "Eltonian noise

hypothesis." However, for the trophic interactions to occur, the organism subject to predation (the food resource) has to be located in the same geographical space as the consumer (Cohen, 1977). This basic assumption could offer a simple solution to including species interactions into ENMs. At broad scales, quantifying prey species richness for a consumer across its geographical range may provide the means to account for trophic interactions in ENMs and to test whether such interactions are influencing species' distributions.

In this paper, we investigate the importance of biotic interactions to estimating species' distributions at broad spatial scales through a case study of sea kraits (*Laticauda*: Reptilia), tropical marine snakes that feed almost exclusively on eels (Ineich et al., 2007). We included the potential distribution of prey species (mostly eels) as a predictor in ENMs of predator species, the sea kraits. We address two questions: (a) are predator models improved when estimates of trophic resources (prey) are included as predictors? and (b) are trophic interactions detectable at broad scales? While most of the knowledge of estimating broad geographical distributions of species is generally based on terrestrial organisms (see Wisz et al., 2013 for a recent review), our study is one of the few to examine the combined effect of abiotic and biotic factors on species' distribution estimates in a marine environment. Furthermore, we infer the importance of trophic interactions in the context of ENMs performance and broad-scale species' distributions.

2 | MATERIALS AND METHODS

2.1 | Study species and data collection

Sea kraits (*Laticauda*: Reptilia) are proteroglyphous (front-fanged) snakes widely distributed along the tropical reefs of eastern Indian Ocean and western Pacific Ocean (Figure 1; Heatwole, 1999; Heatwole, Busack, & Cogger, 2005). Currently, three distinct groups of sea kraits are recognized: the black-banded sea kraits [*L. semifasciata* (Reinwardt in Schlegel, 1837) and *L. schistorhyncha* (Günther, 1874)], the yellow-banded sea kraits [*L. colubrina* (Schneider, 1799), *L. frontalis* (De Vis, 1905), *L. gunyai* (Heatwole et al., 2005) and *L. saintgironsi* (Cogger & Heatwole, 2006)], and the blue-banded sea kraits [*L. laticaudata* (Linnaeus, 1758) and *L. crockeri* (Slevin, 1934)] (Cogger & Heatwole, 2006; Cogger et al., 1987; Heatwole, 1999; Heatwole et al., 2005; Lane & Shine, 2011a,b). All sea krait species (with the exception of *L. crockeri*) display adaptations for marine life (e.g. salt-excreting glands, flattened tail), but, while sea kraits forage at sea, they return to land to mate, lay eggs and digest their prey (Heatwole, 1999). Sea kraits are benthic foragers, exploring burrows in the seafloor and coral reefs in search for anguilliform fish (Brischoux, Bonnet, & Shine, 2007, 2009; Ineich et al., 2007). From a feeding ecology perspective, sea kraits are trophic specialists, with up to 99.6% of their diet consisting of various eel species (Ineich et al., 2007).

Predator occurrence data were comprised of a database of 694 unique records of all *Laticauda* species (Gherghel, Papes, Brischoux, Sahlean, & Strugariu, 2016), further refined based on Heatwole, Grech, and Marsh (2017), that were georeferenced at a resolution of 9 km,

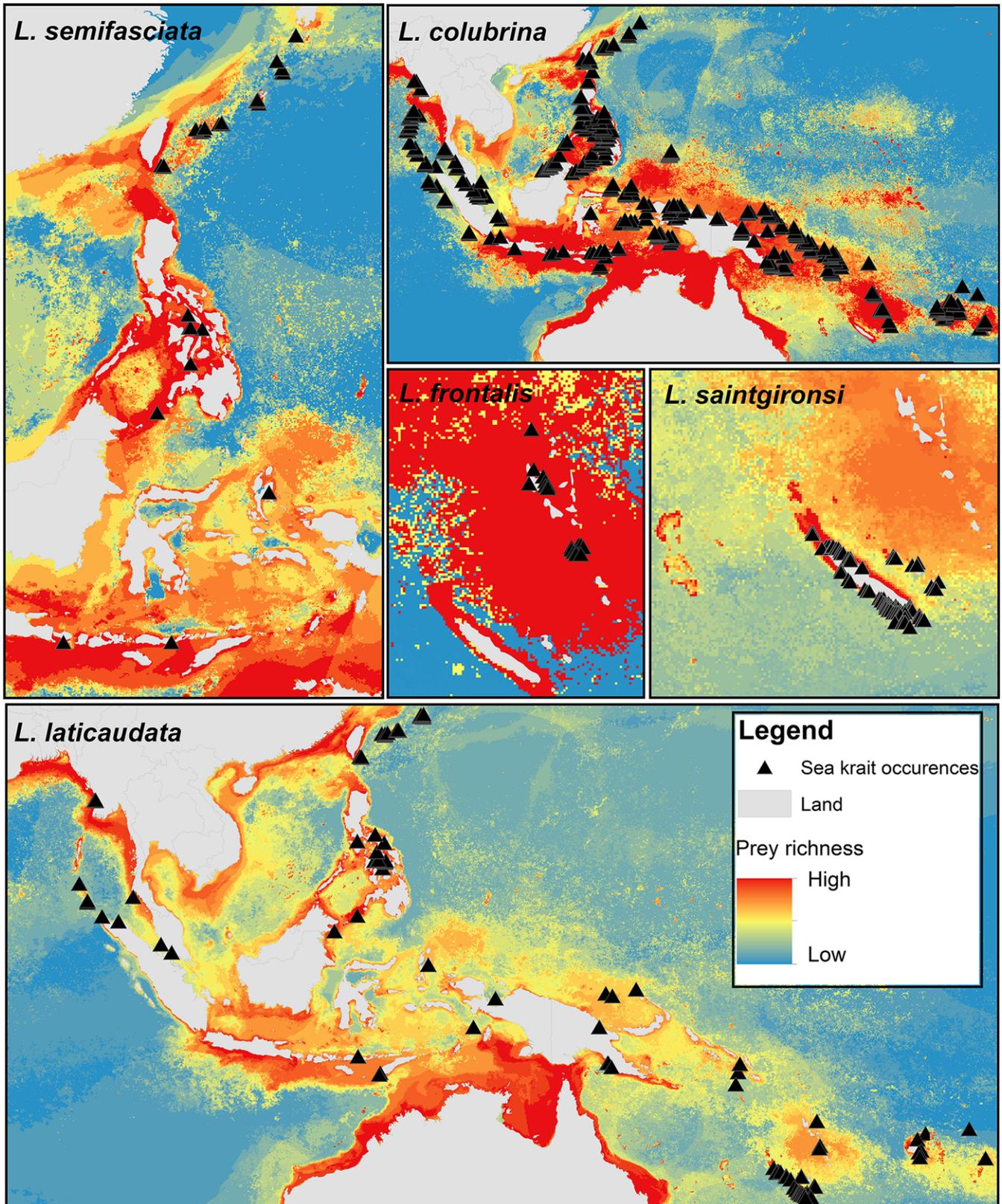


FIGURE 1 Distribution patterns of estimated prey species richness (colour gradient) and occurrence points (black triangles) used to calibrate the ecological niche models of sea kraits (adapted from Gherghel et al., 2016). The colour gradient represents the estimated prey species richness: blue areas were predicted suitable (by ecological niche models) for low numbers of prey species and red areas for high numbers of prey species

corresponding to the resolution of environmental layers used in our ENMs (see Environmental data section for details). We focused our study on *L. colubrina* ($n = 432$), *L. laticaudata* ($n = 107$), *L. frontalis* ($n = 17$), *L. saintgironsi* ($n = 75$) and *L. semifasciata* ($n = 28$), species for which the trophic ecology has been thoroughly described (e.g. Brischoux, Bonnet, Cherel, & Shine, 2011; Brischoux et al., 2007, 2009; Heatwole, 1999; Ineich et al., 2007; Su, Fong, & Tu, 2005). Prey information was compiled from existing literature on feeding ecology of sea kraits (Appendix S1), from which we recorded the prey species in a database (Appendix S2). Our database of prey species (Appendix S2) contained 7538 occurrence records for the 48 species, mostly anguilliform fish: *Abudefduf sexfasciatus* ($n = 402$), *Acanthurus mata* ($n = 98$), *Anarchias allardicei* ($n = 48$), *A. cantonensis* ($n = 22$), *A. seychellensis* ($n = 96$), *Centropyge heraldi* ($n = 142$), *Cirrhitichthys aprinus* ($n = 129$), *Conger cinereus* ($n = 296$), *Ctenochaetus striatus* ($n = 767$), *Echidna delicatula* ($n = 20$), *E. unicolor* ($n = 40$), *Enchelycore pardalis* ($n = 41$), *Enchelynassa canina* ($n = 38$), *Grammistes sexlineatus* ($n = 302$), *Gymnomuraena zebra* ($n = 75$), *Gymnothorax buroensis* ($n = 338$), *G. chilospilus* ($n = 245$), *G. enigmaticus* ($n = 90$), *G. eurostus* ($n = 122$), *G. fimbriatus* ($n = 240$), *G. formosus* ($n = 15$), *G. fuscocomaculatus* ($n = 125$), *G. gracilicauda* ($n = 37$), *G. margaritophorus* ($n = 256$), *G. nudivomer* ($n = 11$), *G. pindae* ($n = 122$), *G. pseudothyroideus* ($n = 176$), *G. reevesii* ($n = 22$), *G. reticularis* ($n = 40$), *G. richardsonii* ($n = 70$), *G. undulatus* ($n = 270$), *G. zonipectis* ($n = 288$), *Halichoeres trimaculatus* ($n = 385$), *Myrichthys maculosus* ($n = 120$), *Myrophis microchir* ($n = 42$), *Parapercis clathrata* ($n = 284$), *P. schauinslandii* ($n = 84$), *Plotosus lineatus* ($n = 397$), *Pterocaesio digramma* ($n = 255$), *Scuticaria tigrina* ($n = 27$), *Strophidon sathete* ($n = 58$), *Thalassoma amblycephalum* ($n = 516$), *Uropterygius concolor* ($n = 104$), *U. fuscoguttatus* ($n = 52$), *U. macrocephalus* ($n = 61$), *U. polyspilus* ($n = 16$), *U. supraforatus* ($n = 31$) and *U. xanthopterus* ($n = 123$). We compiled occurrence data from two online databases, the Global Biodiversity Information Facility (GBIF; www.gbif.org) and the Ocean Biogeographic Information System (OBIS; www.iobis.org). An additional eight prey species mentioned in the literature could not be used in our study due to low numbers of occurrences that made it impossible to estimate their potential distribution with ENMs. We removed spatially duplicate occurrence records at a resolution of 9 km, to match the resolution of the environmental layers (see Environmental data section for details).

2.2 | Environmental data

To model the ecological niches of *Laticauda* species, we extracted from Bio-Oracle (Tyberghein et al., 2012) and Marspec (Sbrocco & Barber, 2013) databases seven variables with 9 km spatial resolution: bathymetry, distance from the shoreline, mean cloud coverage, salinity, and maximum, minimum, and range of the sea surface temperature. These seven variables are expected to strongly influence the distribution of sea kraits (Brischoux, Tingley, Shine, & Lillywhite, 2012, 2013; Heatwole, Grech, Monahan, King, & Marsh, 2012; Heatwole et al., 2005, 2017). Bathymetry informs the model about the limits of foraging depths (sea kraits are benthic feeders); distance from the shoreline quantifies availability of foraging space; mean

cloud coverage is a proxy for precipitation; salinity is representative of physiological limits linked to osmoregulation; and sea surface temperature variables (maximum, minimum, and range) are used to represent thermal physiological limits of sea kraits. The historical biogeography also played an important role in shaping the current distribution of sea kraits (Heatwole et al., 2017), however, this aspect was not the subject of our study as we focused on the interactions of sea kraits with their prey.

To avoid overfitting the prey models, we considered only the variables representing the mean of the given chemical parameter, which reduced the initial dataset to 12 variables: calcite, nitrate, phosphate, silicate, dissolved oxygen, salinity, pH, mean cloud coverage, mean photosynthetically available radiation, mean chlorophyll A, mean sea surface temperature and water clarity. We ran initial ENMs to identify and eliminate variables with low contribution (<5%) to the overall gain in model accuracy (Phillips, Anderson, & Schapire, 2006; Phillips & Dudík, 2008), in an approach akin to backward-stepwise selection (Hastie, Tibshirani, & Friedman 2001). The remaining variables were used to create the final model (see Appendix S2). This process was repeated for each prey species individually to obtain models trained on variables that best fit the available occurrence data.

2.3 | Generation and evaluation of ecological niche models

The ENMs were generated using Maxent 3.3.3k (Phillips & Dudík, 2008; Phillips et al., 2006). Maxent is a machine-learning method that calculates the probability of a species' presence from known presences and randomly selected locations without species presences (pseudo-absences) from the "background" (Phillips & Dudík, 2008; Phillips et al., 2006). We ran models using 75% of the occurrence data to train the models and 25% to test the models. Possible sampling biases were taken into account by using in the modelling experiments a bias file corresponding to the number of occurrences per pixel. We used default options for other algorithm settings (10,000 background samples and feature selection). All model outputs were reported to the Maxent probability of presence value corresponding to 10% training omission error threshold which classified Maxent values above the threshold as present (1) and below as absent (0). Training omission error represents the proportion of occurrences used to train the model that are incorrectly predicted as absent by the model (Fielding & Bell, 1997).

We used the binary, presence-absence predictions obtained for each prey species to create a prey richness map for each studied sea krait species by calculating in ArcGIS 10 (ESRI, 2011) the number of prey species predicted present in each grid cell. The prey species richness maps were used as a biotic variable in the niche models of the sea krait species. The relationship between the probability of predator' presence, as estimated by Maxent models, and prey species richness (sum of Maxent predictions) was tested using Pearson correlation in SAS JMP 12.

The models were evaluated using two metrics: area under the curve (AUC) of the receiver operating characteristic and omission



error. The AUC values range from 0 (no prediction) to 1 (perfect prediction), and 0.5 represents a random prediction (Swets, 1988). Based on AUC, Swets (1988) classified models as useful (AUC >0.7), good (AUC >0.8), and very good (AUC >0.9). However, using AUC to evaluate ENMs has been criticized in recent years (see Jiménez-Valverde, Lobo, & Hortal, 2008; Jiménez-Valverde, 2012; Lobo, Jiménez-Valverde, & Real, 2008; Peterson, Papeş, & Soberón, 2008 for more information). Some modifications have been proposed (see Peterson et al., 2008 for one example), but AUC is still the standard method for evaluating the performance of ENMs (Phillips & Dudík, 2008). The omission error is a straightforward method of evaluating models: a lower percentage of presences that are predicted as absences indicates that the model is better at predicting the species' known distribution.

3 | RESULTS

3.1 | Performance of sea krait and prey models and variable contributions

The sea krait species with the lowest number of prey species was *L. frontalis* ($N = 4$), whereas the sea krait species with the highest number of prey species was *L. saintgironsi* ($N = 26$; see Appendix S2). The mean of test AUC values for prey species models was high (0.9), indicating high model performance (see Appendix S2). Similarly, the mean omission error (16.7%) showed that the prey species models performed well, correctly predicting most of the known occurrences of prey species. We found that, on average, four predictors contributed most to prey species models (see Appendix S2): calcite (47.45%), nitrate (27.16%), mean sea surface temperature (16.92%) and silicate (16.73%).

The abiotic ENMs of the sea kraits (i.e. those not including prey species richness as a predictor) performed well when evaluated with the AUC ($M = 0.99$), however, relatively poorly when evaluated for omission error ($M = 25.18\%$). The high average omission error across the five species studied suggests a limited ability of the abiotic variables to estimate the known distribution of sea kraits (Table 1). The species with lowest sample sizes, *L. semifasciata* ($N = 28$) and *L. frontalis* ($N = 17$), had the highest and third highest omission error, respectively, of the five species studied. This result indicates that models trained with small presence datasets will be predictive of environmental conditions associated with those presences and will have limited power to extrapolate, or correctly predict present known records withheld for testing models (Pearson et al., 2007).

The variables with high contribution to abiotic ENMs of sea kraits were distance from the shoreline ($M = 63.66\%$), bathymetry ($M = 14.42\%$), salinity ($M = 6.82\%$) and minimum sea surface temperature ($M = 6.38\%$); the rest of the variables had <5% mean contribution to model accuracy (Table 1). The biotic ENMs had, on average, lower testing omission error ($M = 22.94\%$; Table 1) than that of the abiotic ENMs, indicating improved model performance. On a species by species basis, the biotic ENMs improved (lower omission error) for two of the five species compared to abiotic

ENMs, including one of the low sample species, *L. semifasciata*. The mean AUC of the biotic ENMs was comparable to that of the abiotic ENMs ($M = 0.99$). In addition, the overall variable contribution to sea krait biotic ENMs changed compared to abiotic ENMs, the most important predictor being distance from the shoreline ($M = 61.5\%$), followed by prey availability ($M = 10.86\%$) and bathymetry ($M = 10.2\%$; Table 1). Overall, in the biotic ENMs, these three variables had an average cumulative contribution of >82%.

3.2 | Prey species distribution patterns

Prey species richness was estimated to be highest along the shores of the western Pacific and eastern Indian Oceans, especially in the Gulf of Bengal, Taiwan, Philippines, Java Sea, Northern Australia and around the Pacific archipelagos (Figure 1). This distribution pattern overlaps well with the known general distribution of *L. semifasciata*, *L. colubrina*, *L. laticaudata* and *L. saintgironsi*. Although *L. frontalis* range overlap with estimated prey species richness was not as clear due to the small number of prey species known ($N = 4$; the feeding ecology of this species is least known among sea kraits), the highest prey species richness coincided with the core of the known range for this sea krait.

Additionally, we found strong relationships between estimated prey species richness and probability of distribution of sea kraits. For all sea krait species analysed, the Maxent probability of presence was strongly correlated with prey species richness: *L. frontalis* ($R = 0.989$, $p < 0.001$) and *L. colubrina* ($R = 0.925$, $p < 0.001$) had the strongest relationship, followed by *L. semifasciata* ($R = 0.366$, $p < 0.001$) and *L. laticaudata* ($R = 0.265$, $p < 0.001$). For *L. saintgironsi* the correlation was weak ($R = 0.093$, $p < 0.001$).

For all sea krait species, the agreement (geographical overlap) between potential distributions obtained with abiotic and biotic ENMs was high (>50%) (Table 2; Figure 2). When prey species richness was included in the models, the proportion of pixels previously predicted suitable by the abiotic ENMs decreased (on average by 25%) and led to a decrease in omission error compared with abiotic ENMs (Tables 1 and 2; Figure 2). On average, the biotic ENMs predicted suitable 4.5% of pixels that were predicted absent by the abiotic ENMs (with highest proportions for *L. frontalis*, 9.31% and *L. semifasciata*, 8.75%; see Table 2 and Figure 2).

4 | DISCUSSION

Ecological niche modelling is used to estimate the potential distribution of species and traditionally studies in this field have been relying on abiotic conditions known or assumed to influence the distribution of species (e.g. temperature, precipitation; Araújo & Peterson, 2012; Peterson et al., 2011). However, recent studies have shown that biotic interactions can influence species' distributions at broad geographical scales (Leathwick & Austin, 2001; Trainor & Schmitz, 2014; Wisz et al., 2013). In our study, we estimated the distribution of sea kraits (*Laticauda* spp.) using both abiotic and biotic variables and compared the models to test whether the inclusion of biotic

TABLE 1 Performance of ecological niche models for five species of sea kraits, measured with testing omission error and AUC, and per cent variable contribution to model accuracy gain

Model	Species	Omission	AUC	Variable contribution (%)							
				Bathymetry	Distance from the shoreline	Cloud coverage (maximum %)	Salinity	Sea surface temperature (max °C)	Sea surface temperature (min °C)	Sea surface temperature (range °C)	Prey species richness
Abiotic	<i>L. colubrina</i>	0.15	0.976	4.3	90.1	0.1	1.1	0.4	3.2	0.8	
	<i>L. frontalis</i>	0.25	0.999	37.3	29.2	8.3	18.5	0.8	0.0	5.9	
	<i>L. latidaudata</i>	0.15	0.989	7.7	78.7	0.4	4.9	2.5	1.8	4.0	
	<i>L. saintgironsi</i>	0.28	0.996	15.4	48.9	6.4	6.8	0.9	17.3	4.3	
	<i>L. semifasciata</i>	0.43	0.997	7.4	71.4	6.7	2.8	0.0	9.6	2.1	
Biotic	<i>L. colubrina</i>	0.07	0.977	5.1	86.9	0.1	1.1	0.5	3.5	0.7	2.2
	<i>L. frontalis</i>	0.25	0.999	29.0	24.0	7.5	18.6	2.2	0.2	3.4	15.0
	<i>L. latidaudata</i>	0.26	0.988	0.8	80.9	0.4	2.2	2.4	0.5	2.6	10.2
	<i>L. saintgironsi</i>	0.28	0.996	10.2	43.4	4.4	1.6	0.9	15.9	1.6	22.0
	<i>L. semifasciata</i>	0.29	0.996	5.8	70.1	5.1	2.6	0.0	9.4	2.0	5.0

TABLE 2 Agreement and disagreement between potential distributions estimated with ecological niche models based on abiotic variables only and abiotic and biotic variables, for five species of sea kraits studied. Agreement is calculated as proportion of pixels predicted present by both abiotic and biotic models and disagreement as proportion of pixels predicted present by one of the two models alone

	<i>L. colubrina</i>	<i>L. frontalis</i>	<i>L. latidaudata</i>	<i>L. saintgironsi</i>	<i>L. semifasciata</i>
% agreement	94.42	83.15	58.31	53.74	53.64
% abiotic	2.80	7.54	39.72	46.18	37.61
% biotic	2.78	9.31	1.97	0.08	8.75

variables improved the model performance for our target species. Because sea kraits are trophic specialists that consume mostly eels (Brischoux et al., 2007; Ineich et al., 2007), the biotic variable we included in the ENMs was sea krait prey species richness. Based on studies of sea krait foraging preferences (Brischoux & Bonnet, 2008; Brischoux et al., 2007, 2009, 2011; Ineich et al., 2007), we expected that prey species richness would improve the model accuracy.

4.1 | Are biotic variables increasing performance of ENMs?

Biotic interactions can affect species distributions at local scales through several mechanisms, such as competition, predation or symbiosis (Araújo & Rozenfeld, 2014). At broad geographical scales, the role of biotic interactions is not well understood but a recent review found that biotic interactions are indeed important in shaping the distribution of species at multiple scales (see Wisz et al., 2013) and called for inclusion of biotic variables in ENMs. In our study, we found that the models trained with relevant biotic information slightly outperformed the abiotic models, at least by one measure of model performance (omission error), and this finding is in line with recent studies that included biotic information in modelling efforts (Bateman, VanDerWal, Williams, & Johnson, 2012; Muñoz-Mas, Martínez-Capel, Alcaraz-Hernández, & Mouton, 2015). Generally, more complex models tend to be overfit and exhibit higher omission error (Radosavljevic & Anderson, 2014), but in our study the models

became more specific with inclusion of prey species richness. The total area predicted present by models that included prey information was smaller, but more specific, thus decreasing both omission error and commission error (areas not suitable for the species but predicted present).

Our study found disagreements between areas predicted suitable for sea kraits by the abiotic and biotic models, especially for *L. latidaudata* and *L. semifasciata* (Figure 2 and Appendix S3), suggesting that regional processes are important in determining how models respond to biotic variables. Further work is needed to understand how regional processes affect ENMs. Another difference between abiotic and biotic ENMs was that the importance of abiotic variables decreased when prey species richness was included in the models, across all studied species, but by different magnitudes. Previous studies have also found that biotic interactions improve estimates of species' distributions (Araújo et al., 2014; Trainor et al., 2014) and suggested that, when possible, biological interactions should be included in models (Feeley, 2015). However, models of each species considered in the current study responded differently to these variables (see Appendix S4), and their inclusion into ENMs as predictors should be carefully evaluated *a priori*, based on the question being investigated. Since biotic factors have been considered more influential to shaping species distributions at lower latitudes than at higher latitudes (MacArthur, 1972; Wallace, 1878), it seems reasonable to consider biotic variables when estimating distributions of species in these geographical areas.

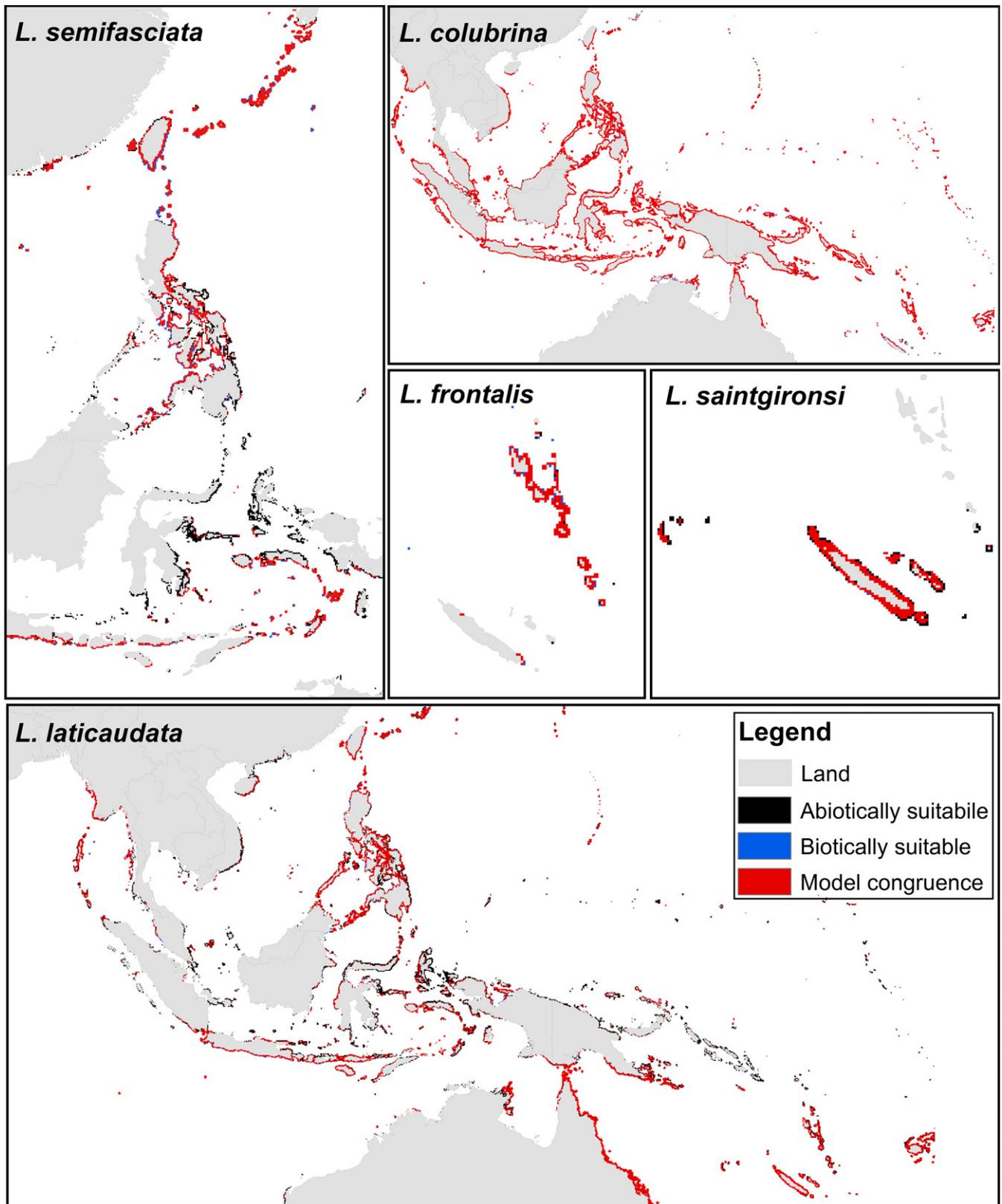


FIGURE 2 Potential distributions of sea kraits predicted by ecological niche models trained with abiotic variables only (abiotic model) and biotic and abiotic variables (biotic model). Red areas represent the agreement between the biotic and abiotic models, black areas represent pixels predicted suitable only by abiotic models, and blue areas pixels predicted suitable only by the biotic models

4.2 | How do prey species shape predator species' distributions? The sea kraits case study

The relationship between predator and prey can strongly influence local abundances and range limits of both predator and prey species (Estes et al., 2011). For example, empirical data have shown that wolves are the main limitation on caribou and moose distributions in northwestern North America (Hayes et al., 2003). Other evidence includes the effects of red fox predation on small marsupials from Australia (Johnson, Isaac, & Fisher, 2007), the presence of rats that trigger shorebird declines worldwide (Jones et al., 2008) and Canadian lynx predation on snowshoe hare (Trainor & Schmitz, 2014; Trainor et al., 2014). Our study showed that the predicted ranges of all five sea krait species overlap with areas that are estimated to have high prey species richness and probability of predator presence was explained ($p < 0.0001$) by the number of prey species estimated. Additionally, the correlation between predator potential distribution and estimated prey species richness suggests that geographical ranges of sea kraits are influenced by distributional patterns of prey species richness. However, regional processes are also important in shaping sea kraits distributions; for example, areas in the Great Barrier Reef of Australia are predicted suitable for the sea kraits but they are not present due to lack of oceanic currents to facilitate migration (Lane & Shine, 2011b), a process known to be important in other sea snakes (Brischoux et al., 2016); or by physiological and physical limits (see Brischoux et al., 2012; Heatwole et al., 2012, 2017 for more details).

At large scale (i.e. continental or oceanic), addition of biotic variables in species' distributions estimates comes with limitations due to the dynamic nature of the data such as direct and indirect interactions between prey and predator, or prey and the environment (Anderson, 2017) that might have cascading effects on ENMs. The limitations include: the general lack of biotic data at large scales and along long environmental gradients; direct and indirect eco-evo feedbacks between prey and predator; and the need for further tuning of modelling techniques to better integrate biotic variables into models. Regardless of these limitations, biotic interactions should be included when the information is available, and the modelling techniques should be tuned to better use these data.

Generally, the importance of predator-prey interactions is thought to manifest primarily at local scales (Soberón, 2010; Soberón & Nakamura, 2009). Yet, in our study, we found that using prey species distributions to estimate predator species distributions at broader geographical scales decreased the mean omission error of model estimates. Sea kraits are trophic specialists, thus we expect that biotic variables would improve the accuracy of ENMs of other species that evolved dietary specialization.

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BIOSKETCHES

Iulian Gherghel is broadly interested in macroecology, evolution, and biogeography. He is studying the effects of incorporating biotic interactions, complex life histories information, and dispersal on ecological niche models. For his PhD, he studies the effects and strength of different agents of selection (biotic and abiotic) at different temporal and spatial scales.

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Author contributions: I.G. conceived and designed the study, with input from all other authors; I.G. and F.B. collected the data; I.G. and M.P. analyzed the data; all authors contributed to the interpretation; and I.G. led the writing, with input from all other authors.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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