Current and future suitable habitats of a range-restricted species group (*Cyrtodactylus chauquangensis*) in Vietnam

Dung Van **Tran**¹, Tuoi Thi **Hoang**¹, Thuong Huyen **Nguyen**¹, Van Bac **Bui**¹, L. Lee **Grismer**², Bao Quang **Tran**^{3*} & Vinh Quang **Luu**^{1*}

Abstract. Climate change is one of the most serious threats to the world's biodiversity. Reptiles with limited dispersal capacities, small geographic ranges, or specialised habitats are considered to be especially vulnerable. In this study, we applied the Maximum Entropy algorithm to predict the current and future suitable habitats of a range-restricted species group (*Cyrtodactylus chauquangensis*) in Vietnam. The models show that the current suitable habitat of *C. chauquangensis* species group mainly covers areas in Ninh Binh, Thanh Hoa, and a part of Nghe An provinces, Vietnam, covering approximately 83,521.53 km². The models also indicate Karst Distance, Mean Diurnal Range, and Precipitation of Driest Month as the top three important variables in generating the potential distribution of *C. chauquangensis* species group under different scenarios. Under the scenario of climate change RCP 4.5, the potential distribution for the group is predicted to decrease significantly, with an average of 59.74% and 65.74% in 2050 and 2070, respectively. For RCP 8.5, the average loss area due to climate change is around 64.18% and 71.44% in 2050 and 2070, respectively. Based on our predictions, suitable habitats in Ninh Binh, Thanh Hoa, and Nghe An provinces could be potential refugia of the group under the impact of climate change. We strongly suggest that these areas be highly prioritised for in-situ conservation measures to safeguard species of the *C. chauquangensis* group in Vietnam.

Key words. bent-toed gecko, climate change, ecological niche modelling, Maxent, potential distribution

INTRODUCTION

Distributional patterns play an important role in understanding the biogeographical, ecological, and conservation aspects of organisms. Ecological niche modelling (ENM) has been broadly applied to project a species distribution by combing occurrence localities and environmental predictors (Anderson et al., 2003; Guisan & Thuiller, 2005). Results of ENM may provide insights into the relationship between species and environmental space, ecological interaction, and speciation (Rissler & Apodaca, 2007). In particular, the ENM approach has been used to tackle various questions in ecological studies, for example, guiding field surveys for rare species (van Schingen et al., 2014; Ngo et al., 2022), supporting taxonomic classification (Raxworthy et al., 2007; Zhang et al., 2014), projecting the distribution of species in the past

²Herpetology Laboratory, Department of Biology, La Sierra University, 4500 Riverwalk Parkway, Riverside, California 92515, USA. lgrismer@lasierra.edu

© National University of Singapore ISSN 2345-7600 (electronic) | ISSN 0217-2445 (print) (van Riemsdijk et al., 2017), revealing ecological niche differentiation between species (Peñalver-Alcázar et al., 2021; Tran et al., 2021; Chan et al., 2022), increasing the efficiency of conservation efforts (van Schingen et al., 2014; Tran et al., 2020), and elucidating drivers of diversification (Chan & Brown, 2020). In particular, ENM has also been frequently applied to assess the risk of climate change on the distribution of species such as amphibians (Milanovich et al., 2010; Ashrafzadeh et al., 2019), birds (Papes, 2007; Vásquez-Aguilar et al., 2021), mammals (Tran et al., 2020; Vu et al., 2020; Trinh et al., 2021; Blair et al., 2022), and reptiles (Bezeng et al., 2018; Ngo et al., 2022).

Previous studies have shown that climate change is one of the main threats to the biodiversity of the world (Paterson et al., 2008; Bellard et al., 2014; Trew & Maclean, 2021). Over a third of global species are predicted to become extinct by 2050 due to climate change (Thomas et al., 2004). The effects of climate change may result in the decrease, or even the disappearance of a species over its historical distribution or the shift of a species' range towards the poles and higher elevations (Walther et al., 2002; Borzée et al., 2019; Vu et al., 2020). Species with limited dispersal capacities, small geographic ranges, or specialised habitats are considered to be more vulnerable to such changes (Thuiller et al., 2005; Pacifici et al., 2015). Reptiles depend closely on environmental conditions (e.g., temperature), thus their distributions are likely to decline significantly under the

Accepted by: Chan Kin Onn

¹Faculty of Forest Resources and Environmental Management, Vietnam National University of Forestry, Xuan Mai, Chuong My, Hanoi, Vietnam; Email: vinhlq@ vnuf.edu.vn, Tel.: + 84 91292350 (*corresponding author)

³Vietnam Administration of Forestry. 2 Ngoc Ha, Ha Noi, Vietnam; Email: <u>baofuv@gmail.com</u>; Tel.: +84 945043274 (*corresponding author)

effects of climate change (Araújo et al., 2006; Bickford et al., 2010). Understanding changes in a species' distribution is crucial to planning conservation actions and management strategies (Bezeng et al., 2018; Ngo et al., 2022).

The bent-toed gecko genus Cyrtodactylus Gray, 1827 is one of the most species-diverse genera in the family Gekkonidae with 330 described species thus far (Uetz et al., 2022) and is the third most speciose vertebrate genus in the world (Grismer et al., 2021a). Over the past decade, the still unrealised diversity of the genus Cyrtodactylus has been demonstrated by the rapid annual increase in the rate at which new species are being described from various geographical areas with different habitats, ecotypes, and topography. The genus extends throughout tropical South Asia, Indochina, the Philippines, the Indo-Australian Archipelago, to the Solomon Islands (Grismer et al., 2021a, b). Most species of Cyrtodactylus occupy habitats with an abundance of rocky substrates and many species have independently evolved varying combinations of suites of characteristics that are adaptive for living exclusively on rocks-either granite or limestone-and locomoting in all planes of orientation (Grismer et al., 2015, 2016; Grismer et al., 2021a, b). Based on the distribution of characteristics and habitat preferences of Cyrtodactylus species, they have been divided into 10 different ecotypes, of which the karst ecotype is the largest and contains the majority of the most recently described species (Grismer et al., 2021a). Cyrtodactylus is also recognised as an excellent group for taxonomic, biogeographic, and ecological research, as well as a model group for lizard evolution and biogeography (Grismer et al., 2021a, b; Grismer et al., 2022).

The Cyrtodactylus chauquangensis group (previously referred to as the C. wayakonei species group [Luu et al., 2011; Nguyen et al., 2015; Brennan et al., 2017; Pham et al., 2019; Schneider et al., 2020; Grismer et al., 2021a]) is composed of species endemic to limestone massifs in northern Indochina, ranging from northern Thailand and Laos to northeastern Vietnam and Yunnan Province in southern China. The group is composed of 17 nominal species and a putative new species (HLM 0357) from northern Thailand (Grismer et al., 2021b). The nominal species of this group, Cyrtodactylus chauquangensis, was described by Hoang et al. (2007) from the karstic region of Chau Quang Village, Quy Hop District, Nghe An Province. So far, 10 species of the Cyrtodactylus chauquangensis group have been discovered in limestone (karst) habitats in Vietnam, of which, one species was assessed in the IUCN Red List as Endangered (C. otai), two species as Vulnerable (C. huongsonensis, and C. bichnganensis), five species as Least Concern (C. bobrovi, C. chauquangensis, C. cucphuongensis, C. puhuensis, C. soni), and two other species (C. sonlaensis, C. taybacensis) have not been evaluated yet (IUCN, 2022).

In this paper, we predict which habitats are currently suitable for a range-restricted species group (*Cyrtodactylus chauquangensis* group) in Vietnam by using the Maximum Entropy algorithm. We also evaluate changes in suitable habitats under climate change scenarios for 2050 and 2070.

From the results of our models, we identify predictors (e.g., karst geology and climatic conditions) that may play an important role in determining suitable habitats for the *C. chauquangensis* group. Additionally, we suggest key areas that should receive high priority for surveying and safeguarding the *C. chauquangensis* group and their future potential refugia under the impact of climate change.

MATERIAL AND METHODS

Collecting occurrence data. Researchers have proposed that species' adaptation to certain environments can be seen in their ecological niches (Mota-Vargas & Rojas-Soto, 2016; Maguire et al., 2018; Smith et al., 2019). This means that separating or grouping certain species together can improve our understanding of a species' ecological niche. Currently, there is a lack of occurrence records of many reptiles and other wildlife species, including the C. chauquangensis species groups. In the study, we employed the location data of 10 species of the bent-toed gecko genus Cyrtodactylus within the C. chauquangensis species group to model their current potential distribution and evaluate the potential effects of climate change on the group. The localities of the species of the C. chauquangensis species group were collected from our field surveys from 2010 to 2021. Additionally, we used records from other publications (Hoang et al., 2007; Ngo & Grismer, 2010; Luu et al., 2011; Ngo & Chan, 2011; Nguyen et al., 2014; Nguyen et al., 2015, 2017; Le et al., 2016; Pham et al., 2019; Grismer et al., 2021a). Initially, we gathered a total of 61 presence records of the group, including C. bichnganensis (1 locality), C. bobrovi (2), C. chauquangensis (1), C. cucphuongensis (3), C. huongsonensis (20), C. otai (3), *C. puhuensis* (25), *C. soni* (4), *C. sonlaensis* (1), and *C.* taybacensis (1). In order to avoid model overfitting bias due to spatial autocorrelation among close-distance localities, we used the "spThin" package (Aiello-Lammens et al., 2015) in R version 4.1.2 to thin the occurrence points within 1 km. Finally, 26 localities were employed for prediction analyses (Fig. 1)

Environmental predictors. The study collected 24 predictors including climatic conditions, land use and land cover (LULC), topography, and karst data to project suitable habitat for the C. chauquangensis species group. For climatic variables, 19 climatic variables were downloaded from the World Clim database (http://www.worldclim.com/; Fick & Hijmans, 2017) with 11 temperature and eight precipitation variables at the resolution of 30 arcseconds. We also obtained data of LULC from the Global Land Cover and Land Use 2019 available at Global Land Analysis & Discovery website (https://glad.umd.edu/dataset/global-land-cover-landuse-v1; Hansen et al., 2022). For topographic variables, we gathered three variables: Elevation, Slope, and Aspect. We extracted the elevation data from Digital Elevation Model (GMTED2010; downloaded from https://earthexplorer.usgs. gov; Danielson & Gesch, 2011), then calculated the Slope and Aspect values by using ArcMap version 10.2 (ESRI, 2013). Regarding karst data, Blair et al. (2022) recently highlighted that a model that incorporates both karst and





RAFFLES BULLETIN OF ZOOLOGY 2023

No.	Name	Sources	Description			
1	Bio02	WorldClim Mean Diurnal Range (Mean of monthly =max tem min temp)				
2	Bio04		Temperature Seasonality (standard deviation *100)			
3	Bio07		Temperature Annual Range (BIO5-BIO6)			
4	Bio10		Mean Temperature of Warmest Quarter			
5	Bio14		Precipitation of Driest Month			
6	Bio15		Precipitation Seasonality (Coefficient of Variation)			
7	Bio16		Precipitation of Wettest Quarter			
8	Bio19		Precipitation of Coldest Quarter			
9	Elevation	Earthexplorer.usgs.gov	Height above sea level			
10	Slope		Degree of rise/run			
11	Aspect		Direction a slope face			
12	Land_Cover	Global Land Analysis & Discovery	Land cover			
13	Karst_Distance	World Karst Aquifer Map	The distance to karst area			

Table 1. The environmental variables used to generate the suitable distribution of the C. chauquangensis species group in the MaxEnt model

climate data can effectively clarify the distribution of species adapted to living in karst landscapes. From our field surveys, the localities of C. chauquangensis group species were only in the karst habitats in central and northern Vietnam. Here, we downloaded the karst layer at the vector data format (polygon) from the World Karst Aquifer Map (Chen et al., 2017), then, extracted it in the study site by ArcMap 10.2. To convert the layer to the raster data format, we used the Euclidean Distance tool in ArcMap 10.2 to generate the distance to the karst areas. The tool generates a raster layer covering the study area from the vector layer of the karst, which indicates the distance from each pixel to the nearest object in the karst layer. The distance value of pixels overlapped by the karst polygons were presented as 0 (Appendix 1). Because of the different resolution of variables, we resampled the collected predictors to the same resolution (nearly 0.9×0.9 km) with the Resample tool in ArcMap 10.2 (ESRI). Since the performance of the species distribution model might be influenced by the background size of variables (VanDerWal et al., 2009; Barve et al., 2011), we extracted the predictors by a box buffering 200 km from our occurrence localities following the suggestion of VanDerWal et al. (2009). We calculated the Pearson's correlation index (r) using ENMTools version 1.4.4 (Warren et al., 2010), then eliminated one variable from each pair of highly correlated variables (|r| > 0.80) to avoid the influence of multicollinearity on the modelling process. Consequently, we used only 13 environmental variables for predictions (Table 1).

To assess the effect of climate change on the distribution of the *C. chauquangensis* species group, we selected future climate change from two general circulation models (GCM): ACCESS1-0 (CSIRO-BOM, Australia), GFDL- CM3 (NOAA, GFDL, USA) as per the suggestion of McSweeney et al. (2015) for the Southeast Asia region. For each GCM, we selected for two climate change scenarios of representative concentration pathways (RCPs): RCP 4.5 and RCP 8.5, representing intermediate and the most severe levels of accumulation of greenhouse gas concentrations in the future climate by the 2050s (average 2041–2060) and by the 2070s (average 2061–2080).

Ecological niche modelling. We used MaxEnt model version 3.4.4 (https://biodiversityinformatics. amnh.org/open source/ maxent/) to project the potential distribution of the C. chauquangensis species group. Applying the automatic setting of MaxEnt might lead to the model overfitting and providing a low precision distribution (Muscarella et al., 2014; Kass et al., 2021). Therefore, we utilised ENMeval package version 2.0.0 (Kass et al., 2021) in R version 4.1.2 to turn the regularisation multiplier values and feature class and select the optimal model. In the study, we turned six feature classes, including L, LQ, H, LQH, LQHP, and LQHPT (L = linear, Q = quadratic, H = hinge, P = product, and T = threshold), and regularisation multiplier values were adjusted from 1 to 5. In each model, the model performance was evaluated by the Jackknife partition method. Consequently, we analysed 30 candidate models and selected the optimal model based on the minimum AICc index (Muscarella et al., 2014; Kass et al., 2021). To assess the good-of-fit of the model, we applied the Area Under Curve (AUC) as suggested by Phillips et al. (2006). The output of the MaxEnt map ranges from 0 to 1, where the higher value represents a higher suitability level. To determine suitable or unsuitable habitat for the species, we used the "Minimum training presence logistic threshold = 0.03" to maximise the areas for conservation purposes. Then, we divided the suitable area into three categories by



Fig. 2. The potential distribution of the *C. chauquangensis* species group under present conditions generated by MaxEnt, A, Minimum training presence logistic threshold; B, 10 percentile training presence logistic threshold.

dividing the suitable value of a pixel equally: low suitability (0.03-0.3), medium suitability (0.3-0.6), and high suitability (>0.6). Additionally, we employed the "10 percentile training presence logistic threshold = 0.4" to identify the priority surveyed areas for the species group. The level of suitability is also determined by dividing equally the pixel value, including low suitability (0.4-0.6), medium suitability (0.6-0.8), and high suitability (>0.8). The threshold normally generates a smaller suitable habitat when converting to the suitable map. To assess the rate of protected suitable habitats of the species group, we overlapped the predicted suitable area and boundary of protected areas downloaded from https://www.protectedplanet.net/en (UNEP-WCMC & IUCN, 2022).

RESULTS

Based on the AICc value (607.77) from the evaluation metric result, we selected the best model for the *C*. *chauquangensis* species group with feature class = Linear (L) and regularisation value = 5. The model's average training AUC = 0.976 ± 0.002 , and testing AUC = 0.973 ± 0.056 demonstrated excellent predictions.

The predicted suitable habitat of the *C. chauquangensis* species group showed discrimination between two different thresholds "Minimum training presence logistic threshold" and "10 percentile training presence logistic threshold". For

the "Minimum training presence logistic threshold", the high and medium suitability areas were mainly found in (i) Ninh Binh, the north of Thanh Hoa, and (ii) a part of Nghe An provinces, with an area of 6,296.94 km² and 15,254.73 km² respectively. The low suitability habitat was estimated to cover 61,969.86 km² in north-eastern (Quang Ninh, Lang Son, Cao Bang, Tuyen Quang provinces) and north-western Vietnam (Son La, Dien Bien, Lao Cai provinces) (Fig. 2A, Table 2).

For suitable habitat of the *C. chauquangensis* species group determined by the "10 percentile training presence logistic threshold", it was significantly narrower than that of the "Minimum training presence logistic threshold" with only 15,829.83 km². The highly suitable category was only predicted in a very small area in Ninh Binh and Thanh Hoa provinces with 426.06 km². The medium and low suitability habitats were 9,532.08 km² and 5,871.69 km² in size respectively, and concentrated in Ha Noi, Ninh Binh, Son La, Thanh Hoa, and Nghe An provinces (Fig. 2B; Table 2).

Overlapping between the current protected network and potential range of the *C. chauquangensis* species group showed that only 4,705.29 km² (equally 5.63%) and 2,198.34 km² (equally 13.89%) of suitable area for the *C. chauquangensis* species group was predicted to be inside the current protected area network under the "minimum training presence logistic threshold", and the "10 percentile

	Present							
Q::4 - L :1:4	Minimum trair	ing presence log	istic threshold	10 percentile training presence logistic threshold				
Suitability	Tatal	Within	n PAs	Tatal	Within PAs			
	Total	km ²	%	- I otal	km ²	%		
Low	61969.86	2042.82	3.30	9532.08	1076.49	11.29		
Medium	15254.73	1540.62	10.10	5871.69	1050.57	17.89		
High	6296.94	1121.85	17.82	426.06	71.28	16.73		
Total	83521.53	4705.29	5.63	15829.83	2198.34	13.89		

Table 2. The suitable habitat area of the C. chauquangensis species group with present environmental variables (Unit: km²).

training presence logistic threshold" respectively (Table 2). There are only a few protected areas covering the high and medium suitability distribution of the *C. chauquangensis* species group, including Cuc Phuong National Park (NP), Ngoc Son–Ngo Luong, Pu Luong, Van Long, Hang Kia–Pa Co, and Pu Huong, Pu Hu Nature Reserves (NR; Fig. 2).

Our results also showed the most important predictors for predicting the suitable habitat of the C. chauquangensis species group. The top three contribution variables were Karst Distance (35%), Bio2 – Mean Diurnal Range (33.4%), and Bio 14 - Precipitation of Driest Month (23.3%). The response curves illustrated the probability of suitability changes following the fluctuation of environmental variables. The response curve to Karst Distance revealed that the C. chauquangensis species group was highly dependent on habitat in karst mountains. The higher suitable probabilities mostly occurred within the karst area (Fig. 3A). For both the Mean Diurnal Range, and Precipitation of Driest Month, the suitable habitat showed a negative relationship (Figs. 3B, C). Furthermore, the most favoured precipitation of the driest month of the species group was below around 5 mm (Fig. 3C).

Under the RCP4.5 scenarios, the potential distribution of the *C. chauquangensis* species group was predicted to decrease significantly with an average of 59.74% and 65.74% in 2050 and 2070 respectively (Table 4, Fig. 4). The predicted areas in Lai Chau, Dien Bien, Son La, and parts of the predicted areas in Nghe An provinces may be rendered unsuitable. In Ninh Binh, Thanh Hoa, and central Nghe An provinces, the high and medium suitability areas of the species group could be partly replaced by low suitability areas or even totally disappear (Table 3, Fig. 4). In particular, the potential distribution projected by the ACCESS1-0 model could be decreased by approximately 46,927.35 km² in 2050 and 54,981.18 km² in 2070. For the GFDL-CM3 model, the loss of potential areas was predicted around 52,871.13 km² and 54,832.14 km² in 2050 and 2070, respectively (Table 4).

In terms of the scenarios of RCP8.5, the potential area of the species group was projected as more severe compared to the project under the RCP4.5 scenario (Tables 3, 4; Fig. 4). Our models showed that the average loss area due to



Fig. 3. The response curves of the top three highest contribution predictors for the *C. chauquangensis* species group model. The red line shows the mean response of 25 replicates in the Maxent model, and the blue band illustrates the standard deviation. A, Karst distance; B, Bio2 – Mean diurnal range; C, Bio 14 – Precipitation of Driest Month.



Fig. 4. The potential distribution of the C. chauquangensis species group under climate change scenarios.

climate change was around 64.18% and 71.44% of the present distribution in 2050 and 2070, respectively. In particular, under the ACCESS1-0 model, the loss of suitable areas accounted for 81.69% (around 68,227.92 km²) in 2050, and 75.10% (around 62,728.02 km²). Most of the high and medium suitability areas were projected to disappear or turn into low suitability areas (Table 3; Fig. 4). The majority of suitable habitat for the species in the group under both climate models was predicted to concentrate on the karst area in Ninh Binh and central Nghe An provinces (Fig. 4). Our results also showed a qualitative consistency across the different climate change models and scenarios.

DISCUSSION

Recently, the MaxEnt model has been widely applied to generate the potential distribution of species. Several studies have applied the model successfully to predict the potential distribution of reptiles (Ngo et al., 2019; Chan et al., 2022; Ngo et al., 2022). With a high value of AUC_{training} and AUC_{testing} (> 0.9), the model showed a high performance in predicting suitable habitat (Phillips et al., 2006; Lobo et al., 2008). It is emphasised that the MaxEnt model is useful for identifying suitable habitat for the *C. chauquangensis* species group with limited occurrence data.

ENM generates potential species distribution based on the relationship between known occurrence localities and environmental predictors (Guisan & Thuiller, 2005). In terms of occurrence data, most researchers normally collect the occurrence localities at the species level to run models. However, occurrence data is still very limited due to being range-restricted and the fact that many species have not been intensely studied, which is a great challenge for developing ENM (Anderson et al., 2016; Peterson et al., 2018). Recently, Smith et al. (2019) suggested that adaptation to local conditions and sharing of environmental tolerances could be reflected in ecological niches, thus splitting taxa or combining related taxa could improve ecological niche estimation. The strategy for grouping occurrence records above the species level in estimating ecological niches of species also has been applied in several previous studies (e.g., Raxworthy et al., 2007; Mota-Vargas & Rojas-Soto, 2016). In this study, the C. chauquangensis species group contains endemic species adapted to limestone habitats in northern Indochina (Grismer et al., 2021b). Previous studies suggested that the predicted suitable habitat of clade models is both larger (Mota-Vargas & Rojas-Soto, 2016; Maguire et al., 2018; Collart et al., 2021) and also smoother than combined subclade models (Maguire et al., 2018). For conservational purposes, we used the occurrence localities of 10 species in the C. chauquangensis group with very limited occurrence localities of each species to generate suitable habitat models for the group in the present and also assess the impact of climate change on the group in Vietnam.

The predicted present distribution of the *C. chauquangensis* species group with the minimum training presence logistic threshold covered most of the occurrence records of the group

RAFFLES BULLETIN OF ZOOLOGY 2023

	ACCESS1-0				GFDL-CM3			
Suitability	RCP4.5		RCP8.5		RCP4.5		RCP8.5	
	2050	2070	2050	2070	2050	2070	2050	2070
Low	36037.71	28490.94	15190.74	20177.10	30465.72	28652.94	42461.82	26892.81
Medium	556.47	49.41	102.87	579.96	184.68	36.45	2033.91	21.06
High	0	0	0	36.45	0	0	50.22	0
Total	36594.18	28540.35	15293.61	20793.51	30650.40	28689.39	44545.95	26913.87

Table 3. The suitable habitat area of the C. chauquangensis species group under climate change scenarios (Unit: km²).

Table 4. The change of suitable habitat area of the C. chauquangensis species group under climate change scenarios (Unit: km²).

	RCP	Present	2050			2070			
Model		Suitable area	Suitable area	Change	%	Suitable area	Change	%	
ACCESS1-0	4.5	83521.53	36594.18	-46927.35	-56.19	28540.35	-54981.18	-65.83	
GFDL-CM3	4.5	83521.53	30650.40	-52871.13	-63.30	28689.39	-54832.14	-65.65	
Average			33622.29	-49899.24	-59.7 4	28614.87	-54906.66	-65.7 4	
ACCESS1-0	8.5	83521.53	15293.61	-68227.92	-81.69	20793.51	-62728.02	-75.10	
GFDL-CM3	8.5	83521.53	44545.95	-38975.58	-46.67	26913.87	-56607.66	-67.78	
Average			29919.78	-53601.75	-64.1 8	23853.69	-59667.84	-71.4 4	

(Fig. 2). It showed a high predictive performance for the group. The current high and medium suitability habitats of the species group are concentrated in two distinctive blocks: i) the karst area in Ninh Binh and Thanh Hoa provinces, and ii) the karst area in central Nghe An province. The karst variables contributed the most to the models, showing a crucial role of the variable in the habitat selection of the *C. chauquangensis* species group, as discussed below. The discontinuity of the karst mountains between Thanh Hoa and Nghe An provinces might explain why the potential distribution of the *C. chauquangensis* species group in Ninh Binh and Thanh Hoa provinces was predicted separately from the suitable area in Nghe An province.

The results of our ENM model can locate areas that provide suitable habitats for focal species but have not yet been surveyed (Pearson et al., 2007; Thorn et al., 2009). To date, only a few studies have reported the successful application of ENM to find new populations of rare reptiles in northern Vietnam (e.g., van Schingen et al., 2016; Ngo et al., 2019, 2022). Therefore, we suggest that the high and medium suitability habitats in Ninh Binh, Thanh Hoa, and Nghe An provinces should receive high priority for conducting surveys to explore new populations and/or new distributional records of these species, providing sufficient data to assess and update population status in the IUCN Red List. We also highly recommend using finer-scale environmental variables for the models involving the *C. chauquangensis* species group, as finer-scale analyses could be very important to help

researchers, conservationists, and managers by identifying appropriate suitable locations throughout the range of the different species (Blair et al., 2022). The finer-scale model should include microclimatic data, a high resolution of vegetation layers, and intraspecific information when these data are available. A sufficiently powerful computer is also needed to run a finer-scale analysis with the many complex processes of the ENMs model.

Our model also generated an overprediction area in northeast Vietnam, where no Cyrtodactylus species are currently known. Such an overprediction area was considered low suitability habitat, and occurred only under the minimum training presence logistic threshold (Fig. 2A). North-eastern Vietnam is mainly covered by a karst mountain range (see Fig. 1), and is the environmental refugia of Goniurosaurus species (Ngo et al., 2022). With the highly strict threshold (the 10-percentile training presence logistic threshold) the optimal distribution of the C. chauquangensis species group was restricted to Ninh Binh, Thanh Hoa, and central Nghe An provinces, while the overprediction has been excluded (Fig. 2B). It would be more useful to spend more effort to find new populations of the species group in the optimal areas instead of the overpredicted areas, and thus a strict model can aid in the discovery of new populations with reduced investigation effort and resources (e.g. time, budget). Hence, we recommend using an appropriate threshold of the model for each specific conservation objective.

Our model showed that the most important variable to predict the suitable habitat of the C. chauquangensis species group was the karst habitat, with Bio2 - Mean Diurnal Range and Bio 14 – Precipitation of Driest Month coming in second and third respectively. Limestone karsts are the home of various endemic species, and are globally vital landscapes (Clements et al., 2006). In a recent study, Blair et al. (2022) emphasised the significance of karst geology to predict suitable habitat for Francois's langur, a primate that has adapted to limestone landscapes in northern Vietnam. The research also demonstrated the potential of limestone karst areas to serve as refuges for species adapted to such environments under the impacts of climate change. Due to the physical stability of habitat, karst-dwelling species may exhibit greater resilience to climate change in comparison to those adapted to forest environments. In the karstic area, microclimate heterogeneity could occur and create microrefugia at various scales, which can allow species to survive under extreme climatic conditions, leading to the reduction of the extinction threat of climate change (Suggitt et al., 2018). So far, the C. chauquangensis species group has been only recorded in limestone massifs in northern Indochina (Grismer et al., 2021b). The C. chauquangensis species group may be too specialised to survive or slowly adapt to other habitats. We argue that protecting karst environments will play an essential role in protecting the C. chauquangensis species group under climate change, besides other anthropogenic threats (Luu & Lo, 2018). However, the karst landscapes are facing several threats, especially cement mining (Clements et al., 2006; Hughes, 2017). Urgent actions to protect the limestone karsts should be planned and implemented promptly (Clements et al., 2006). Furthermore, we believe that the species group's decreased suitable habitat was most likely due to other habitat types located between karst areas that were not represented in the current karst data map. The karst variable used in the model was still at a relatively coarse scale, while various microhabitats/microclimates may be supported by the karst topography at a finer scale (Blair et al., 2022). Therefore, we highly recommend using a higher resolution of the karst variables when it is available for further ENM analysis on karst-adapted species.

One of the consequences of climate change is that the suitable range of species could decline or disappear (Vu et al., 2020; Trinh et al., 2021; Blair et al., 2022; Ngo et al., 2022). Previous studies have also reported that the distribution of fauna in the karst mountain ecosystem could shift or retract under the impact of climate change in northern Vietnam (Trinh et al., 2021; Blair et al., 2022; Ngo et al., 2022), or in other types of ecosystems in Vietnam (Tran et al., 2020; Vu et al., 2020; Yang et al., 2021). The distributions of species in the Gekkonidae, such as Gekko japonicus (Kim et al., 2020) and the Eublepharidae, such as Goniurosaurus lichtenfelderi (Ngo et al., 2022), are also expected to decrease or become isolated as a result of climate change. Our results with the model of the C. chauquangensis species group habitat distribution is consistent with the trend of habitat contraction under climate change.

Under the impact of climate change, the suitable habitats in Ninh Binh, Thanh Hoa, and Nghe An provinces could be potential refugia for the C. chauquangensis species group in 2050 and 2070, although the suitability level in the area is likely to turn from high to low suitability (Fig. 4). With high emission scenarios of RCP8.5, the predicted habitat of the species group might be impacted more seriously compared to the RCP4.5 scenarios. In particular, the suitable habitat of the C. chauquangensis species group is projected to decrease over time. The suitable habitat that will disappear under RCP8.5 scenarios was predicted to be around 64.18% and 71.44% in 2050 and 2070, respectively, while for RCP4.5, the area of habitat loss was approximately 59.74% in 2050 and 65.74% in 2070 (Tables 3, 4). Our results highlight the importance and urgency of appropriate conservation solutions in the context of climate change. Research and the implementation of management measures, which require collaboration between researchers and authorities, are essential to protect the populations of the C. chauquangensis species group and their habitat.

Our analysis of the overlap between the current suitable habitat of the C. chauquangensis species group and the existing protected area network in Vietnam revealed that the current network of protected areas in Vietnam is insufficient to cover the highly suitable habitat of the species group. Only a minority of the potential range of this species group was predicted to be inside protected areas, including Cuc Phuong NP, Van Long NR (Ninh Binh Province), Thuong Tien, Ngoc Son-Ngo Luong, Hang Kia-Pa Co NRs (Hoa Binh Province), Pu Luong, Pu Hu NRs (Thanh Hoa Province), and Pu Huong NR, a part of Pu Mat NP (Nghe An Province; see Fig. 2). Therefore, we highly suggest that these areas should be given high priority as key areas for protecting the C. chauquangensis species group. Additionally, the current network of protected areas is inadequate for conserving the suitable range of the C. chauquangensis species group under projected effects of climate change in the future. A large amount of suitable habitat within the existing protected areas is likely to decrease and/or turn into habitat that has a low suitability level (Fig. 4).

CONCLUSION

In the current study, the current suitable habitat of the *C. chauquangensis* species group is predicted to mainly cover areas in Ninh Binh, Thanh Hoa, and a part of Nghe An province, Vietnam with an area of approximately 83,521.53 km². The model's most important environmental variables are Karst Distance, Mean Diurnal Range, and Precipitation of Driest Month. The potential distribution of the group is projected to shrink rapidly with an average of 59.74% and 65.74% in 2050 and 2070 respectively, under the RCP 4.5 scenario. For the RCP 8.5 scenario, the potential loss of habitat area of the species group was projected to be more severe compared to the project under the RCP4.5 scenario, at around 64.18% and 71.44% of present distribution loss in 2050 and 2070, respectively. Based on the model results, we recommend that the suitable areas in Ninh Binh, Thanh

Hoa, and Nghe An provinces should receive high priority for extensive surveys to discover new populations as well as conservation actions to protect the species group from the effects of climate change.

ACKNOWLEDGEMENTS

We thank Ngoan V. Ha, Oanh V. Lo, Johnny Souwideth, Quang H. Nguyen, Tung T. Tran, Phanh A. Trang for their assistance in the field. Many thanks to Kin Onn Chan and one anonymous reviewer for improving previous versions of the manuscript. This research is funded by the National Foundation for Science and Technology Development (NAFOSTED, Grant No. 106-NN.06-2021.28), Rufford Foundation (Grant No. 31850-1), and Idea Wild. Research of Thuong Huyen Nguyen in Vietnam National University of Forestry is supported by Vingroup Innovation Foundation.

LITERATURE CITED

- Aiello-Lammens ME, Boria RA, Radosavljevic A, Vilela B, & Anderson RP (2015) spThin: An R package for spatial thinning of species occurrence records for use in ecological niche models. Ecography, 38: 541–545.
- Anderson RP, Araújo MB, Guisan A, Lobo JM, Martínez-Meyer E, Peterson AT, & Soberón J (2016) Are species occurrence data in global online repositories fit for modeling species distributions? The case of the Global Biodiversity Information Facility (GBIF). Final Report of the Task Group on GBIF Data Fitness for Use in Distribution Modelling. GBIF Secretariat, Global Biodiversity Information Facility (GBIF), 27 pp.
- Anderson RP, Lew D, & Peterson AT (2003) Evaluating predictive models of species' distributions: criteria for selecting optimal models. Ecological Modelling, 162: 211–232.
- Araújo MB, Thuiller W & Pearson RG (2006) Climate warming and the decline of amphibians and reptiles in Europe. Journal of Biogeography, 33: 1712–1728.
- Ashrafzadeh MR, Naghipour AA, Haidarian M, Kusza S & Pilliod DS (2019) Effects of climate change on habitat and connectivity for populations of a vulnerable, endemic salamander in Iran. Global Ecology and Conservation, 19: e00637.
- Barve N, Barve V, Jiménez-Valverde A, Lira-Noriega A, Maher SP, Peterson AT, Soberón J & Villalobos F (2011) The crucial role of the accessible area in ecological niche modeling and species distribution modeling. Ecological Modelling, 222: 1810–1819.
- Bellard C, Leclerc C, Leroy B, Bakkenes M, Veloz S, Thuiller W & Courchamp F (2014). Vulnerability of biodiversity hotspots to global change. Global Ecology and Biogeography, 23: 1376–1386.
- Bezeng BS, Tesfamichael SG & Dayananda B (2018) Predicting the effect of climate change on a range-restricted lizard in southeastern Australia. Current Zoology, 64: 165–171.
- Bickford D, Howard SD, Ng DJJ & Sheridan JA (2010) Impacts of climate change on the amphibians and reptiles of Southeast Asia. Biodiversity and Conservation, 19: 1043–1062.
- Blair ME, Nguyen TA, Le MD, Liu Z, Meng T, Horning N, Sterling EJ, Thach HM, Xu M & Galante PJ (2022) Karst as an abiotic driver of François' langur distribution, with predictions for biological communities on karst under climate change. Frontiers of Biogeography, 14: e51838.
- Borzée A, Andersen D, Groffen J, Kim H, Bae Y & Jang Y (2019) Climate change-based models predict range shifts in

the distribution of the only Asian plethodontid salamander: *Karsenia koreana*. Scientific Reports, 9: 1–9.

- Brennan IG, Bauer AM, Van TN, Wang Y, Wang W, Zhang YP & Murphy RW (2017) Barcoding utility in a mega-diverse, cross-continental genus: keeping pace with *Cyrtodactylus* geckos. Scientific Reports, 7: 1–11.
- Chan KO & Brown RM (2020) Elucidating the drivers of genetic differentiation in Malaysian torrent frogs (Anura: Ranidae: *Amolops*): a landscape genomics approach. Zoological Journal of the Linnean Society, 190: 65–78.
- Chan KO, Sind LI, Thong LI, Ananthanarayanan S, Rasu S, Aowphol A, Rujirawan A, Anuar S, Mulcahy D, Grismer JL & Grismer LL (2022) Phylogeography of mangrove pit vipers (Viperidae, *Trimeresurus erythrurus-purpureomaculatus* complex). Zoologica Scripta, 51: 664–675.
- Chen Z, Auler AS, Bakalowicz M, Drew D, Griger F, Hartmann J, Jiang G, Moosdorf N, Richts A, Stevanovic Z, Veni G & Goldscheider N (2017) The World Karst Aquifer Mapping project: Concept, mapping procedure and map of Europe. Hydrogeology Journal, 25(3): 771–785.
- Clements R, Sodhi NS, Schilthuizen M & Ng PKL (2006) Limestone karsts of Southeast Asia: imperiled arks of biodiversity. BioScience, 56: 733–742.
- Collart F, Hedenäs L, Broennimann O, Guisan A & Vanderpoorten A (2021) Intraspecific differentiation: Implications for niche and distribution modelling. Journal of Biogeography, 48: 415–426.
- Danielson JJ & Gesch DB (2011) Global multi-resolution terrain elevation data 2010 (GMTED2010). A Report Submitted to the U.S. Geological Survey, Virginia, USA, 23 pp.
- ESRI (2013) ArcGIS Desktop: Release 10.2. Environmental Systems Research Institute, Redlands.
- Fick SE & Hijmans RJ (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology, 37: 4302–4315.
- Gray JE (1827) XI. A synopsis of the genera of Saurian reptiles, in which some new genera are indicated, and the others reviewed by actual examination. The Philosophical Magazine, 2(7): 54–58.
- Grismer LL, Poyarkov NA, Quah ESH, Grismer JL & Wood Jr PL (2022) The biogeography of bent-toed geckos, *Cyrtodactylus* (Squamata: Gekkonidae). PeerJ, 10: e13153.
- Grismer LL, Wood Jr PL, Poyarkov NA, Le MD, Kraus F, Agarwal I, Oliver PM, Nguyen SN, Nguyen TQ, Karunarathna S, Welton LJ, Stuart BL, Luu VQ, Bauer AM, O'Connell KA, Quah ESH, Chan KO, Ziegler T, Ngo H, Nazarov RA, Aowphol A, Chomdej S, Suwannapoom C, Siler CD, Anuar S, Tri NV & Grismer JL (2021a) Phylogenetic partitioning of the third-largest vertebrate genus in the world, *Cyrtodactylus* Gray, 1827 (Reptilia; Squamata; Gekkonidae) and its relevance to taxonomy and conservation. Vertebrate Zoology, 71: 101–154.
- Grismer LL, Wood Jr PL, Quah ESH, Anuar S, Ngadi E & Norhayati A (2015) A new insular species of rock gecko (*Cnemaspis boulenger*) from Pulau Langkawi, Kedah, Peninsular Malaysia. Zootaxa, 3985: 203–218.
- Grismer LL, Wood PL, Aowphol A, Cota M, Murdoch ML, Aguilar C & Grismer MS (2016) Taxonomy, phylogeny, and distribution of *Bronchocela rayaensis* (Squamata: Agamidae) on the Thai-Malay Peninsula. Zootaxa, 4092: 414–420.
- Grismer L, Wood PL, Poyarkov NA, Le, MD, Karunarathna S, Chomdej S, Suwannapoom CQiS, Liu S & Che J (2021b) Karstic landscapes are foci of species diversity in the world's thirdlargest vertebrate genus *Cyrtodactylus* Gray, 1827 (Reptilia: Squamata; Gekkonidae). Diversity, 13: 1–15.
- Guisan A & Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. Ecology Letters, 8: 993–1009.
- Hansen MC, Potapov PV, Pickens AH, Tyukavina A, Hernandez-Serna A, Zalles V, Turubanova S, Kommareddy I, Stehman

SV, & Song XP (2022) Global land use extent and dispersion within natural land cover using Landsat data. Environmental Research Letters, 17(3): 034050.

- Hoang XQ, Orlov NL, Ananjeva NB, Johns AG, Hoang NT & Dau QV (2007) Description of a new species of the genus *Cyrtodactylus* Gray, 1827 (Squamata: Sauria: Gekkonidae) from the karst of north central Vietnam. Russian Journal of Herpetology, 14: 98–106.
- Hughes AC (2017) Understanding the drivers of Southeast Asian biodiversity loss. Ecosphere, 8(1): e01624.
- IUCN (2022) The IUCN Red List of Threatened Species. Version 2021-3. https://www.iucnredlist.org (Accessed 6 June 2022).
- Kass JM, Muscarella R, Galante PJ, Bohl CL, Pinilla Buitrago GE, Boria RA, Soley Guardia M & Anderson RP (2021) ENMeval 2.0: redesigned for customizable and reproducible modeling of species' niches and distributions. Methods in Ecology and Evolution, 12: 1602–1608.
- Kim DI, Park IK, Bae SY, Fong JJ, Zhang YP, Li SR, Ota H, Kim JS & Park D (2020) Prediction of present and future distribution of the Schlegel's Japanese gecko (*Gekko japonicus*) using MaxEnt modeling. Journal of Ecology and Environment, 44: 1–8.
- Le DT, Nguyen TQ, Le MD & Ziegler T (2016) A new species of *Cyrtodactylus* (Squamata: Gekkonidae) from Ninh Binh Province, Vietnam. Zootaxa, 4162: 268–282.
- Lobo JM, Jiménez Valverde A & Real R (2008) AUC: a misleading measure of the performance of predictive distribution models. Global Ecology and Biogeography, 17: 145–151.
- Luu QV & Lo VO (2018) A new record of *Cyrtodactylus soni* Le, Nguyen, Le & Ziegler, 2016 (Reptilia: Squamata: Gekkonidae) from Hoa Binh province and threat assessment. Academia Journal of Biology, 40: 90–95.
- Luu VQ, Nguyen TQ, Do HQ & Ziegler T (2011) A new *Cyrtodactylus* (Squamata: Gekkonidae) from Huong Son limestone forest, Hanoi, northern Vietnam. Zootaxa, 3129: 39–50.
- Maguire KC, Shinneman DJ, Potter KM & Hipkins VD (2018) Intraspecific niche models for ponderosa pine (*Pinus ponderosa*) suggest potential variability in population-level response to climate change. Systematic Biology, 67: 965–978.
- McSweeney CF, Jones RG, Lee RW & Rowell DP (2015) Selecting CMIP5 GCMs for downscaling over multiple regions. Climate Dynamics, 44: 3237–3260.
- Milanovich JR, Peterman WE, Nibbelink NP & Maerz JC (2010) Projected loss of a salamander diversity hotspot as a consequence of projected global climate change. PLoS ONE, 5: e12189.
- Mota-Vargas C & Rojas-Soto OR (2016) Taxonomy and ecological niche modeling: Implications for the conservation of wood partridges (genus *Dendrortyx*). Journal for Nature Conservation, 29: 1–13.
- Muscarella R, Galante PJ, Soley Guardia M, Boria RA, Kass JM, Uriarte M & Anderson RP (2014) ENM eval: An R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. Methods in Ecology and Evolution, 5: 1198–1205.
- Ngo HN, Le TQ, Pham ML, Nguyen TQ, Le MD, van Schingen M & Ziegler T (2019) First record of the Cat Ba Tiger Gecko, *Goniurosaurus catbaensis*, from Ha Long Bay, Quang Ninh Province, Vietnam: Microhabitat selection, potential distribution, and evidence of threats. Amphibian and Reptile Conservation, 13: 1–13.
- Ngo HN, Nguyen HQ, Phan TQ, Nguyen TQ, Gewiss LR, Rödder D & Ziegler T (2022) Modeling the environmental refugia of the endangered Lichtenfelder's Tiger Gecko (*Goniurosaurus lichtenfelderi*) towards implementation of transboundary conservation. Frontiers of Biogeography, 14: e51167.

- Ngo VT & Chan KO (2011) A new karstic cave-dwelling *Cyrtodactylus* Gray (Squamata: Gekkonidae) from northern Vietnam. Zootaxa, 3125: 51–63.
- Ngo TV & Grismer LL (2010) A new karst dwelling *Cyrtodactylus* (Squamata: Gekkonidae) from Son La Province, northwestern Vietnam. Hamadryad, 35: 84–95.
- Nguyen SN, Yang JX, Le TNT, Nguyen LT, Orlov NL, Hoang CV, Nguyen TQ, Jin JQ, Rao DQ & Hoang TN (2014) DNA barcoding of Vietnamese bent-toed geckos (Squamata: Gekkonidae: *Cyrtodactylus*) and the description of a new species. Zootaxa, 3784: 48–66.
- Nguyen TQ, Le MD, Pham AV, Ngo HN, Hoang CV, Pham CT & Ziegler T (2015) Two new species of *Cyrtodactylus* (Squamata: Gekkonidae) from the karst forest of Hoa Binh Province, Vietnam. Zootaxa, 3985: 375–390.
- Nguyen TQ, Pham AV, Ziegler T, Ngo HT & Le MD (2017) A new species of *Cyrtodactylus* (Squamata: Gekkonidae) and the first record of *C. otai* from Son La Province, Vietnam. Zootaxa, 4341: 25–40.
- Pacifici M, Foden WB, Visconti P, Watson JEM, Butchart SHM, Kovacs KM, Scheffers BR, Hole DG, Martin TG & Akçakaya HR (2015) Assessing species vulnerability to climate change. Nature Climate Change, 5: 215–224.
- Papes M (2007) Ecological niche modeling approaches to conservation of endangered and threatened birds in Central and Eastern Europe. Biodiversity Informatics, 4: 14–26.
- Paterson JS, Araújo MB, Berry PM, Piper JM & Rounsevell MDA (2008) Mitigation, adaptation, and the threat to biodiversity. Conservation Biology, 22: 1352–1355.
- Pearson RG, Raxworthy CJ, Nakamura M & Peterson AT (2007) Predicting species distributions from small numbers of occurrence records: A test case using cryptic geckos in Madagascar. Journal of Biogeography, 34: 102–117.
- Peñalver-Alcázar M, Jiménez-Valverde A & Aragón P (2021) Niche differentiation between deeply divergent phylogenetic lineages of an endemic newt: implications for Species Distribution Models. Zoology, 144: 125852.
- Peterson AT, Asase A, Canhos DAL, de Souza S & Wieczorek J (2018) Data leakage and loss in biodiversity informatics. Biodiversity Data Journal, 6: e26826.
- Pham AV, Le MD, Ziegler T & Nguyen TQ (2019) A new species of *Cyrtodactylus* (Squamata: Gekkonidae) from northwestern Vietnam. Zootaxa, 4544: 360–380.
- Phillips SJ, Anderson RP & Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecological Modelling, 190: 231–259.
- Raxworthy CJ, Ingram CM, Rabibisoa N & Pearson RG (2007) Applications of ecological niche modeling for species delimitation: A review and empirical evaluation using day geckos (*Phelsuma*) from Madagascar. Systematic Biology, 56: 907–923.
- Rissler LJ & Apodaca JJ (2007) Adding more ecology into species delimitation: Ecological niche models and phylogeography help define cryptic species in the black salamander (*Aneides flavipunctatus*). Systematic Biology, 56: 924–942.
- Schneider N, Luu VQ, Sitthivong S, Teynie A, Nguyen TQ & Ziegler T (2020) Two new species of *Cyrtodactylus* (Squamata: Gekkonidae) from northern Laos, including new finding and expanded diagnosis of *C. bansocensis*. Zootaxa, 4822: 503–530.
- Smith AB, Godsoe W, Rodríguez-Sánchez F, Wang HH & Warren D (2019) Niche estimation above and below the species level. Trends in Ecology and Evolution, 34: 260–273.
- Suggitt AJ, Wilson RJ, Isaac NJB, Beale CM, Auffret AG, August T, Bennie JJ, Crick HQP, Duffield S, Fox R, Hopkins JJ, Macgregor NA, Morecroft MD, Walker KJ & Maclean IMD

(2018) Extinction risk from climate change is reduced by microclimatic buffering. Nature Climate Change, 8: 713–717.

- Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFN, De Siqueira MF, Grainger A & Hannah L (2004) Extinction risk from climate change. Nature, 427: 145–148.
- Thorn JS, Nijman V, Smith D & Nekaris KAI (2009) Ecological niche modelling as a technique for assessing threats and setting conservation priorities for Asian slow lorises (Primates: *Nycticebus*). Diversity and Distributions, 15: 289–298.
- Thuiller W, Lavorel S & Araújo MB (2005) Niche properties and geographical extent as predictors of species sensitivity to climate change. Global Ecology and Biogeography, 14: 347–357.
- Tran DV, Vu TT, Tran BQ, Nguyen MD, Vu PT, Tran TH, Nguyen HT, Pham TV & Nguyen TC (2020) Modelling the change in the distribution of the black-shanked douc, *Pygathrix nigripes* (Milne-Edwards) in the context of climate change: Implications for conservation. Raffles Bulletin of Zoology, 68: 769–778.
- Tran DV, Terui S, Nomoto K & Nishikawa K (2021) Ecological niche differentiation of two salamanders (Caudata: Hynobiidae) from Hokkaido Island, Japan. Ecological Research, 36: 281–292.
- Trew BT & Maclean IMD (2021). Vulnerability of global biodiversity hotspots to climate change. Global Ecology and Biogeography, 30: 768–783.
- Trinh DH, Nguyen AT, Le MD, Li X, Cao NTH & Blair ME (2021) Assessment of climate change impacts on one of the rarest apes on Earth, the Cao Vit Gibbon *Nomascus nasutus*. Frontiers of Biogeography, 14: e53320.
- Uetz P, Freed P, Aguilar R & Hošek J (2022) The Reptile Database. http://www.reptile-database.org. (Accessed on 6 June 2022).
- UNEP-WCMC & IUCN (2022) Protected Planet: The World Database on Protected Areas (WDPA), Cambridge, UK: UNEP-WCMC and IUCN. www.protectedplanet.net. (Accessed 8 June 2022).
- van Riemsdijk I, Arntzen JW, Bogaerts S, Franzen M, Litvinchuk SN, Olgun K & Wielstra B (2017) The Near East as a cradle of biodiversity: A phylogeography of banded newts (genus *Ommatotriton*) reveals extensive inter- and intraspecific genetic differentiation. Molecular Phylogenetics and Evolution, 114: 73–81.

- van Schingen M, Ihlow F, Nguyen TQ, Ziegler T, Bonkowski M, Wu Z & Rödder D (2014) Potential distribution and effectiveness of the protected area network for the crocodile lizard, *Shinisaurus crocodilurus* (Reptilia: Squamata: Sauria). Salamandra, 50: 71–76.
- van Schingen M, Le MD, Ngo HT, Pham CT, Ha QQ, Nguyen TQ & Ziegler T (2016) Is there more than one Crocodile Lizard? An integrative taxonomic approach reveals Vietnamese and Chinese *Shinisaurus crocodilurus* represent separate conservation and taxonomic units. Der Zoologische Garten, 85: 240–260.
- VanDerWal J, Shoo LP, Graham C & Williams SE (2009) Selecting pseudo-absence data for presence-only distribution modeling: How far should you stray from what you know? Ecological Modelling, 220: 589–594.
- Vásquez-Aguilar AA, Ornelas JF, Rodríguez-Gómez F & Cristina MGM (2021) Modeling future potential distribution of Buffbellied Hummingbird (*Amazilia yucatanensis*) under climate change: Species vs. subspecies. Tropical Conservation Science, 14: 19400829211030830.
- Vu TT, Tran DV, Tran HTP, Nguyen MD, Do TA, Ta NT, Cao HT, Pham NT & Phan DV (2020) An assessment of the impact of climate change on the distribution of the grey-shanked douc *Pygathrix cinerea* using an ecological niche model. Primates, 61: 267–275.
- Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin JM, Hoegh-Guldberg O & Bairlein F (2002). Ecological responses to recent climate change. Nature, 416: 389–395.
- Warren DL, Glor RE & Turelli M (2010) ENMTools: A toolbox for comparative studies of environmental niche models. Ecography, 33: 607–611.
- Yang L, Shi KC, Ma C, Ren GP & Fan PF (2021) Mechanisms underlying altitudinal and horizontal range contraction: The western black crested gibbon. Journal of Biogeography, 48: 321–331.
- Zhang Y, Chen C, Li L, Zhao C, Chen W & Huang Y (2014) Insights from ecological niche modeling on the taxonomic distinction and niche differentiation between the blackspotted and red-spotted tokay geckoes (*Gekko gecko*). Ecology and Evolution, 4: 3383–3394.

APPENDIX



