

Distribution modelling and conservation assessment for helmeted terrapins (*Pelomedusa* spp.)

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Abstract. For decades, the genus *Pelomedusa* has been thought of as containing only a single species that is widely distributed in sub-Saharan Africa, the Arabian Peninsula, and Madagascar. However, ten species and up to five candidate species have been recognized recently. For these taxa, ecological information is scarce and distribution ranges are often only incompletely known. In this study, ecological niche spaces were estimated for eight *Pelomedusa* species, using a maximum entropy algorithm and geographical, climatic, and topographic information. Using the obtained models and Schoener's D and Hellinger's I indices, areas of sympatry between species were estimated and candidate areas for possibly overlooked taxa were identified. Furthermore, differences in niche spaces between species were assessed. The ecological niche models revealed geographical spaces that match the predicted niche of the eight examined species. However, for *P. subrufa* sensu stricto, the distribution range of the introduced populations in Madagascar was not predicted. Our models, together with statistical analyses, indicate that the studied *Pelomedusa* species occupy different geographical spaces. Areas of sympatry with significant niche overlap were identified between some species pairs. Yet, *Pelomedusa* species are generally allopatrically or parapatrically distributed. A minimum of five candidate regions possibly harbouring unknown taxa were identified. Our results provide a better understanding of the distribution ranges of *Pelomedusa* species and, thus, can serve as a basis for conservation planning.

Key words. Africa, Arabian Peninsula, Ecological Niche Modelling, MAXENT.

Introduction

Complexes of cryptic species require special consideration in conservation planning because unrecognised species can be rare, endangered, and may therefore need special conservation strategies (BICKFORD et al. 2007). Assessing distribution patterns of cryptic taxa is often difficult because many locality records can be misidentified. Helmeted terrapins (genus *Pelomedusa*) represent an excellent example for this: For a long time, these terrapins were identified as a single widespread species, *Pelomedusa subrufa* (BONNATERRE, 1789) sensu lato. It was thought to be distributed in a vast range, encompassing sub-Saharan Africa, the southwestern Arabian Peninsula, and Madagascar (IVERSON 1992, GASPERETTI et al. 1993). However, recent studies have demonstrated that helmeted terrapins represent a diverse species complex (VARGAS-RAMÍREZ et al. 2010, WONG et al. 2010, FRITZ et al. 2011, 2014, PETZOLD et al. 2014, NAGY et al. 2015) with currently 10 named species and up to another

five unnamed candidate species in continental Africa and Arabia (FRITZ et al. 2014, PETZOLD et al. 2014, NAGY et al. 2015). The helmeted terrapins from Madagascar are now understood as introduced populations of *P. subrufa* sensu stricto (VARGAS-RAMÍREZ et al. 2010, WONG et al. 2010, PETZOLD et al. 2014). However, without genetic verification, many of the old records of helmeted terrapins cannot be identified with a certain species, which is why the distribution ranges of many taxa are only incompletely known.

Based on known locality data, distribution modelling can improve this situation. Among other biogeographical analyses (RAXWORTHY et al. 2007, RISSLER & APODACA 2007, NAKAZATO et al. 2010), distribution modelling relating verified locality and environmental data has generally been applied to identify regions where rare or undiscovered species may occur (ANDERSON et al. 2002, FERRIER et al. 2002, RAXWORTHY et al. 2003, 2007, SIQUEIRA et al. 2009), to recognize environmental differences among species (KOZAK et al. 2008), to identify regions of high ende-

micity and conservation value (RISSLER et al. 2006), and to support conservation planning (e.g., ARAÚJO & WILLIAMS 2000, FERRIER et al. 2002). Based on the premise that the observed distribution of a species provides useful information as to its environmental requirements (PEARSON & DAWSON 2003), this approach associates known distributional information with a set of environmental variables to characterize the range of habitat conditions (the realized niche sensu HUTCHINSON 1957). Thus, ecological niche modelling (ENM) utilizes environmental conditions at known presence localities of a target species to assemble a model of its ecological tolerances that can be used to predict the geographical space that fulfils the same requirements (ACKERLY 2003, PEARSON et al. 2007). However, the results from ENM must be interpreted cautiously because factors like geographical barriers, biotic interactions, and demographic history are often not considered, implying that species rarely occupy all areas with suitable environments (ANDERSON et al. 2002, PEARSON & DAWSON 2003, ARAÚJO & PEARSON 2005, PHILLIPS et al. 2006). Regardless of these limitations, distribution models have been shown to provide highly informative biogeographical information (e.g., FLEISHMAN et al. 2002, BOURG et al. 2005, RAXWORTHY et al. 2007), especially if researchers adopt a conservative interpretation of model results as areas similar to those from which a species is known (PEARSON et al. 2007).

Based on genetically verified locality data for *Pelomedusa* species (PETZOLD et al. 2014), we perform in the present paper ENM and climatic niche analyses (i) to predict the ecological niches and geographical spaces for several species of helmeted terrapins, (ii) to identify areas of sympatry, and (iii) to assess ecological variation among species. However, we excluded from our modelling approach the unnamed candidate species and two named species (*P. gehafie*, *P. somalica*) for which only one or two collection sites are known (PETZOLD et al. 2014, NAGY et al. 2015) due to the sensitivity of ecological niche model approaches to small sample sizes (PEARSON et al. 2007, WISZ et al. 2008). As an additional aim, we try to identify areas with further, as yet possibly overlooked *Pelomedusa* species.

Materials and methods

Estimation of climatic niche

The climatic niche was analysed in two ways. In an ENM approach, the climate niche was projected across a geographical region using the georeferenced locality data for each *Pelomedusa* species from PETZOLD et al. (2014). However, locality data for the introduced Malagasy populations of *P. subrufa* sensu stricto were excluded. In addition, a point-based analysis was conducted utilizing univariate and multivariate statistics for specific conditions using climate variables and altitude alone. Bioclimatic variables and altitude were taken from WorldClim version 1.4 with a resolution of 30 arcseconds (HIJMAN et al. 2005). In order to reduce effects of overfitting and multi-collinearity of predictors (HEIKKINEN et al. 2006), correlated variables

were identified using R v.2.9.2. For doing so, climatic and altitude data across Africa and the Arabian Peninsula were extracted for 10^5 randomly generated points using the 'Create Random Points' command in ArcGIS v.10.2. (ESRI Spatial Analyst), and a Pearson correlation coefficient was estimated for each pair of variables. Due to the expanse of the area of study, this procedure was repeated three times. For the pair of variables that exceeded a threshold of $r = 0.75$ (KALKVIK et al. 2011), the variable that was biologically most meaningful was integrated. Based on the results of the three repetitions, the following eleven variables were included in the analyses: (1) annual mean temperature, (2) mean diurnal range, (3) isothermality, (4) maximum temperature of the warmest month, (5) minimum temperature of the coldest month, (6) annual precipitation, (7) precipitation of the wettest quarter, (8) precipitation of the driest quarter, (9) precipitation of the warmest quarter, (10) precipitation of the coldest quarter, and (11) altitude.

Niche modelling, overlap, and areas of distribution

Niche modelling was used to identify areas with climatic and topographic conditions resembling those regions for which verified records of the different *Pelomedusa* species exist. Models were created using MAXENT v.3.3.3k, which applies a maximum entropy algorithm to estimate distributions based on niche characteristics (PHILLIPS et al. 2006, PHILLIPS & DUDÍK 2008). Maximum entropy is useful when absence data is lacking and performs better than other distribution modelling algorithms when the number of data points is limited (ELITH et al. 2006, PEARSON et al. 2007, WISZ et al. 2008). Our niche modelling included Africa, Madagascar, and the Arabian Peninsula, i.e., the whole distribution range of all *Pelomedusa* species. Only a few genetically verified occurrence points are available for *Pelomedusa barbata*, *P. kobe*, *P. neumanni*, *P. olivacea*, *P. schweinfurthi*, and *P. variabilis* (PETZOLD et al. 2014). To increase sample size for these species, a minimum convex polygon (MCP) was created using the genetically verified records from PETZOLD et al. (2014). This sampling was enriched with additional *Pelomedusa* records within each polygon, which were allocated to the respective species (Supplementary figs S1+S2). In order to increase the number of sites for *P. barbata* and *P. schweinfurthi*, records immediately adjacent to the polygons were also included (Table 1). Additional locality data were obtained from HerpNet (<http://www.herpnet.org>) and EMYSys (<http://emys.geo.orst.edu/>; Supplementary table S1). To assess the accuracy of each model and due to the low number of localities, the jackknife data partitioning approach (PEARSON et al. 2007) was used. As described by these authors, independent MAXENT models were run with one of the localities excluded in each case. For each model, the lowest presence threshold was used and the ability to predict the excluded locality assessed. For doing so, the program PVALUECOMPUTE.EXE (PEARSON et al. 2007) was used, and a p-value was calculated for each species.

Table 1. Model contributions of the bioclimatic variables and altitude for the *Pelomedusa* species (percentages) and results of model evaluation. Bioclimatic variables: ALT – altitude; AMT – annual mean temperature; AP – annual precipitation; IT – isothermality; MDR – mean diurnal range; MTCM – minimum temperature of the coldest month; MTWM – maximum temperature of the warmest month; PCQ – precipitation of the coldest quarter; PDQ – precipitation of the driest quarter; PWaQ – precipitation of the warmest quarter; PWQ – precipitation of the wettest quarter. n – number of records; O.r. – omission rate; AUC – area under the curve of ROC plots.

Rank	<i>barbata</i>	<i>galeata</i>	<i>kobe</i>	<i>neumannii</i>	<i>olivacea</i>	<i>schweinfurthi</i>	<i>subrufa</i>	<i>variabilis</i>
1	MTCM 26.2	PDQ 34.7	IT 22.6	IT 57.1	PCQ 21.0	IT 31.1	MTCM 34.3	MTCM 73.5
2	MDR 20.1	IT 18.4	ALT 22.3	ALT 22.0	PWQ 19.6	PCQ 18.8	ALT 27.1	MDR 15.8
3	AP 19.3	AMT 16.9	PDQ 16.8	MTCM 5.9	PDQ 14.6	PWQ 16.1	MTWM 11.8	ALT 4.5
4	PWQ 17.0	MTCM 11.1	PCQ 14.2	AP 2.7	AMT 11.8	MTCM 14.0	PCQ 6.0	AP 3.9
5	ALT 13.1	ALT 7.0	MDR 10.1	MDR 2.5	MDR 11.6	PWQ 7.6	IT 5.5	AMT 0.5
6	PWQ 1.6	PWQ 4.1	MTWM 8.0	AMT 2.5	PWQ 10.0	MDR 4.9	PWQ 4.3	IT 0.4
7	PDQ 0.9	MDR 3.4	AP 3.4	MTWM 2.3	ALT 5.1	AP 4.9	MDR 3.5	PDQ 0.4
8	AMT 0.7	PWQ 1.6	PWQ 1.3	PWQ 1.8	AP 2.6	ALT 1.3	PDQ 2.5	PWQ 0.4
9	PCQ 0.7	MTWM 1.0	MTCM 1.1	PDQ 1.7	IT 1.5	PDQ 1.1	AMT 2.3	PCQ 0.3
10	IT 0.3	AP 0.9	PWQ 0.1	PCQ 1.2	MTCM 1.2	MTWM 0.1	PWQ 1.7	MTWM 0.2
11	MTWM 0.1	PCQ 0.8	AMT 0.1	PWQ 0.3	MTWM 1.0	AMT 0.0	AP 1.0	PWQ 0.1
n	11	23	10	13	18	10	16	12
O.r.	1 of 11 p<0.001	2 of 23 p<0.001	1 of 10 p<0.001	2 of 13 p<0.001	2 of 18 p<0.001	1 of 10 p<0.001	1 of 16 p<0.001	1 of 12 p<0.001
AUC	0.991	0.997	0.984	0.990	0.990	0.992	0.955	0.991

Additionally, because all included species were represented by more than ten locality records, a model evaluation was performed using the area under the curve (AUC) of the receiver-operating characteristic (ROC) plot. For this, the occurrence data were randomly partitioned into training (75%) and test (25%) data sets. The results of each model were summarized as averages of 100 bootstrap replicates. All analyses were run with a convergence threshold of 1.0×10^{-5} with 1,000 iterations. The regularization multiplier was set at 0.5 to obtain a more localized output distribution that will be a closer fit to the given presence records (RIVERA et al. 2011). For each species, the minimum training presence was used as the threshold for generating binary prediction maps of suitable climatic niche. A jackknife resampling test for evaluating the importance of each variable was performed, and to examine how each variable affected the MAXENT prediction, individual response curves were examined. Disjunct areas of major overprediction were excluded from further analyses in this context (but see below). Niche overlaps of lineages were estimated using two different measures of similarity, Schoener's D and the I statistic, based on Hellinger distance. Each metric is calculated by comparing the estimates of habitat suitability from the ENMs generated by MAXENT for each grid cell of the study area after normalizing each ENM, so that all suitability scores sum up to 1. Both similarity tests range from 0 (no overlap between predicted environmental tolerances of species) to 1 (all grid cells are estimated to be equally suitable for both species). The ecological interpretation of D implies that the suitability scores are proportional to species abundance, while I simply treats the two ENMs as probability distributions (WARREN et al. 2010). Further-

more, range overlap between species was calculated using the average of all minimum training presences as a threshold. This metric and niche overlap were computed using ENMTOOLS v.1.4.3 (WARREN et al. 2008, 2010; available at <http://enmtools.blogspot.com>). In addition, the geographical distribution of each species was estimated by means of the extent of occurrence (EOO) and the area of occupancy (AOO). These estimators are used in some criteria for determining the threat category of a species (IUCN 2012). The EOO for each species was calculated in km² from the MCPs using the GeoCAT portal (BACHMAN et al. 2011; <http://geocat.kew.org/>) and, in addition, using ArcGIS from the geographical space that fulfils the predicted ecological niche. The AOO was calculated using the GeoCAT portal. The EOO is defined as "the area contained within the shortest continuous imaginary boundary, which can be drawn to encompass all the known, inferred or projected sites of present occurrence of a taxon", and the AOO "as the area within its 'extent of occurrence', which is occupied by a taxon" (IUCN 2012), for both, excluding cases of vagrancy.

Identification of candidate areas for possibly unknown additional *Pelomedusa* species

For some species, ecological niche modelling has guided the discovery of isolated areas of environmental suitability that are not actually occupied by the species being modelled (RAXWORTHY et al. 2007). Species rarely occupy all regions with suitable environments due to historical and ecological constraints like geographical barriers or biotic interactions (e.g., interspecific competition, predation

pressure or dispersal abilities). Such factors, which can play a key role in shaping the geographical ranges of species (PETERSON 2001, SVENNING & SKOV 2004, ARAÚJO & PEARSON 2005, RAXWORTHY et al. 2007), are not considered in our modelling approach. However, disjunct overpredicted regions can be valuable indicators for unrecognised distribution ranges or even overlooked taxa. RAXWORTHY et al. (2003, 2007) have pointed out that especially in poorly studied regions with many local endemics, isolated areas of overprediction can correspond to the ranges of unknown taxa. Here we adopt this approach as a means to identify candidate areas where possibly unknown species of *Pelomedusa* might occur. For doing so, we compare our disjunct areas of overprediction with published locality records for helmeted terrapins from the HerpNet data portal (<http://www.herpnet.org>) and the world turtle database of the EMySsystem data portal (<http://emys.geo.orst.edu>). All used records are shown in Supplementary figure S2. We hypothesize that isolated areas of overprediction potentially harbour additional candidate species of *Pelomedusa*, especially if records of helmeted terrapins exist from these areas. Moreover, records of helmeted terrapins both outside the contiguous and isolated regions predicted for the studied *Pelomedusa* species could correspond to additional unrecognised taxa.

Point-based analysis

To establish whether significant differences exist among the climatic spaces of different species, univariate (ANOVA) and multivariate analyses of variance (MANOVA) and parametric discriminant analysis (PDA) were performed using occurrence points. For comparing the multidimensional climatic values between records, altitude and climatic values were extracted for each site using ArcGIS. A one-way analysis of variance (ANOVA) was used on each of the 10 environmental variables and altitude to test for significant differences between species. Subsequently, a MANOVA was calculated using all variables simultaneously to assess whether significant overall differences exist among the ecological spaces occupied by the individual species. Furthermore, the relative contributions of environmental variables and altitude to the discrimination of the species were quantified by a PDA. Divergences were visualized using the centroid for each lineage. All sampling locations representing explicit climatic and altitude data were plotted on the main discriminant dimensions. All statistical analyses were performed in SPSS v.19.0.

Results

Estimation of climatic niche and niche modelling, overlap, and areas of distribution

The jackknife data partitioning validation revealed high success rates (i.e., low omission rates) and showed that all models were significantly better than random expectations

(Table 1). Furthermore, the AUC values for the test data set were robust and revealed high specificity for each model. The minimum probability of occurrence for training points ranged from 0.017 for *Pelomedusa galeata* to 0.381 for *P. subrufa* (Supplementary figs S3–S10). In the obtained models, the predicted ecological niche of each species was affected, with different strength, by virtually all environmental variables (Table 1). The minimum temperature of the coldest month made the largest contribution to *P. barbata*, *P. subrufa*, and *P. variabilis*, isothermality was most important for *P. kobe*, *P. neumanni*, and *P. schweinfurthi*, precipitation of the coldest quarter was most important for *P. olivacea*, and precipitation of the driest quarter for *P. galeata* (Table 1).

For characterizing the geographical ranges fulfilling the predicted ecological niches of the studied *Pelomedusa* species (Fig. 1), the classification of sub-Saharan regions by LINDER et al. (2012) will be followed here. The predicted distribution of *P. olivacea* ranges along the western Sudanian Region. The predicted main area included a savannah belt from Senegal to southern Chad (Fig. 1A). A major, significantly overpredicted disjunct area was revealed between southern Sudan and northern South Sudan (Supplementary fig. S3), corresponding to the eastern Sudanian Region. Additional but smaller disjunct overpredicted areas were also indicated along the coast of Angola, in eastern Zambia and northernmost Zimbabwe, in northern Mozambique, Malawi, Tanzania, Kenya, Somalia, Ethiopia, and in western Madagascar. For *P. neumanni*, the model predicted two main areas (Fig. 1A): one located within the Ethiopian and Somali Regions, and a second one in the northern Zambezian Region of the eastern Democratic Republic of the Congo, Uganda, Tanzania, and Kenya (Fig. 1A). Disjunct small overpredicted areas were indicated in northern and central Madagascar, northern Somalia, and western Angola (Supplementary fig. S4). The occurrence of *P. galeata* was predicted all over the Southern Africa Region, extending into the southeastern corner of the Zambezian Region (Fig. 1A). Disjunct small overpredicted areas were indicated along the coast of the western Maghreb, in the southwestern Arabian Peninsula, Eritrea, Ethiopia, Somalia, Kenya, Malawi, and southern Madagascar (Supplementary fig. S5).

The predicted distribution of *P. barbata* extends along the southern coast of the Arabian Peninsula from Saudi Arabia through Yemen to Oman (Fig. 1B). Further disjunct overpredicted areas were revealed on the southern Red Sea coast of Africa, the coastal regions of the Horn of Africa, and inland in the border region of Kenya and Ethiopia (Supplementary fig. S6). The occurrence of *P. schweinfurthi* was predicted for a large region encompassing parts of eastern and southern Ethiopia, Sudan, South Sudan, the northeastern Democratic Republic of the Congo, northern Uganda, and northern Kenya and adjacent Somalia (Fig. 1B). This range corresponds to the crossroads of several biogeographical regions of LINDER et al. (2012). Small disjunct overpredicted areas for *P. schweinfurthi* were suggested for several regions in West Africa and the cen-

tral Democratic Republic of the Congo (Supplementary fig. S7). *Pelomedusa subrufa* was predicted for a large area corresponding to the Zambezi Region and the Kalahari Subregion, and parts of the Natal and Namib Subregions of the Southern African Region of LINDER et al. (2012). Small disjunct overpredicted areas were also revealed for Chad, Sudan, the East African countries, the southwestern Arabian Peninsula, and inland Madagascar (Supplementary fig. S8). However, the species was not predicted for any of the regions in northern, western and southern Madagascar, from where introduced populations of *P. subrufa* are known (cf. the EMYSsystem map and PETZOLD et al. 2014).

The occurrence of *P. variabilis* (Fig. 1C) was predicted for the Guinean Subregion and the coastal Congolian Subregion of the Congolian Region of LINDER et al. (2012). In addition, major suitable areas were suggested for the southern and northern Red Sea coasts, southern Somalia and adjacent Kenya and coastal Tanzania, northwestern Kenya, and the border region of the Congo Republics (Supplementary fig. S9). For *P. kobe*, the northeastern part of the Zambezi region and parts of the Somalian Region were revealed as suitable (Fig. 1C). Disjunct overpredicted areas were found in western Angola and Namibia as well as Yemen (Supplementary fig. S10).

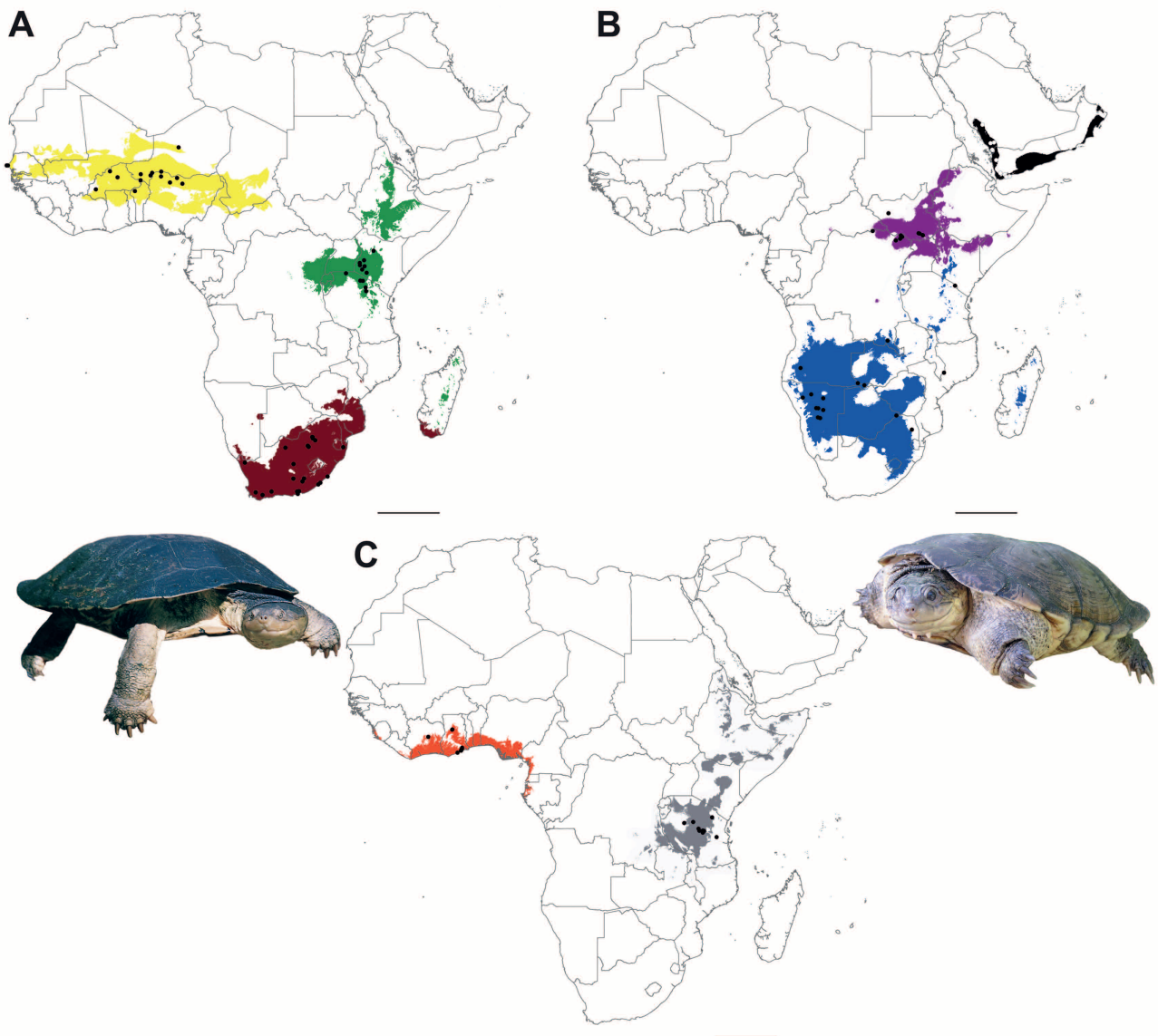


Figure 1. Environments modelled as suitable using MAXENT for A) *Pelomedusa olivacea* (yellow), *P. neumanni* (green), and *P. galeata* (brown); B) *P. barbata* (black), *P. schweinfurthi* (purple), and *P. subrufa* (blue); and C) *P. variabilis* (orange) and *P. kobe* (grey). Ranges are based on 10 environmental variables and altitude. Minimum training presence thresholds used to separate the map into binary predictions (suitable: coloured, unsuitable: not coloured). Major overpredicted disjunct areas except Madagascar are not shown. Black (or white) dots: records used for developing the models. Scale bars = 1,000 km. Inset (left): *P. galeata*, photo: W. R. BRANCH, inset (right): *P. subrufa*, photo: A. SCHLEICHER.

Table 2. Percentage of geographical overlap in niche spaces predicted by MAXENT and measures of niche overlap (Schoener's D and Hellinger's I indices) between eight species of *Pelomedusa*.

Species pair	% overlap	I	D
<i>P. barbata</i> vs <i>P. galeata</i>	0.0	0.000	0.000
<i>P. barbata</i> vs <i>P. kobe</i>	0.0	0.000	0.000
<i>P. barbata</i> vs <i>P. neumanni</i>	0.0	0.000	0.000
<i>P. barbata</i> vs <i>P. olivacea</i>	0.0	0.000	0.000
<i>P. barbata</i> vs <i>P. schweinfurthi</i>	0.0	0.000	0.000
<i>P. barbata</i> vs <i>P. subrufa</i>	0.0	0.000	0.000
<i>P. barbata</i> vs <i>P. variabilis</i>	0.0	0.000	0.000
<i>P. galeata</i> vs <i>P. kobe</i>	0.0	0.000	0.000
<i>P. galeata</i> vs <i>P. neumanni</i>	0.0	0.000	0.000
<i>P. galeata</i> vs <i>P. olivacea</i>	0.0	0.000	0.000
<i>P. galeata</i> vs <i>P. schweinfurthi</i>	0.0	0.000	0.000
<i>P. galeata</i> vs <i>P. subrufa</i>	39.6	0.266	0.176
<i>P. galeata</i> vs <i>P. variabilis</i>	0.0	0.000	0.000
<i>P. kobe</i> vs <i>P. neumanni</i>	25.3	0.222	0.179
<i>P. kobe</i> vs <i>P. olivacea</i>	0.0	0.000	0.000
<i>P. kobe</i> vs <i>P. schweinfurthi</i>	3.8	0.031	0.025
<i>P. kobe</i> vs <i>P. subrufa</i>	8.3	0.043	0.019
<i>P. kobe</i> vs <i>P. variabilis</i>	0.0	0.000	0.000
<i>P. neumanni</i> vs <i>P. olivacea</i>	0.0	0.000	0.000
<i>P. neumanni</i> vs <i>P. schweinfurthi</i>	4.4	0.037	0.030
<i>P. neumanni</i> vs <i>P. subrufa</i>	7.2	0.042	0.020
<i>P. neumanni</i> vs <i>P. variabilis</i>	0.0	0.000	0.000
<i>P. olivacea</i> vs <i>P. schweinfurthi</i>	0.0	0.000	0.000
<i>P. olivacea</i> vs <i>P. subrufa</i>	0.0	0.000	0.000
<i>P. olivacea</i> vs <i>P. variabilis</i>	1.6	0.004	0.002
<i>P. schweinfurthi</i> vs <i>P. subrufa</i>	0.0	0.000	0.000
<i>P. schweinfurthi</i> vs <i>P. variabilis</i>	0.0	0.000	0.000
<i>P. subrufa</i> vs <i>P. variabilis</i>	0.0	0.000	0.000

The revealed environmental niches of the individual *Pelomedusa* species are mostly non-overlapping or at least little overlapping, indicating that allopatry or parapatry constitute the general spatial configurations (Fig. 2, Table 2). However, a large area of geographical niche overlap was revealed in eastern South Africa for *P. galeata* and *P. subrufa* (39.6%; $I = 0.266$, $D = 0.176$). Moreover, significant overlap was also suggested for the East African species *P. kobe* and *P. neumanni* (25.3%; $I = 0.222$, $D = 0.179$). The largest extents of occurrence (EOO) were found for *P. subrufa*, *P. olivacea*, and *P. galeata*, and the smallest for *P. barbata* and *P. variabilis* (Table 3). Furthermore, distinctly smaller areas of occupancy (AOO) were revealed for all species (Table 3).

Identification of candidate areas for possibly unknown additional *Pelomedusa* species

Seven disjunct overpredicted major areas (I–VII in Fig. 3) containing records for helmeted terrapins were identi-

Table 3. Extents of occurrence (EOO) and areas of occupancy (AOO) in km². MCP – minimum convex polygon.

Species	EOO		AOO
	MAXENT	MCP	
<i>P. barbata</i>	320190	66154	44000
<i>P. galeata</i>	1435633	858795	92000
<i>P. kobe</i>	860929	83956	40000
<i>P. neumanni</i>	991562	128206	48000
<i>P. olivacea</i>	2283126	1292791	72000
<i>P. schweinfurthi</i>	906026	180989	40000
<i>P. subrufa</i>	2674085	3313210	64000
<i>P. variabilis</i>	475410	99671	40000

fied. These areas often correspond well to the statistically defined biogeographical regions of sub-Saharan Africa of LINDER et al. (2012). Area I matches largely the Namib and southwest Angola Subregions of the Southern African Region, area II falls within the Congolian Subregion of the Congolian Region, and area III is located in the eastern part of the Sudanian Region. In this area lies the only known collection site for candidate species B of PETZOLD et al. (2014), which represents a highly distinct genetic lineage. Candidate species B was not described as a new species because only one specimen is known. Area IV corresponds to the Ethiopian Subregion, and area V largely matches the Horn Subregion of the Somalian Region. Area V embraces the two genetically verified records of *P. somalica*. This species consists of two highly distinct genetic lineages recorded from two neighbouring sites; it corresponds most likely to two distinct taxa (PETZOLD et al. 2014). Due to the paucity of records, *P. somalica* was not included in the present modelling. Area VI lies in the eastern Somalian Region and the northeastern Zambezian Region, and area VII in the eastern inland portion of the Zambezian Region.

Additional records for helmeted terrapins fall neither within any of the areas modelled for the eight *Pelomedusa* species nor in any major disjunct area of overprediction (Figs 1+3). Among others, such outliers were identified for the Democratic Republic of the Congo. A new candidate species was recently described from the southeastern part of this country (NAGY et al. 2015).

Point-based analysis

One-way analysis of variance (ANOVA) revealed for all ten climate variables and altitude significant differences between species (Supplementary table S2). Furthermore, multivariate analyses of variance (MANOVA) indicated significant overall differences among the ecological spaces of the eight species (Wilks' lambda = 0.0001, $F = 23.083$, $p < 0.001$). The two statistical tests indicate species-specific ecological preferences. This is also underlined by the PDA results (Fig. 4). The two first canonical scores of the PDA explained 80.8% of environmental variation among

the eight studied species. For the 61.5% of the variation explained by the first axis, minimum temperature of the coldest month and isothermality were the most important variables. For the 19.3% of the variation explained by the second axis, maximum temperature of the warmest month and annual mean temperature were most important. The first axis shows a gradient from subtropical sites with marked cold winters to tropical sites with warmer temperatures, and the second axis reflects a gradient from regions with low annual mean temperatures to regions with high annual mean temperatures. Another MANOVA analysis, using the classification function coefficients as dependent variables and species as categorical variables, confirmed

differences in the environmental spaces of the eight species (Wilks' lambda = 0.526, $F = 0.189$, $p = 0.05$).

Discussion

Species are present at a certain point because it fulfils three crucial conditions: (1) abiotic and (2) biotic conditions are favourable, and (3) the point is reachable for the species under consideration (SOBERÓN & PETERSON 2005). Condition (2) refers to interactions with other species that modify the species' ability to maintain populations. This embraces a wide range of co-occurring taxa that may serve

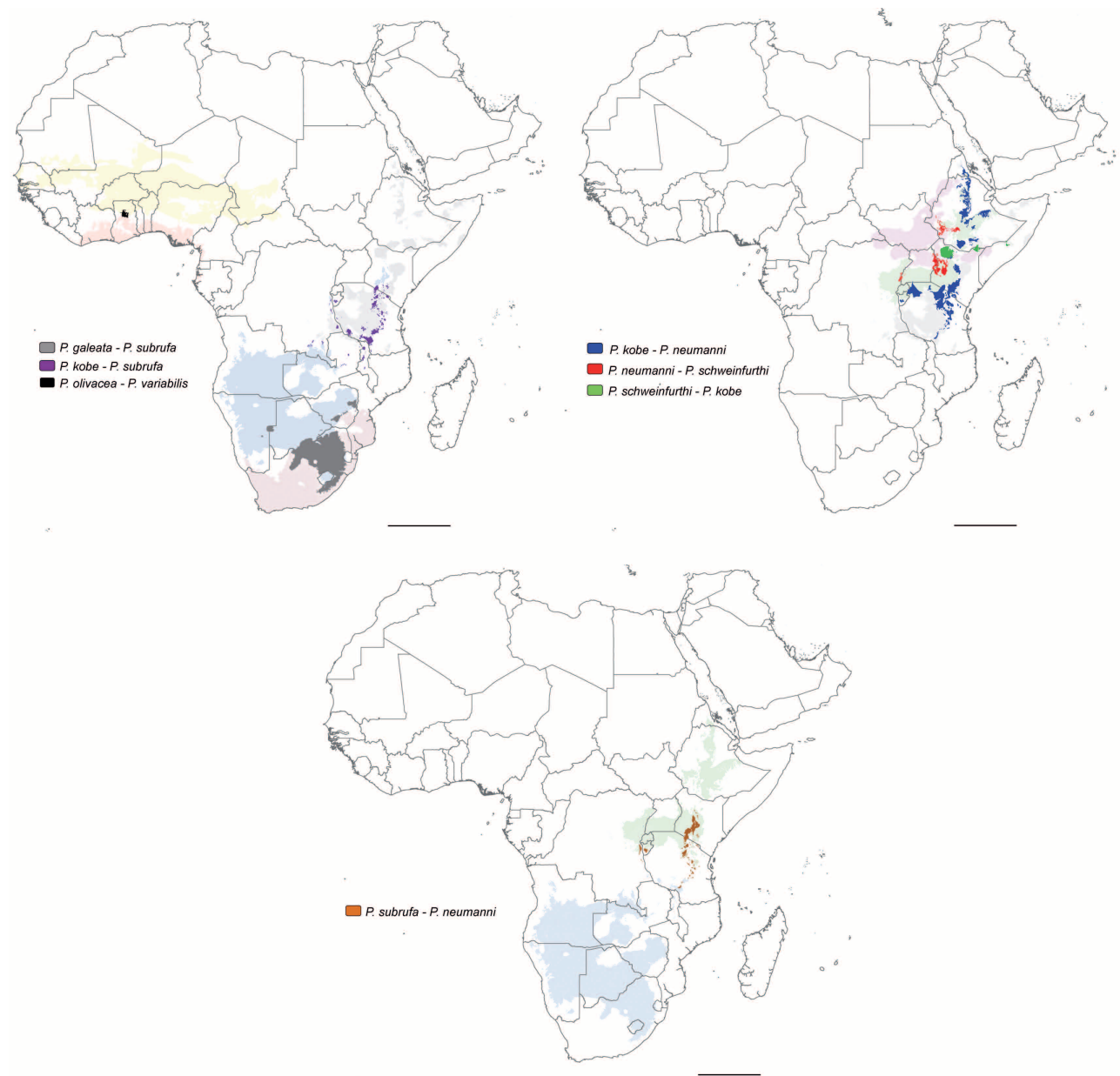


Figure 2. Overlap between predicted distributions of the *Pelomedusa* species as determined by their ecological niche models. Scale bars = 1,000 km.

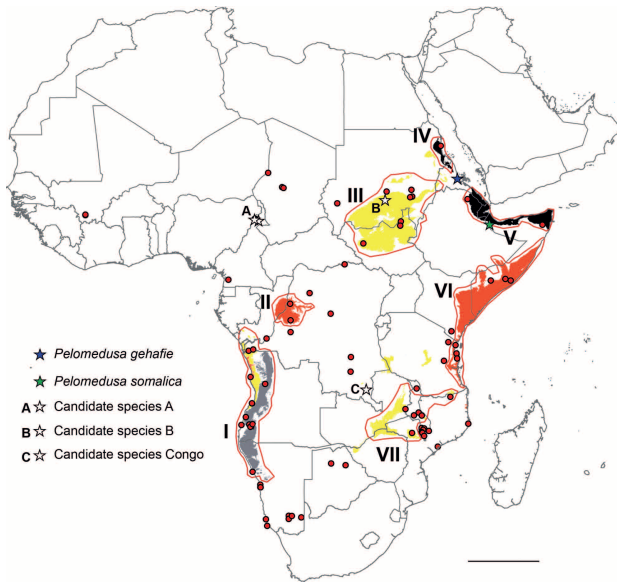


Figure 3. Major disjunct overpredicted areas for *Pelomedusa barbata* (black), *P. kobe* (grey), *P. olivacea* (yellow), and *P. variabilis* (orange). Red dots: records of *Pelomedusa* falling outside the modelled species' ranges and outside the overpredicted areas. Red lines enclose major overpredicted regions containing *Pelomedusa* records. For explanation of numbered areas see text. Scale bar = 1,000 km.

as food, competitors, enemies or as vectors or triggers of diseases. The performed analyses in this study focused on abiotic conditions and information on the biotic interaction of each species is lacking. However, due to the fact that biotic factors robustly correlate with abiotic factors (OWENS et al. 2012) and their impact disappears in large-scale analyses (SOBERÓN & NAKAMURA 2009), we consider our developed models as meaningful approximations.

The apparent correlation between the environments modelled as suitable for each species and biogeographical regions of sub-Saharan Africa indicates their congruency with general patterns. This suggests that the revealed ecological niches of the different taxa reflect real differences. Our statistical analyses (ANOVA, MANOVA, PDA) also corroborated the ecological niche models, supporting the notion that these species inhabit significantly different climatic envelopes (Fig. 4). Moreover, the fact that the relative contributions of each environmental variable and altitude are species-specific (Table 1) suggests that the species are not ecologically compatible. Such ecological differentiation, together with allopatric or parapatric distribution of the species (Fig. 1), indicates habitat isolation that prevents or limits gene flow. In spite of this, large areas of potential sympatry were revealed for a few species pairs (Fig. 2, Table 2). In line with our modelling results, the study by PETZOLD et al. (2014) already suggested the sympatric occurrence of up to three species of *Pelomedusa* in the Arusha

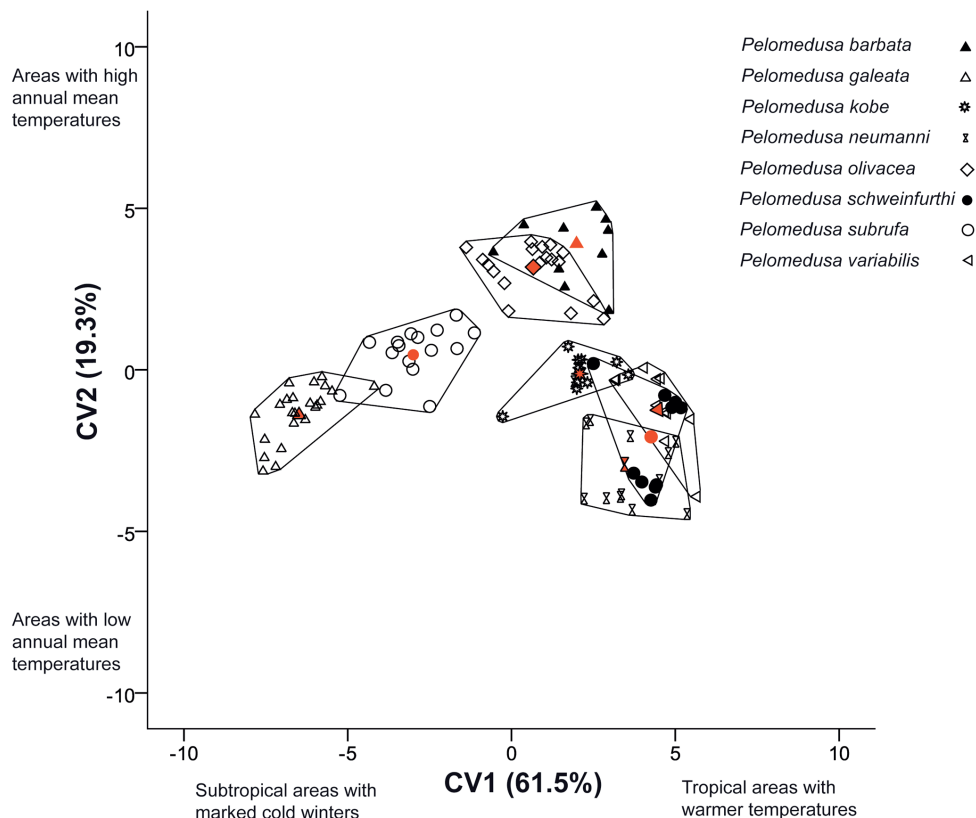


Figure 4. Discriminant analysis of the climatic spaces of eight species of *Pelomedusa*. Percentages of the explained variation are given for both axes (CV – coefficient of variation). Total variation explained: 80.8%. Group centroids in red.

region of Tanzania, which was confirmed by our models (Fig. 2). We suggest that intensive surveys should be conducted in the potential regions of sympatry to confirm or reject sympatric or even syntopic occurrences of different *Pelomedusa* species there.

We also identified disjunct overpredicted areas of considerable size in which unspecific *Pelomedusa* records are located (Fig. 3). Such a situation can be indicative of previously unrecognised species (RAXWORTHY et al. 2003, 2007), and the genetic and morphological screening of helmeted terrapins from these areas would be the consequent next step.

However, there are also caveats regarding the reliability of our ecological niche models. Introduced populations of *P. subrufa* sensu stricto are widely distributed in northern, western, and southern Madagascar (cf. the EMySystem map and PETZOLD et al. 2014). Yet, our model for *P. subrufa* did not predict the occurrence of the species there (Fig. 1B), but for other areas of Madagascar. This underlines that ecological niche models are approximations that should not be trusted blindly.

Even if our models are used under this premise for assessing the conservation status, they clearly indicate that the IUCN Threat Categories of the studied *Pelomedusa* species need to be revised. Until now, all helmeted terrapins are still treated as a single widely distributed species by the IUCN, which is why helmeted turtles are not listed in the IUCN Red List of Threatened Species (IUCN 2014a). This corresponds to the Threat Category “Least Concern, LR/lc” (BOYCOTT & BOURQUIN 2008).

The extent of occurrence (EOO) and the area of occupancy (AOO) are both used as measures for assessing the conservation status of a species (MACE et al. 2008, IUCN 2014b). According to our calculations, the EOOs and AOOs (Table 3) per se do not qualify any studied species for red-listing, because then EOOs < 20,000 km² or AOOs < 2,000 km² would be required. However, we assume that our calculations for the AOOs using the approach of BACHMAN et al. (2011) are by far too optimistic. All *Pelomedusa* species depend on the presence of freshwater habitats and are therefore neither common nor widespread all over the inferred areas of occurrence. Moreover, surface freshwater is scarce and dwindling in the ranges of some *Pelomedusa* species. This is, for instance, true for *P. barbata*, a species endemic to the southwestern Arabian Peninsula. PETZOLD et al. (2014) already pointed out that this species is most probably endangered, and our AOO value does not necessarily contradict this view.

As is obvious, our results constitute a first effort towards a better understanding of the distribution ranges of *Pelomedusa* species. The resulting models and statistical analyses are “under development” and awaiting new field data that could improve details and resolution.

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Note added in proof

In the meantime, *Pelomedusa neumanni* has been recorded from southern Ethiopia (Omo Region), i.e. from the immediate proximity of its predicted ecological niche. However, further to the north in Ethiopia, two deeply divergent genetic lineages of *P. somalica* (two distinct candidate species) were found in regions within the ecological niche of *P. neumanni* (Oromia Region). At the eastern border of the predicted ecological niche of *P. subrufa* sensu stricto in South Africa, this species has been found at another site (Mpumalanga Province), so that the latter species has now been recorded twice in northeastern South Africa (FRITZ et al. 2015).

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Supplementary material

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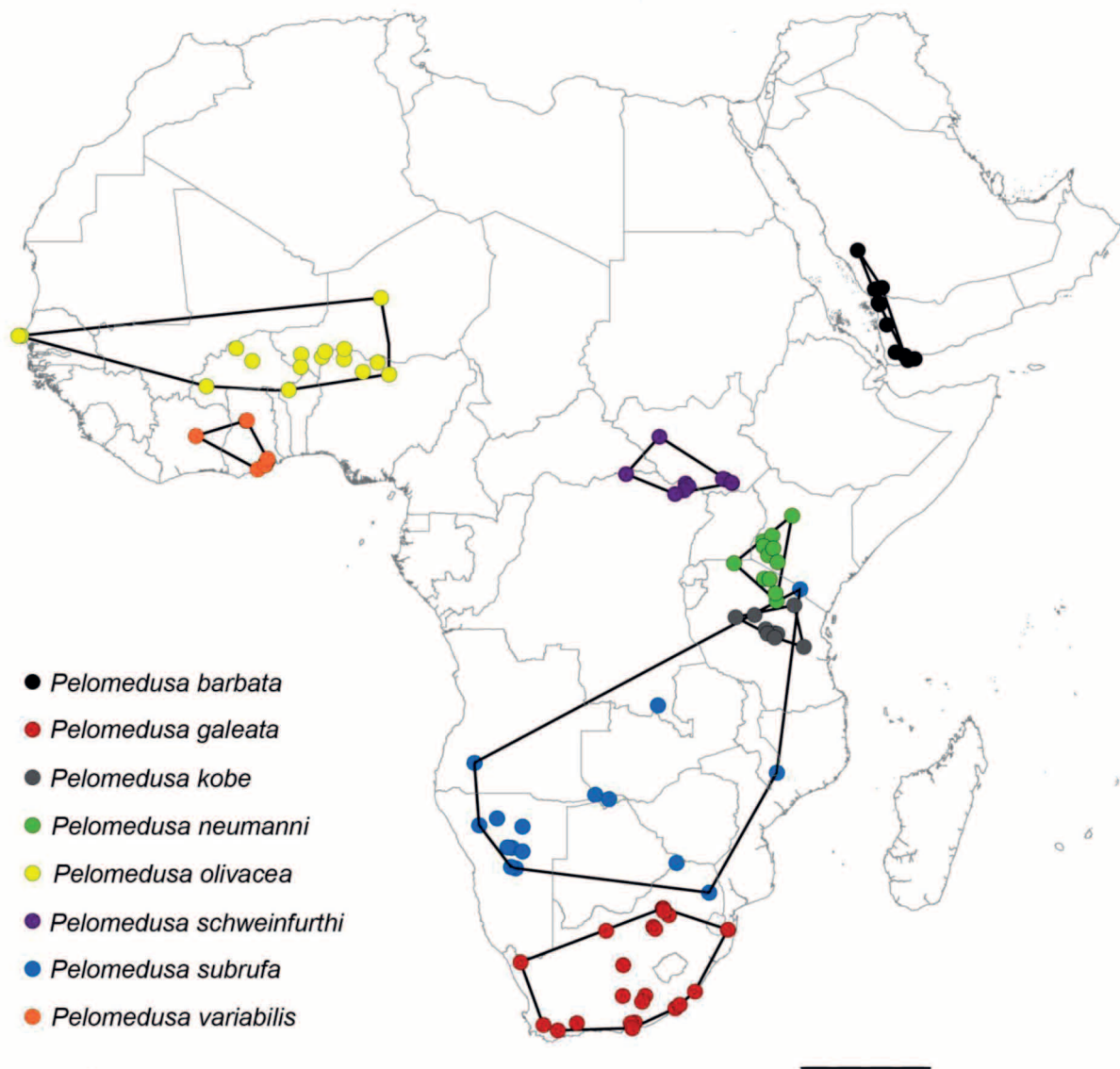
Supplementary figure S1. Minimum convex polygons enclosing records used to develop the ecological niche models.

Supplementary figure S2. Records of *Pelomedusa* from HerpNet (<http://www.herpnet.org>), EMySystem (<http://emys.geo.orst.edu/>), and PETZOLD et al. (2014).

Supplementary figures S3–S10. Environments modelled as suitable for *Pelomedusa olivacea*, *P. neumanni*, *P. galeata*, *P. barbata*, *P. schweinfurthi*, *P. subrufa*, *P. variabilis*, and *P. kobe* using MAXENT.

Supplementary table S1. Additional records of *Pelomedusa* species used for ENM.

Supplementary table S2. Statistics of univariate one-way analysis of variance (ANOVA) among *Pelomedusa* species for each environmental variable and altitude.



Supplementary figure S1. Minimum convex polygons enclosing records used to develop the ecological niche models.



Supplementary figure S2. Records for *Pelomedusa* from HerpNet (<http://www.herpnet.org>), EMYSsystem (<http://emys.geo.orst.edu/>), and PETZOLD et al. (2014). The allochthonous populations of *Pelomedusa subrufa* sensu stricto on Madagascar were excluded. The internet resources were accessed on 16 April 2013.



Supplementary figure S3. Environments modelled as suitable for *Pelomedusa olivacea* using MAXENT. Minimum training presence = 0.074.



Supplementary figure S4. Environments modelled as suitable for *Pelomedusa neumanni* using MAXENT. Minimum training presence = 0.162.



Supplementary figure S5. Environments modelled as suitable for *Pelomedusa galeata* using MAXENT. Minimum training presence = 0.017.



Supplementary figure S6. Environments modelled as suitable for *Pelomedusa barbata* using MAXENT. Minimum training presence = 0.351.



Supplementary figure S7. Environments modelled as suitable for *Pelomedusa schweinfurthi* using MAXENT. Minimum training presence = 0.297.



Supplementary figure S8. Environments modelled as suitable for *Pelomedusa subrufa* using MAXENT. Minimum training presence = 0.381.



Supplementary figure S9. Environments modelled as suitable for *Pelomedusa variabilis* using MAXENT. Minimum training presence = 0.152.



Supplementary figure S10. Environments modelled as suitable for *Pelomedusa kobe* using MAXENT. Minimum training presence = 0.280.

Supplementary table S1. Additional records of *Pelomedusa* species used for ENM (data from HerpNet and EMYSsystem).

Species	Provenance	Source
<i>Pelomedusa barbata</i>	Saudi Arabia: N17°01.00 E42°50.00	HerpNet
<i>Pelomedusa barbata</i>	Saudi Arabia: N17°01.20, E42°49.80	EMYSsystem
<i>Pelomedusa barbata</i>	Saudi Arabia: N18°00.00, E42°34.80	EMYSsystem
<i>Pelomedusa barbata</i>	Yemen: N13°01.20, E44°54.00	EMYSsystem
<i>Pelomedusa barbata</i>	Yemen: N13°06.00, E045°22.80	EMYSsystem
<i>Pelomedusa barbata</i>	Yemen: N13°34.80, E44°01.80	EMYSsystem
<i>Pelomedusa barbata</i>	Yemen: N15°30.00, E43°25.20	EMYSsystem
<i>Pelomedusa kobe</i>	Tanzania: S06°09.00, E35°34.20	EMYSsystem
<i>Pelomedusa kobe</i>	Tanzania: S4°52.80, E34°09.00	EMYSsystem
<i>Pelomedusa kobe</i>	Tanzania: S5°52.20, E34°55.20	EMYSsystem
<i>Pelomedusa kobe</i>	Tanzania: S6°10.20, E35°04.20	HerpNet
<i>Pelomedusa kobe</i>	Tanzania: S6°10.20, E35°40.20	EMYSsystem
<i>Pelomedusa kobe</i>	Tanzania: S6°10.99, E35°45.00	EMYSsystem
<i>Pelomedusa kobe</i>	Tanzania: S6°27.00, E35°34.20	EMYSsystem
<i>Pelomedusa neumanni</i>	Kenya: N0°03.00, E34°46.80	EMYSsystem
<i>Pelomedusa neumanni</i>	Kenya: N0°12.00, E35°28.01	HerpNet
<i>Pelomedusa neumanni</i>	Kenya: N0°12.00, E35°28.20	EMYSsystem
<i>Pelomedusa neumanni</i>	Kenya: N0°40.80, S35°07.20	EMYSsystem
<i>Pelomedusa neumanni</i>	Kenya: N0°42.00, E35°22.80	EMYSsystem
<i>Pelomedusa neumanni</i>	Kenya: S1°09.00, E35°46.20	EMYSsystem
<i>Pelomedusa neumanni</i>	Tanzania: S2°20.00, E34°50.00	HerpNet
<i>Pelomedusa neumanni</i>	Tanzania: S2°21.31, E35°12.57	HerpNet
<i>Pelomedusa neumanni</i>	Tanzania: S3°21.24, E35°36.73	EMYSsystem
<i>Pelomedusa olivacea</i>	Burkina Faso: N12°57.00; W1°04.98	EMYSsystem
<i>Pelomedusa olivacea</i>	Burkina Faso: N13°51.00, W2°12.00	EMYSsystem
<i>Pelomedusa olivacea</i>	Nigeria: N12°12.00, E6°40.20	EMYSsystem
<i>Pelomedusa olivacea</i>	Nigeria: N12°51.28, E7°42.68	HerpNet
<i>Pelomedusa olivacea</i>	Nigeria: N13°48.00, E5°22.80	EMYSsystem
<i>Pelomedusa olivacea</i>	Nigeria: N14°09.01, E8°30.99	HerpNet
<i>Pelomedusa olivacea</i>	Togo: N10°54.00, E0°24.00	EMYSsystem
<i>Pelomedusa schweinfurthi</i>	Democratic Republic of the Congo: N3°37.20, E28°34.20	EMYSsystem
<i>Pelomedusa schweinfurthi</i>	Democratic Republic of the Congo: N3°52.80, E29°12.00	EMYSsystem
<i>Pelomedusa schweinfurthi</i>	Democratic Republic of the Congo: N4°10.16, E29°30.41	EMYSsystem
<i>Pelomedusa schweinfurthi</i>	Democratic Republic of the Congo: N4°22.20, E29°18.00	EMYSsystem
<i>Pelomedusa schweinfurthi</i>	South Sudan: N4°24.00, E32°34.20	EMYSsystem
<i>Pelomedusa schweinfurthi</i>	South Sudan: N4°24.29, E32°32.83	HerpNet
<i>Pelomedusa schweinfurthi</i>	South Sudan: N4°42.00, E31°55.20	EMYSsystem
<i>Pelomedusa variabilis</i>	Ghana: N5°39.00, E0°10.80	EMYSsystem
<i>Pelomedusa variabilis</i>	Ghana: N5°39.00, E0°11.00	HerpNet
<i>Pelomedusa variabilis</i>	Ghana: N6°06.00, E0°01.02	HerpNet
<i>Pelomedusa variabilis</i>	Ghana: N6°06.00, E0°01.20	EMYSsystem
<i>Pelomedusa variabilis</i>	Ghana: N8°46.77, W1°28.082	HerpNet

Supplementary table S2. Statistics of univariate one-way analysis of variance (ANOVA) among *Pelomedusa* species for each environmental variable and altitude. AMT – annual mean temperature; MDR – mean diurnal range; IT – isothermality; MTWM – maximum temperature of warmest month; MTCM – minimum temperature of coldest month; AP – annual precipitation; PWQ – precipitation of wettest quarter; PDQ – precipitation of driest quarter; PWaQ – precipitation of warmest quarter; PCQ – precipitation of coldest quarter; ALT – altitude.

Bioclimatic variable	Mean Square	F	df	Sig.
AMT	25810.27	26.114	7	0.0001
MDR	4487.94	9.618	7	0.0001
IT	1367.46	102.64	7	0.0001
MTWM	22482.36	16.082	7	0.0001
MTCM	57239.33	52.854	7	0.0001
AP	1553605.7	14.792	7	0.0001
PWQ	291588.09	16.017	7	0.0001
PDQ	25456.49	12.253	7	0.0001
PWaQ	100033.53	7.904	7	0.0001
PCQ	349107.62	20.107	7	0.0001
ALT	4274818.72	11.782	7	0.0001