SALAMANDRA **57**(4): 464–474
30 October 2021 | ISSN 0036–3375

SALAMANDRA
German Journal of Herpetology

Vulnerability of an endemic Tiger Gecko (*Goniurosaurus huuliensis*) to climate change: modeling environmental refugia and implications for in-situ conservation

Hai Ngoc Ngo[1,4,5], Huy Quoc Nguyen[1,3], Tien Quang Phan[2], Hieu Minh Tran[2], Truong Quang Nguyen[2,3], Thomas Ziegler[4,5] & Dennis Rödder[6]

[1)] Vietnam National Museum of Nature, Vietnam Academy of Science and Technology, 18 Hoang Quoc Viet Road, Hanoi, Vietnam

[2)] Institute of Ecology and Biological Resources, Vietnam Academy of Science and Technology, 18 Hoang Quoc Viet Road, Hanoi, Vietnam

[3)] Graduate University of Science and Technology, Vietnam Academy of Science and Technology, 18 Hoang Quoc Viet Road, Hanoi, Vietnam

[4)] Institute of Zoology, University of Cologne, Zülpicher Str. 47b, 50674 Cologne, Germany

[5)] Cologne Zoo, Riehler Str. 173, 50735, Cologne, Germany

[6)] Herpetology Section, Zoologisches Forschungsmuseum Alexander Koenig (ZFMK), Adenauerallee 160, 53113, Bonn, Germany

Corresponding author: Hai Ngoc Ngo, e-mail: ngohai2709@gmail.com

Manuscript received: 6 April 2021
Accepted: 23 August 2021 by Alexander Kupfer

Abstract. Detailed information on potentially suitable habitats and forecasted alterations thereof under climate change scenarios are critical for the conservation planning of endangered taxa, in particular those with small distribution ranges. The Huu Lien Tiger Gecko, *Goniurosaurus huuliensis*, is a is a micro-endemic species in northern Vietnam. The species is listed in the IUCN Red List as Critically Endangered and in CITES Appendix II due to habitat loss and overexploitation for the international pet trade. Climate change has been globally acknowledged to impact on many species and it likely has negative influences on *G. huuliensis*. In this study, an ensemble modeling technique is employed, trained with climate and vegetation cover conditions, to identify the contemporary potential distribution of this species and assess its alterations under different climate change scenarios. Our predictions suggest that the current potential distribution of *G. huuliensis* mostly covers the known sites of occurrence and their surroundings. These areas will narrow significantly and/or shift towards higher latitudes under novel climate conditions as can be expected according to future IPCC scenarios. To safeguard in-situ populations of *G. huuliensis* in the context of the potentially severe impacts, we provide a core refugia map that identifies key regions for priority conservation measures, including Lang Son Province and small sites in Bac Giang and Thai Nguyen Provinces, northern Vietnam. We highly recommend that the Huu Lien Nature Reserve be selected as a "centre" to kick-off conservation actions for the target species.

Key words. Squamata, Eublepharidae, climate, core refugia, Ensembles of Small Models (ESMs), Huu Lien Nature Reserve, potential distribution, vegetation.

Introduction

The Huu Lien Tiger Gecko, *Goniurosaurus huuliensis* Orlov, Ryabov, Nguyen, Nguyen & Ho, 2008, which is one of five known *Goniurosaurus* species in Vietnam, has only been recorded from the type locality in the Huu Lien Nature Reserve (NR), Lang Son Province (Orlov et al. 2008, Nguyen et al. 2009, Nguyen 2011). This endemic species is found in the evergreen forest on isolated karst formations at altitudes from 300 to 370 m a.s.l. (Orlov et al. 2008). Although discovered recently, *G. huuliensis* was assessed as Critically Endangered (CR) in the IUCN Red List of Threatened Species (Nguyen 2018), and this species was included in CITES (the Convention on International Trade in Endangered Species of Wild Fauna and Flora) Appendix II and the Vietnam Government's Decree No. 06/2019/ND-CP (Group IIB) in 2019 (Ngo et al. 2019b).

Recent investigations provided convincing evidence for the endangered status of *G. huuliensis*. In particular, this habitat specialist has, to date, only been recorded from a very small karstic range within the Huu Lien Nature Reserve, with the estimated extent of occurrence (EOO) being 30 km^2 (Orlov et al. 2008, Nguyen et al. 2009, Nguyen 2018). Similar to other Tiger Geckos, the effective population status of *G. huuliensis* is expected to be extremely small (Ngo et al. 2016, 2019a, b). Furthermore, wild Tiger

© 2021 Deutsche Gesellschaft für Herpetologie und Terrarienkunde e.V. (DGHT), Germany
Open access at https://www.salamandra-journal.com

Geckos, including *G. huuliensis*, have been locally overharvested for the international pet trade (Ngo et al. 2019a, b). These severe impacts may be driving this species to the brink of extinction.

Climate change is a global threat to biodiversity and ecosystems, which drives large-scale shifts in species distribution, and may lead to a decline of species abundance, and even extirpation or extinction of many terrestrial organisms (Huggett 2004, Thomas et al. 2004, Parmesan 2006, Huey et al. 2009, Monastersky 2014, Pimm et al. 2014, Urban 2015, Taylor & Kumar 2016, Markle & Kozak 2018, Weiskopf et al. 2020). Besides direct anthropogenic impacts, climate change may also affect *G. huuliensis* in a negative manner. On the one hand, as a poikilothermic lizard, basic physiological functions, such as locomotion, growth and reproduction are determined mainly by environmental conditions (Araújo et al. 2006, Fitzgerald et al. 2018, Ngo et al. 2019a, Vicente et al. 2019). On the other hand, a species within a small distribution range and a habitat specialist being dependent on specific ecological niches will be less capable of responding to novel environmental conditions as a result of climate change (Huggett 2004, Orlov et al. 2008, Sandel et al. 2011, Pimm et al. 2014, Markle & Kozak 2018). Thus, this target species is considered to be particularly susceptible to climate change.

To date, no in-situ conservation action has yet been implemented to protect wild populations of *G. huuliensis*. General conservation plans have already been proposed for all Tiger Geckos (Ngo et al. 2019b). However, in-situ conservation measures have been only conducted to safeguard another threatened congener, *Goniurosaurus catbaensis*, from northern Vietnam, after Ngo et al. (2016, 2019a) provided detailed insights into its population status and utilized microhabitat, and Le et al. (2017) used a Maxent approach to predict its potential distribution for conservation.

A considerable gap between designing general conservation plans and practical application of conservation measures can limit the efficiency level of conservation efforts (Dudley & Parish 2006). In fact, conservationists normally encounter an obstacle for priority conservation efforts when trying to identify where potentially suitable habitats and core refugia are (Baumgartner et al. 2018), even though all populations should be protected in the same manner. Recently, the development of species distribution models (SDMs), based on species' geographic coordinates and their environmental data, have been able to predict the potential distributions of species (Guisan & Zimmermann 2000, Guisan & Thuiller 2005). Several techniques to compute SDMs have been recently applied for some rare lizards in Vietnam (van Schingen et al. 2016, Le et al. 2017, Ngo et al. 2019a, Ngo et al. 2021). However, the modelling of endangered or rare species has its limitations when only a few recorded occurrences are combined with many predictor variables, which may lead to the model overfitting (Breiner et al. 2015). Recently, the ensembles of small models (ESMs) approach, a novel strategy of fitting SDMs, has been employed to overcome the limitations of using a single SDM technique and improve the qualitative outcome of predictions where only a small number of presence coordinates is available (Breiner et al. 2015, Cola et al. 2017).

The present study aims to predict the potential distribution of *G. huuliensis* based on geographic locations and environmental variables (including climate and vegetation data) under both current conditions and different future scenarios. The ESMs technique is employed to compute the models and to project the ensemble through space and time. We hypothesize that the currently suitable area of *G. huuliensis* will shrink significantly under the impacts of climate change. We also intend to identify potential core refugia of *G. huuliensis*, based on the simulated outcomes, to improve the efficacy of in-situ conservation measures.

Materials and methods

Study area

The study area (within 20–24°N and 104–109°E) with altitudes ranging from 1 to 2,139 m a.s.l. (Fig. 1) was selected as the background area, encompassing all known distribution ranges of the five *Goniurosaurus* species occurring in northern Vietnam (Grismer et al. 1999, Vu et al. 2006, Orlov et al. 2008, Ziegler et al. 2008, Nguyen et al. 2009, Nguyen 2011). *Goniurosaurus huuliensis* is known only from the karst forest at its type locality in the Huu Lien NR, Lang Son Province, northern Vietnam (Orlov et al. 2008). Further populations of *G. huuliensis* are expected to be found in surrounding areas, including all districts of Lang Son Province and adjoining provinces (e.g., Bac Giang, Cao Bang, Quang Ninh and Bac Giang Provinces), where we directly observed karst habitats resembling those known from the type locality.

Data collection

Occurrence data of *G. huuliensis* were compiled from literature, direct observations, and interviews with local people (Orlov et al. 2008). We conducted field surveys in the Huu Lien NR in April and August 2019, and from June to July 2020. An extensive initiative interviewing local people was carried out in July 2020 in all districts of Lang Son and surrounding provinces (Bac Giang, Cao Bang, Quang Ninh, Thai Nguyen) in order to possibly detect as yet unrecorded populations of *G. huuliensis.*

Coordinates of each captured individual were recorded with a GPS Garmin 64, but will be shared upon request. A total of 80 occurrence records in the WGS84 projection of *G. huuliensis* were initially collected. However, several records were removed to reduce the density of recorded locations by using spatial filtering in the packages "dismo" and "sp" in R v 3.1.2 (R Core Team 2018) due to duplicates or near-duplicates for some localities. Only one occurrence locality was randomly selected within each 1-km square. Spatial filtering can improve the quality of prediction models by decreasing geographical bias, autocorrelation effects, and uncertainty (Veloz 2009, Radosavljevic & Anderson 2014). A total of 27 representative occurrence points were finally used for modelling.

For environmental data, we selected bioclimatic and vegetation cover variables. Nineteen climatic variables for current (averages between 1960–1990, version 1.4) and future conditions from the Coupled Model Intercomparison Project Phase 5 (CMIP5) were obtained from Worldclim (https://www.worldclim.org/) (Hijmans et al. 2005). To predict the future potential distribution of the target species, we selected future climatic data from two general circulation models (GCM), including Community Climate System Model version 4 (CCSM4) (Gent et al. 2011) and Beijing Climate Center – Climate System Model 1-1 (BCC-CSM 1-1) (Wu et al. 2014) as expected for the 2050s (average 2041–2060) and the 2070s (average 2061–2080). 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, were used for each model, respectively (Moss et al. 2010, van Vuuren et al. 2011). For vegetation cover data, we extracted the Normalized Difference Vegetation Index (NDVI) and Enhanced Vegetation Index (EVI) from within the study area using Moderate Resolution Imaging Spectroradiometer (MODIS) sensor data from five years, 2015 to 2019 (https://earthexplorer.usgs.gov/). The mean, maximum, minimum, median, range, standard deviations (STD), and mean, maximum, minimum of warmest and coldest quarters for the enhanced vegetation index (EVI) and normalized difference vegetation index (NDVI) were generated using Quantum GIS (QGIS Version 3.12.0, Development Team. 2020, available at http://qgis.osgeo.org [downloaded on 25 March 2020]).

Eleven variables were eventually kept for the prediction approaches based on the selection previously made by Ngo et al. (2021) for another tiger gecko, *G. lichtenfelderi*. Particularly, six climatic variables (i.e., Bio-2: Mean Diurnal Temperature Range, Bio-3: Isothermality, Bio-9: Mean Temperature of Driest Quarter, Bio-15: Precipitation Seasonality, Bio-18: Precipitation of Warmest Quarter, Bio-19: Precipitation of Coldest Quarter) were used to train the climatic model, while five remaining variables of vegetation cover (e.g., NDVI of Mean Coldest Quarter, NDVI of Minimum Coldest Quarter, NDVI of Minimum Warmest Quarter, NDVI of STD, and EVI of Range) were used for a separate model based on the vegetation structure. The climate and vegetation cover variables were used separately to model the potential distribution, in order to account for both broad-scale climatic factors delimiting the species' potential distribution and fine-scale habitat availability within this potential distribution. Future scenarios of potential vegetation structure are not available for limiting these variables. This procedure allowed us to disentangle the potential impact of climate change from those of land-use changes, which are largely unpredictable.

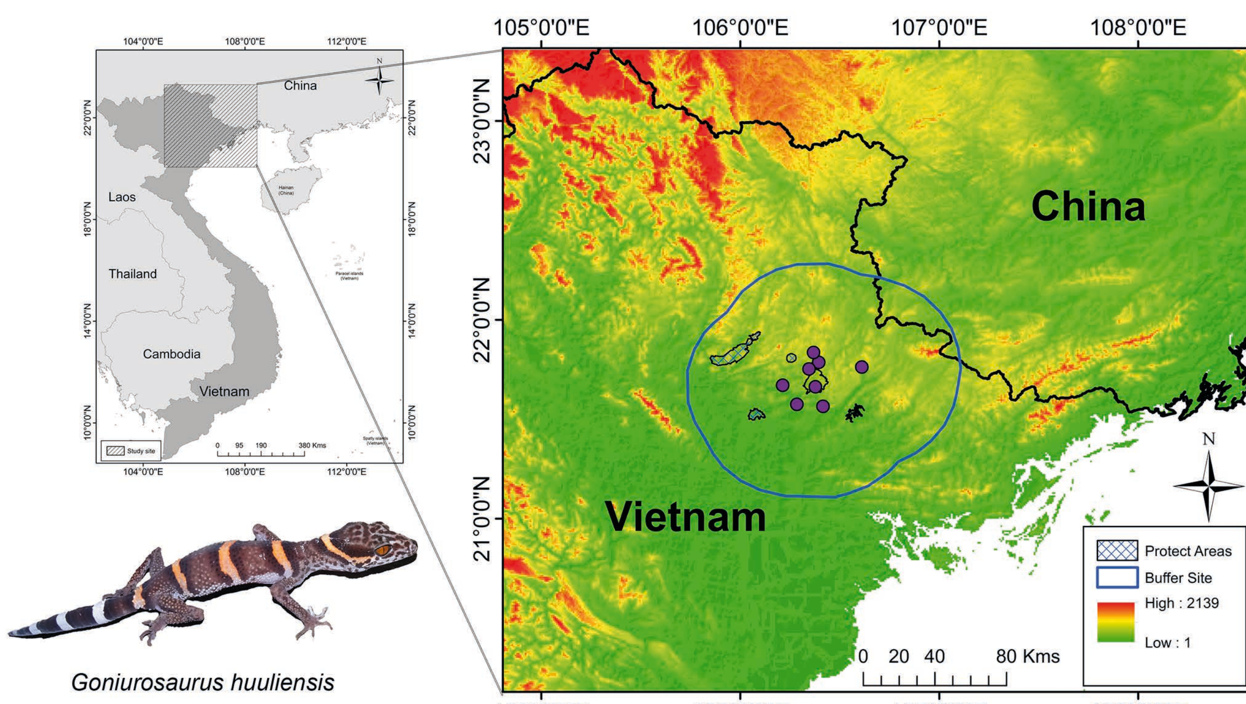


Figure 1. Map of study site in northern Vietnam and southern China, including the selected buffer representing a radius of 50 km around occurrence points (violet circles) of *Goniurosaurus huuliensis*.

Species distribution modelling

We fitted the ensembles of small models with six modelling techniques: artificial neural network (ANN), classification tree analysis (CTA), generalized linear models (GLM), generalized additive models (GAM), generalized boosting regression models (GBM), and maximum entropy modelling (Maxent). All models were calibrated with the R package "ecospat" ver. 3.1 (Breiner et al. 2015, Cola et al. 2017). To build an Ensemble of Small Models, we used subsets of the environmental predictors to create bivariate predictor combinations. In particular, six climate and five vegetation predictors resulted in 15 and 10 bivariate models (BiVa) in each of six selected modelling techniques, respectively (step-1, Supplementary Fig. S1). In step-2, we evaluated each of these bivariate models using a cross-validated model evaluation index as a Somers' D (Breiner et al. 2015). Bivariate models with a Somers' D lower than 0 (i.e., AUC < 0.5) were set to zero and not used to build ESMs. One ESM prediction was built for each modelling technique in step-3 (i.e., ANN-ESM based on bivariate ANN models, CTA-ESM on bivariate CTA models, etc.). In the final steps (Steps 4 and 5), we built a final ensemble prediction (EP-ESM) – the fitted ESM by averaging across these ESMs, again using Somers' D as a weighting factor (Supplementary Fig. S1) (Breiner et al. 2015).

All models were calibrated with presence-only data and 10,000 random background points selected within a buffer area. As the buffer we defined an area with a radius of 50 km around the occurrence points using the R packages "dismo" and "raster". The fitted ESM was also projected to areas beyond the selected buffer within the study area to show up alternative potential refugia in the context of future climate change. Fifteen-fold cross-validation, with subsets of 70% training data and 30% test data, was used to evaluate the models. We used three adjustment indices to evaluate model performance, including the AUC of the Receiver Operating Characteristic Curve to discriminate presence from absence (or background), which was then used to build a Somers' D ($D = 2 \times (AUC - 0.5)$) (Fielding & Bell 1997, Lobo et al. 2008, Elith & Graham 2009), TSS is particularly (TSS = sensitivity + specificity – 1) useful for the modelling of rare species and can be used to compare different modelling techniques (Allouche et al. 2006). In these indices, values closer to 1.0 indicate better model performance (Breiner et al. 2015).

To assess the predictive capabilities of our ensemble model projections, multivariate environmental similarity surface (MESS) analyses were used to quantify potential extrapolation errors (Elith et al. 2010). The respective MESS functions of the "ecospat" package were used (Cola et al. 2017). The MESS analysis compares the environmental similarity of any given grid cell within the study site to a reference set of grid cells of chosen predictor variables. It is used to identify extrapolation in areas with novel environmental conditions beyond the training range of the models, as is indicated by negative values (Elith et al. 2010, 2011). In this study, similarity/novelty was classified into four levels: "< -10" (high extrapolation), "-10–0" (low extrapolation – margin), "0–10" (low interpolation – margin) and "> 10" (high interpolation). We also performed MESS analyses to create maps for each future climate scenario and to evaluate the alteration of novel climatic conditions from the reference conditions under the current climate model.

Core refugia

The core refugia for *G. huuliensis* were identified within highly suitable areas in terms of climate, which have values above the 10% training presence threshold (high occurrence probability). This is a stricter criterion for converting the probability maps to binary maps with smaller suitable habitats. We also identified buffer refugia with the least-suitable environmental conditions with values above the minimum presence threshold (intermediate occurrence probability). They were all combined with suitable areas as identified in the model based on vegetation indices. To identify priority areas and assess the effectiveness of the protected areas for safeguarding the target species, we collected all shapefiles of nature reserves within the occurrence region of *G. huuliensis* from https://www.protectedplanet.net/ (accessed in June 2019) (Fig. 1). The identified environmental refugia for the target species were afterwards layered with the protected area.

Results

As a result of our extensive interviews, we documented the occurrence of *G. huuliensis* in four districts of Lang Son Province (including the Huu Lien NR) and another district in Thai Nguyen Province, northern Vietnam. According to local people, all animals were found in the evergreen forest on karst formations. They were observed moving or resting on rocky cliffs or hiding in crevices.

Regarding the model evaluation, Maxent.Phillips-ESM and ANN-ESM were the best models, showing the highest mean values of adjustment indices with low variation, while GLM-ESM exhibited the lowest value of these indices with high variation (Supplementary Figs S2–S3). Compared to these, the fitted ensemble models (EP-ESMs) of climate and vegetation improved the accuracy of prediction as indicated with higher average values of adjustment indices. In particular, TSS, AUC and Somers'D in the fitted EP-ESMs performed well with average values of 0.80, 0.92 and 0.83 in the climate model, respectively (Supplementary Fig. S2). These values were relatively lower in the vegetation model (0.71, 0.88 and 0.75, respectively) (Supplementary Fig. S3). All selected climate and vegetation variables significantly influenced the prediction and their contribution rates were approximately equal (Supplementary Tables S1–S2).

Under current climatic conditions, the potential distribution of *G. huuliensis* covers mainly the sites of occurrence and their surroundings within the buffer area. We recorded a few additional potential sites beyond the buffer area in Vinh Phuc Province, northern Vietnam, and in border areas between China and Vietnam (Cao Bang Province) (Fig. 2A). The suitable climate range covers a total area of 63,773 km², of which approximately 42.5% (27,124 km²) represent highly suitable habitat (Fig. 2B). However, within the buffer area, the suitable habitat only covers 9,577 km² (about 15% of the total suitable area). With regard to the vegetation model, suitable habitats of *G. huuliensis* are relatively scattered within the study site, but they are also gathered mainly around the occurrence sites. In particular, in the buffer area, the suitable area of vegetation covers 6,874 km² within the intermediate suitable site of climate, accounting for 71.8% (Figs 2A–2B–4). In terms of the MESS analysis, the buffer area is filled by a large area of interpolated habitat, covering 9,620 km² (approximately 65.0%) in the current climate model and 8,250 km² (approximately 56%) in the vegetation model, whereas we only recorded a very small area of extrapolation in both these models (Figs 2C–2D).

With respect to future predictions, in general, the climatically suitable area of each future scenario fluctuated depending on RCPs (e.g., 4.5 and 8.5) and periods (by the 2050s and 2070s). Under future climate scenarios, each predicted a significantly smaller area of the potential distribution compared to the contemporary one and implied a shift towards higher latitudes in the future (Figs 2–3–4). However, we recorded a novel case of the CCSM4 –

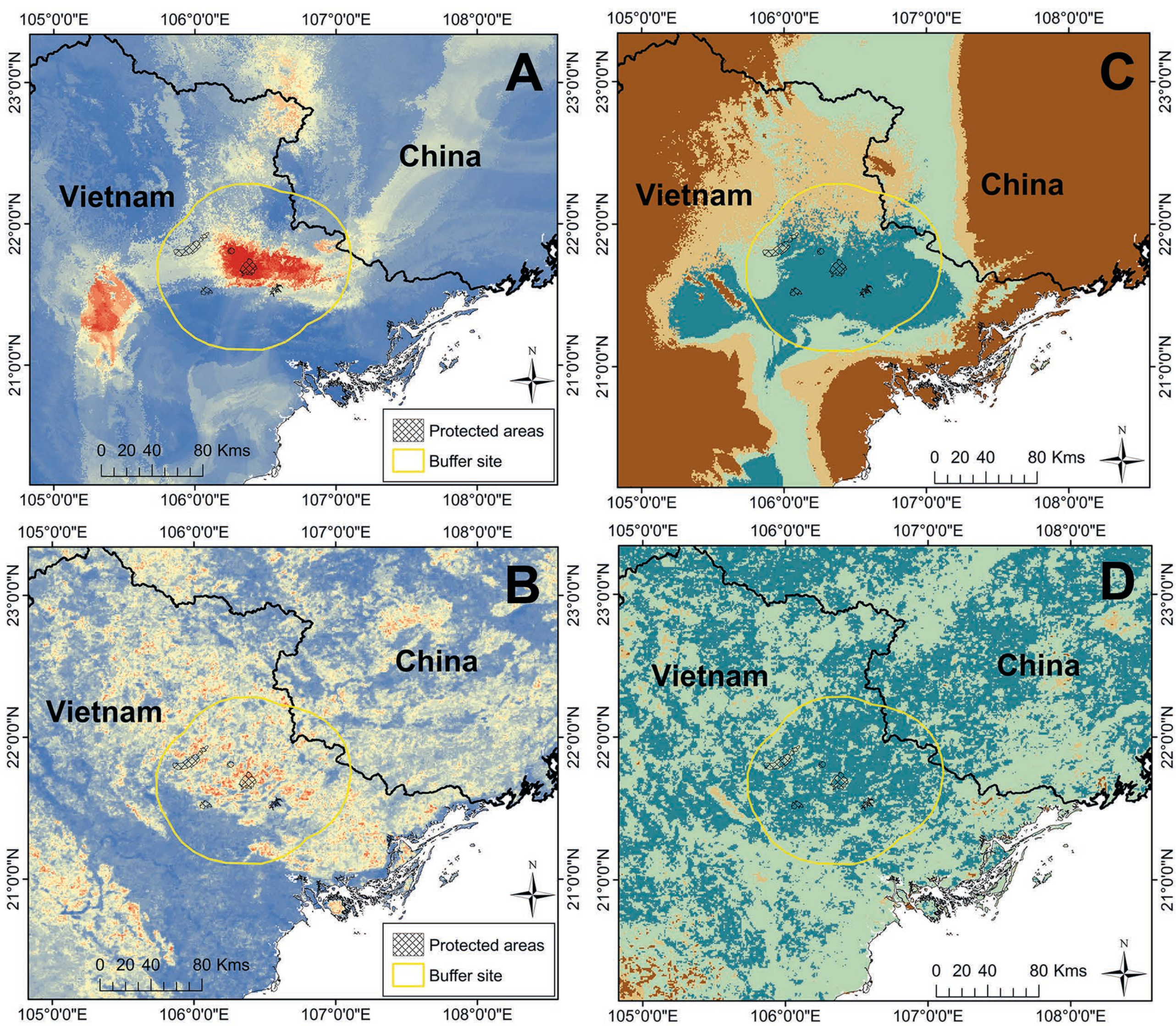


Figure 2. Projected potential distribution for *Goniurosaurus huuliensis* following (A) the climate model; (B) the vegetation model (blue to red colours indicate higher suitability). Multi-Environment Similarity Surface (MESS) map of novel habitat following (C) the climate model; (D) the vegetation model (teal colour represents high interpolation habitat, aqua colour – low interpolation, coral colour – low extrapolation, brown colour – high extrapolation).

RCP 4.5 scenario by the 2050s, covering 10,311 km² of the suitable area within the buffer. Afterwards, this suitable area contracted considerably under the same conditions by the 2070s (Fig. 4). The range contraction is expected to be largest under the RCP8.5 scenario by the 2070s. In particular, the CCSM4 circulation model suggests that the potential distribution may cover only 3,507 km² (representing 24% suitable area of the current model) (Figs 3D–4), while in the BCC-CSM 1-1 model, no highly suitable habitat for *G. huuliensis* was documented (0 km²) and the intermediate suitable habitat within the buffer was only 2,555 km² (Figs 3D–4). Given the MESS projections, interpolated habitats within the current climate-based potential distribution of *G. huuliensis* will be gradually replaced by high novelty (extrapolated) habitats in the future (Supplementary Figs S4–S5). It is noteworthy that novel climatic conditions were recorded in most of the entire buffer area under the RCP 8.5 scenarios by the 2070s (Supplementary Figs S4A4–S4B4).

Discussion

Prediction models

Comparing the adjustment indices of TSS, AUC and Somers' D, we confirmed that the ensemble SDM significantly

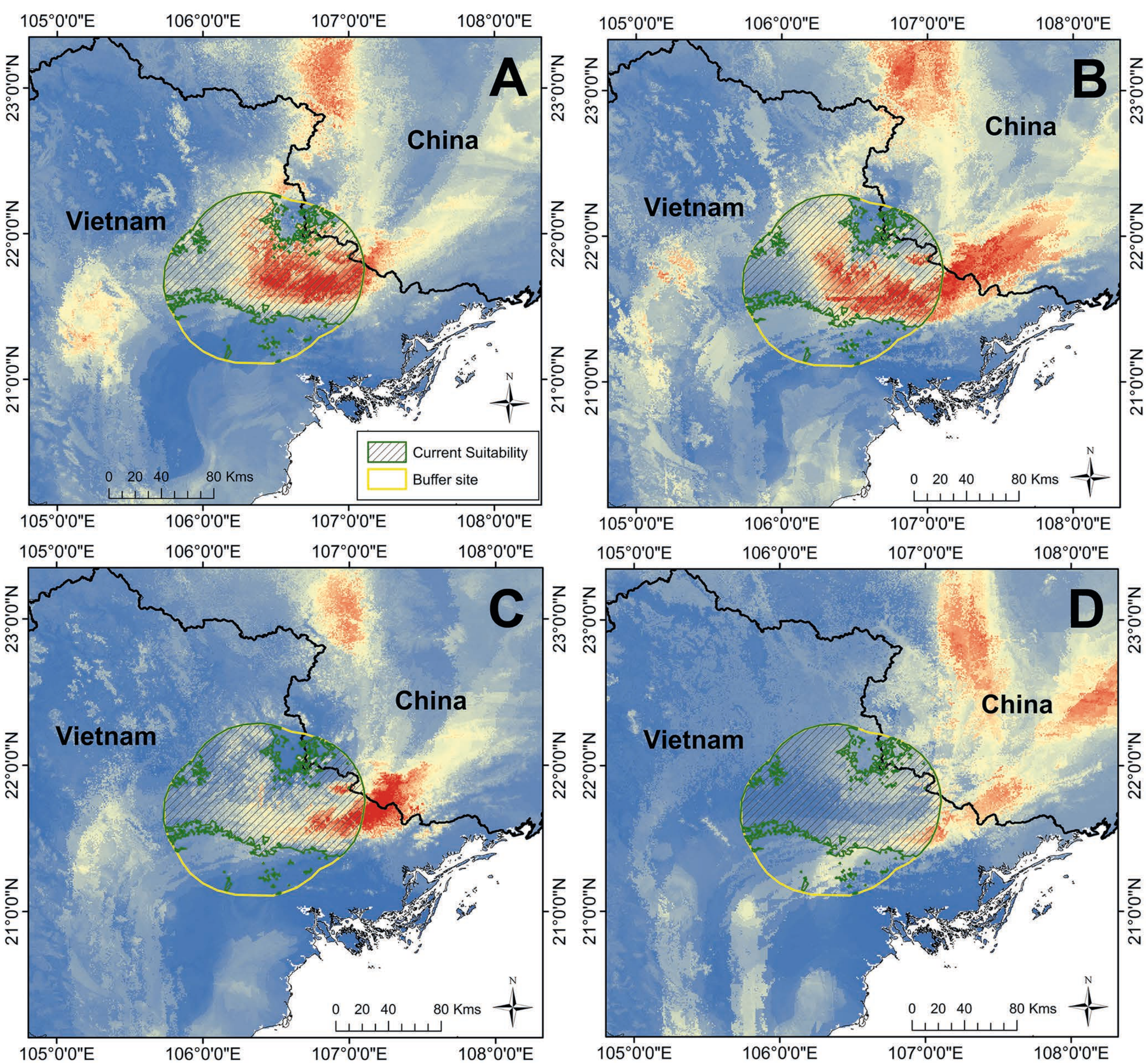


Figure 3. Projected potential distribution for *Goniurosaurus huuliensis* under different future climate scenarios (blue to red colours indicate higher suitability). The average map of two circulation models of BCC_CSM-1-1 and CCSM4 in the scenario of (A), RCP-4.5 by the 2050s; (B) RCP-4.5 by the 2070s; (C) RCP-8.5 by the 2050s; (D) RCP-8.5 by the 2070s.

improved the accuracy of model prediction for rare species. In particular, the average values of these indices in the fitted ensemble models (EP-ESMs) of climate and vegetation were generally higher than for a single modelling technique (Supplementary Figs S2–S3).

All selected climate and vegetation variables influenced the predictions, and their contributions were approximately equal in each ensemble model (Supplementary Tables S1–S2). However, the specific biological relationships between the selected environmental variables (macroclimate and vegetation cover) and the species remain unclear. Studies on two Tiger Gecko congeners, *G. catbaensis* and *G. lichtenfelderi*, recently described their microhabitat use and identified vegetation (canopy coverage) and ambient parameters (temperature, humidity, weather condition) as the most important characteristics (Ngo et al. 2019a, Ngo et al. in press). Therefore, it is undeniable that the selected environmental variables, which might play important roles in the natural history of *G. huuliensis*, constrain the current distribution range and even have effects on evolutionary processes (see also Pyron & Burbrink 2009, Rödder & Engler 2011, Zhang et al. 2014, Rato et al. 2015, Heidari 2019, Nogueira et al. 2019, Sheu et al. 2020).

In this study, we found in the current MESS map that novel climatic conditions will impact on most sites of occurrence of the other three Vietnamese Tiger Geckos (namely *G. catbaensis, G. lichtenfelderi*, and *G. luii*), and that the potential distribution of *G. huuliensis* does not or only slightly overlaps their occurrence sites (Orlov et al. 2008, Ziegler et al. 2008, Nguyen et al. 2009, Nguyen 2011, Ngo et al. 2019a, Ngo et al. 2021). The climate-based potential distribution of the granite-adapted *G. lichtenfelderi*, as simulated by the Maxent approach, showed that it does not overlap with the extent of occurrence of any karst-dwelling Tiger Gecko in Vietnam, apart from *G. catbaensis* (Ngo et al. 2021). We assume that macroclimatic niche divergence may have a central role in explaining the diversification in *Goniurosaurus* (Grinnell 1917, Rödder & Engler 2011, Fisher-Reid et al. 2012).

Implications for conservation

Under the future potential impacts of climate change, the potential distribution of *G. huuliensis* tends to narrow and shift towards higher latitudes in the border area between China and Vietnam. Similar changes were also previously predicted by using the Maxent approach for *G. catbaensis* and *G. lichtenfelderi* (Le et al. 2017, Ngo et al. 2021). Since all *Goniurosaurus* species are locally-distributed specialists adapted to unique ecological niches (Nguyen et al. 2009, Nguyen 2011, Ngo et al. 2016, 2019a, 2021, Ngo et al. in press), we only identified currently suitable areas within the selected buffer that can serve as refugia for sustainable in-situ conservation rather than areas suitable for colonization. Based on the forecasted climate and vegetation maps, we have generated a core-refugia map that identifies key regions for priority conservation. The green patches in the map (Fig. 5) represent highly suitable habitats with regard to both climate and vegetation, mostly in areas in Lang Son Province and at small sites in Bac Giang and Thai Nguyen Provinces, northern Vietnam. The yellow areas indicating

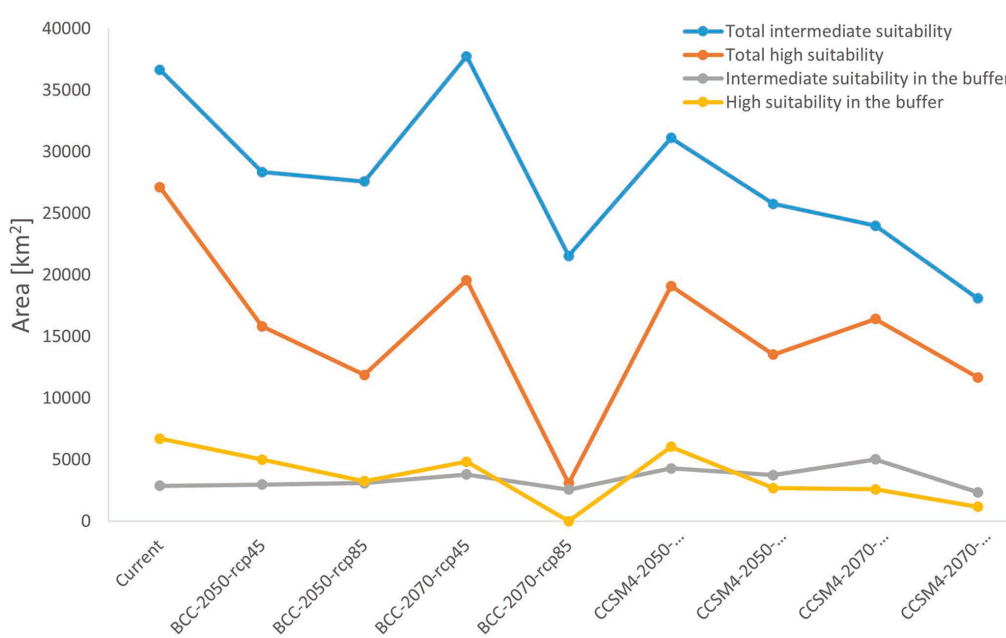


Figure 4. Projected habitable areas of suitable categories for *Goniurosaurus huuliensis* under different climate conditions of current and future scenarios (blue line represents the total areas of intermediate suitability within the study site; orange line the total areas of high suitability within the study site; grey line the areas of intermediate suitability in the buffer; yellow line the areas of high suitability in the buffer).

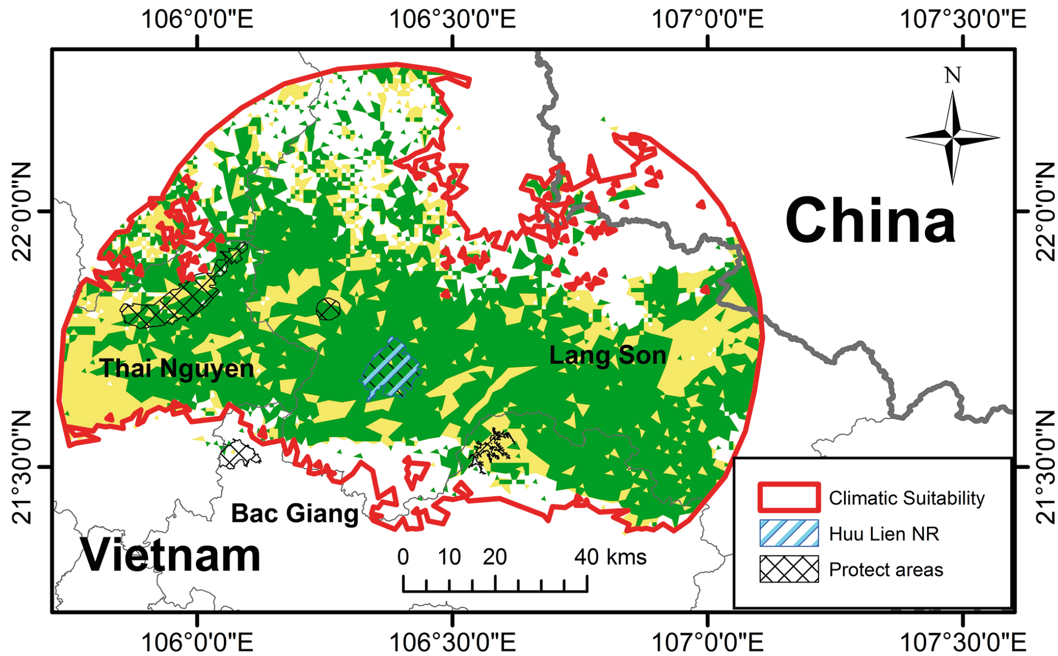


Figure 5. Proposed refugia throughout the range of *Goniurosaurus huuliensis* under the current model (green areas indicate core habitats of suitable vegetation within yellow areas of high climatic suitability and red lines cover all climatically suitable areas in the buffer area).

the intermediate level of climate suitability should be considered buffers of the core refugia (Fig. 5).

There are three nature reserves (namely Bac Me, Huu Lien and Than Sa – Phuong Hoang) within the selected green patches (Fig. 5). However, the target species has been found only in the Huu Lien NR. A large area of evergreen forest in the Huu Lien NR is rigorously protected by local people and rangers, and wild populations of *G. huuliensis* may potentially be found in previously overlooked but suitable areas there (Ngo et al. pers. obs). Thus, the Huu Lien NR plays a very important role and should be considered a "centre" for the initiation of in-situ conservation programs for *G. huuliensis*.

However, our interviews with local rangers showed that dealers are usually contacted by local hunters from the Huu Lien NR with offers of desired quantities and prices for each wild specimen. Captured animals were then handed over to the dealers in places outside the nature reserve to evade stringent inspections by local rangers. As a consequence of these illegal actions, large numbers of wild animals were collected, leading to a potentially significant decline of the wild population of *G. huuliensis* (Ngo et al. 2019a, b). Furthermore, we observed other anthropogenic impacts on the karst habitat of *G. huuliensis*, such as expanding road construction and illegal timber logging.

Thus, we recommend the establishment of a species and habitat conservation area for the threatened species *G. huuliensis*. The core-protection area should be selected from within the green patches in the core-refugia map with the "Huu Lien NR-Center" (Fig. 5). However, this suggestion may not be the best option to protect the species effectively. In fact, our selection of core refugia is only based on the outcome of our climatic and vegetation models. To enhance the practical applicability of in-situ conservation measures, conservationists should be provided with detailed biological information on the target species, such as population status, habitat requirements, and threats as well. At the moment, to mitigate the anthropogenic impacts on wild populations and their habitat, we strongly propose that monitoring of the illegal trade and protecting natural forests be intensified, as well as community education on the value of biodiversity be enhanced.

Two other lizards, *Gekko canhi* and *Scincella apraefrontalis*, were recently discovered in the Huu Lien NR (Nguyen et al. 2010, Rösler et al. 2010, Ngo et al. pers. obs). We assume that these endemic species, being sympatric with *G. huuliensis*, are likewise being negatively affected in the context of climate change. Therefore, these lizard species will also benefit from improved conservation measures in the region.

Acknowledgements

For supporting fieldwork and issuing relevant permits, we thank the authorities and forest management departments of the Huu Lien Nature Reserve in Lang Son Province, and of Bac Giang and Thai Nguyen Provinces. We are grateful to T. Pagel and C. Landsberg (Cologne Zoo), S. V. Nguyen (IEBR, Hanoi), L. V. Vu, and T. T. Nguyen (VNMN, Hanoi) for their support of conservation-based biodiversity research in Vietnam. We are very thankful to A. Bauer (Villanova University) and L. Grismer (La

Sierra University) for their constructive reviews, which improved the manuscript. Field surveys were partially funded by Cologne Zoo and the Wildlife Conservation Society with the John Thorbjarnarson Fellowship for Reptile Research. Cologne Zoo is a partner of the World Association of Zoos and Aquariums (WAZA): Conservation Project 07011, 07012 (Herpetodiversity Research, Amphibian and Reptilian Breeding and Rescue Stations). This research was partially supported by the Vietnam Academy of Science and Technology (Project code NVCC09.07/21-21). Research of H. N. Ngo in Germany is funded by the German Academic Exchange Service (DAAD).

References

Allouche, O., A. Tsoar & R. Kadmon (2006): Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS). – Journal of Applied Ecology, **43**: 1223–1232.

Araújo, M. B., W. Thuillerand & R. G. Pearson (2006): Climate warming and the decline of amphibians and reptiles in Europe. – Journal of Biogeography, **33**: 1712–1728.

Baumgartner, J., M. Esperón-Rodríguez & L. J. Beaumont (2018): Identifying in situ climate refugia for plant species. – Ecography, **41**: 1–14.

Breiner F. T., A. Guisan, A. Bergamini & M. P. Nobis (2015): Overcoming limitations of modelling rare species by using ensembles of small models. – Methods in Ecology and Evolution, **6**: 1210–1218.

Cola V. D., O. Broennimann, B. Petitpierre, F. T. Breiner, M. D'Amen, C. Randin, R. Engler, J. Pottier, D. Pio, A. Dubuis, L. Pellissier, R. G. Mateo, W. Hordijk, N. Salamin & A. Guisan (2017): Ecospat: An R package to support spatial analyses and modeling of species niches and distributions. – Ecography, **40**: 01–14.

Dudley, N. & J. Parish (2006): Closing the gap. Creating ecologically representative protected area systems: A guide to conducting the gap assessments of protected area systems for the convention on biological diversity. – Secretariat of the Convention on Biological Diversity, Montreal, Technical Series no. **24**: 108 PP.

Elith, J. & C. H. Graham (2009): Do they? How do they? Why do they differ? On finding reasons for differing performances of species distribution models. – Ecography, **32**: 66–77.

Elith, J., M. Kearney & S. Phillips (2010): The art of modeling range-shifting species. – Methods in Ecology and Evolution, **1**: 330–342.

Elith, J., S. J. Phillips, T. Hastie, M. Dudík, Y. E. Chee & C. J. Yates (2011): A statistical explanation of Maxent for ecologists. – Diversity and Distributions, **17**: 43–47.

Fielding, A. H. & J. F. Bell (1997): A review of methods for the measurement of prediction errors in conservation presence/absence models. – Environmental Conservation, **24**: 38–49.

Fisher-Reid, M. C., K. H. Kozak & J. J. Wiens (2012): How is the rate of climatic-niche evolution related to climatic-niche breadth? – Evolution, **66**: 3836–3851

Fitzgerald, L. A., D. Walkup, K. Chyn, E. Buchholtz, N. Angeli & M. Parker (2018): The future for reptiles: advances and challenges in the anthropocene. – Encyclopedia of the Anthropocene, **3**: 163–174.

Gent, P. R., G. Danabasoglu, L. J. Donner, M. M. Holland, E. C. Hunke, S. R. Jayne, D. M. Lawrence, R. B. Neale, P. J. Rasch, M. V. P. H. Worley, Z. L. Yang & M. Zhang (2011): The Community Climate System Model Version 4. – Journal of Climate, **24**: 4973–4991.

Grinnell, J. (1917): The niche-relationships of the California thrasher. – Auk, **34**: 427–433.

Grismer, L. L., B. E. Viets & L. J. Boyle (1999): Two new continental species of *Goniurosaurus* (Squamata: Eublepharidae) with a phylogeny and evolutionary classification of the genus. – Journal of Herpetology, **33**: 382–393.

Guisan, A. & W. Thuiller (2005): Predicting species distribution: Offering more than simple habitat models. – Ecological Letters, **8**: 993–1009.

Guisan, A. & N. E. Zimmermann (2000): Predictive habitat distribution models in ecology. – Ecological Modelling, **135**: 147–186.

Heidari, N. (2019): Ecological niche differentiation between *Acanthodactylus micropholis* and *A. khamirensis* (Sauria: Lacertidae) in southern Iran. – Zoology Apologia, **36**: e27357.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones & A. Jarvis (2005): Very high resolution interpolated climate surfaces for global land areas. – International Journal Climatology, **25**: 1965–1978.

Huey, R. B., C. A. Deutsch, J. J. Tewksbury, L. J. Vitt, P. E. Hertz, H. J. Álvarez Pérez & T. Garland (2009): Why tropical forest lizards are vulnerable to climate warming. Proceedings of the Royal Society B: Biological Sciences, **276**: 1939–1948.

Huggett, R. J. (2004): Fundamentals of Biogeography (Routledge Fundamentals of Physical Geography). – Taylor & Francis Group.

Le, Q. T., X. C. Le, M. H. Le, A. T. Tran, T. H. Chu, Q. T. Nguyen & N. H. Ngo (2017): Existing status and impact of climate change to the distribution of *Goniurosaurus catbaensis*. – Proceedings of the 7th National Scientific Conference on Ecology and Biological Resources, Hanoi.

Lobo, J. M., A. Jimenez-Valverde & R. Real (2008): AUC: a misleading measure of the performance of predictive distribution models. – Global Ecology and Biogeography, **17**: 145–151.

Markle, T. M. & K. H. Kozak (2018): Low acclimation capacity of narrow-ranging thermal specialists exposes susceptibility to global climate change. – Ecology and Evolution, **8**: 4644–4656.

Monastersky, M. (2014): Life – a status report: Species are disappearing quickly – but researchers are struggling to assess how bad the problem is. – Nature, **516**: 158.

Moss, R. H., J. A. Edmonds, K. A. Hibbard, M. R. Manning, S. K. Rose, D. P. Van Vuuren, T. R. Carter, S. Emori, M. Kainuma, T. Kram & G. A. Meehl (2010): The next generation of scenarios for climate change research and assessment. – Nature, **463**: 747–756.

Ngo, N. H., Q. H. Nguyen, Q. T. Phan, Q. T. Nguyen, L. R. Gewiss, D. Rödder & T. Ziegler (2022): Modeling the environmental refugia of the endangered Lichtenfelder's Tiger Gecko (*Goniurosaurus lichtenfelderi*) towards implementation of transboundary conservation. – Frontiers of Biogeography, **14.1**: e51167.

Ngo, N. H., Q. H. Nguyen, Q. T. Phan, Q. T. Nguyen, L. R. Gewiss, D. Rödder & T. Ziegler (in press): First ecological assessment of the endangered Lichtenfelder's tiger gecko

(*Goniurosaurus lichtenfelderi*) from northern Vietnam: Micro-habitat selection and Macro-climatic niches comparison between island and mainland populations. – Amphibia-Reptilia.

Ngo, H. N., Q. T. Le, L. M. Pham, D. M. Le, M. van Schingen & T. Ziegler (2019a): First record of the Cat Ba tiger gecko, *Goniurosaurus catbaensis*, from Ha Long Bay, Quang Ninh Province, Viet Nam: Microhabitat selection, potential distribution, and evidence of threats. – Amphibian & Reptile Conservation, **13**: 1–13.

Ngo, N. H., Q. T. Nguyen, Q. T. Phan, M. van Schingen & T. Ziegler (2019b): A case study on trade in threatened Tiger Geckos (*Goniurosaurus*) in Vietnam including updated information on the abundance of the Endangered *G. catbaensis*. – Nature Conservation, **33**: 1–19.

Ngo, H. N., T. Ziegler, T. Q. Nguyen, C. T. Pham, T. T. Nguyen, M. D. Le & M. van Schingen (2016): First population assessment of two cryptic tiger geckos (*Goniurosaurus*) from Northern Vietnam: Implications for conservation. – Amphibian & Reptile Conservation, **10**: 34–45.

Nguyen T. Q. (2011): Systematics, ecology, and conservation of the lizard fauna in northeastern Vietnam, with special focus on *Pseudocalotes* (Agamidae), *Goniurosaurus* (Eublepharidae), *Sphenomorphus* and *Tropidophorus* (Scincidae) from this country. – PhD thesis, University of Bonn, Bonn, Germany.

Nguyen, T. Q. (2018): *Goniurosaurus huuliensis*. The IUCN Red List of Threatened Species 2018: e.T18917702A18917704.

Nguyen, T. Q., V. S. Nguyen, W. Böhme & T. Ziegler. (2010): A new species of *Scincella* (Squamata: Scincidae) from Vietnam. – Folia Zoologica, **59**: 115–121.

Nguyen, S. V., C. T. Ho & T. Q. Nguyen (2009): Herpetofauna of Vietnam – Edition Chimaira, Frankfurt am Main.

Nogueira, T. D. A. C., W. E. Ayala, J. S. Dayrell, R. D. Fraga & I. L. Kaefer (2019): Scale-dependent estimates of niche overlap and environmental effects on two sister species of Neotropical snakes. – Studies on Neotropical Fauna and Environment, **54**: 121–132.

Orlov, N. L., S. A. Ryabov, T. T. Nguyen, T. Q. Nguyen & C. T. Ho (2008): A new species of *Goniurosaurus* (Sauria: Gekkota: Eublepharidae) from north Vietnam. – Russian Journal of Herpetology, **15**: 229–244.

Parmesan, C. (2006): Ecological and evolutionary responses to recent climate change. – Annual Review of Ecology, Evolution, and Systematics, **37**: 637–669.

Pimm, S. L., C. N. Jenkins, R. Abell, T. M. Brooks, J. L. Gittleman, L. N. Joppa, P. H. Raven, C. M. Roberts, & J. O. Sexton (2014): The biodiversity of species and their rates of extinction, distribution, and protection. – Science, **334**: 1246752.

Pyron, R. A. & F. T. Burbrink (2009): Lineage diversification in a widespread species: roles for niche divergence and conservatism in the Common Kingsnake, *Lampropeltis getula*. – Molecular Ecology, **18**: 3443–3457.

Radosavljevic, A. & R. P. Anderson (2014): Making better Maxent models of species distributions: complexity, overfitting and evaluation. – Journal of Biogeography, **41**: 629–643.

Rato C., D. J. Harris, A. Perera, S. B. Carvalho, M. A. Carretero & D. Rödder (2015): A combination of divergence and conservatism in the niche evolution of the Moorish Gecko, *Tarentola mauritanica* (Gekkota: Phyllodactylidae). – PLoS ONE, **10**: e0127980.

Rödder D. & J. O. Engler (2011): Quantitative metrics of overlaps in overlaps in Grinnellian niches: advances and possible drawbacks. – Global Ecology and Biogeography, **20**: 915–927.

Rösler H., T. Q. Nguyen, K. V. Doan, C. T. Ho, T. T. Nguyen & T. Ziegler (2010): A new species of the genus *Gekko* Laurenti (Squamata: Sauria: Gekkonidae) from Vietnam with remarks on *G. japonicus* (Schlegel). – Zootaxa, **2329**: 56–68.

RStudio Team. (2018): RStudio: Integrated Development for R. RStudio, Inc., Boston, MA, USA. Available at: http://www.rstudio.com/.

Sandel, B., L. Arge, B. Dalsgaard, R. G. Davies, K. J. Gaston, W. J. Sutherland & J. C. Svenning (2011): The influence of late Quaternary climate-change velocity on species endemism. – Science, **334**: 660–664.

Sheu, Y., J. P. Zurano, M. A. Ribeiro-Junior, T. C. Ávila-Pires, M. T. Rodrigues, G. R. Colli & F. P. Werneck (2020): The combined role of dispersal and niche evolution in the diversification of Neotropical lizards. – Ecology and Evolution, **10**: 2608–2625.

Taylor, S. & L. Kumar (2016): Global climate change impacts on Pacific islands terrestrial biodiversity: a review. – Tropical Conservation Science, **9**: 203–223.

The Government of Vietnam (2019): Decree No. 06/2019/ND-CP of the Government of Vietnam on management of threatened and rare wild plants and animals, dated on 18 March 2019, Hanoi.

Thomas, C. D., A. Cameron, R. E. Green, M. Bakkenes, L. J. Beaumont, Y. C. Collingham, B. F. N. Erasmus, M. F. D. Siqueira, A. Grainger, L. Hannah, L. Hughes, B. Huntley, A. S. Van Jaarsveld, G. F. Midgley, L. Miles, M. A. Ortega-Huerta, A. T. Peterson, O. L. Phillips & S. E. Williams (2004): Extinction risk from climate change. – Nature, **427**: 145–148.

Urban, M. C. (2015): Accelerating extinction risk from climate change. – Science, **348**: 571–573.

van Schingen, M., Q. Q. Ha, C. T. Pham, T. Q. Le, Q. T. Nguyen, M. Bonkowski & T. Ziegler (2016): Discovery of a new crocodile lizard population in Vietnam: Population trends, future prognoses and identification of key habitats for conservation. – Revue Suisse de Zoologie, **123**: 241–251.

Van Vuuren, D. P., J. Edmonds, M. Kainuma, K. Riahi, A. Thomson, K. Hibbard, G. C. Hurtt, T. Kram, V. Krey, J. Lamarque, T. Masui, M. Meinshausen, N. Nakicenovic, S. J. Smith & S. K. Rose (2011): The representative concentration pathways: an overview. – Climatic Change, **109**: 5–31.

Veloz, S. D. (2009): Spatially autocorrelated sampling falsely inflates measures of accuracy for presence-only niche models. – Journal of Biogeography, **36**: 2290–2299.

Vicente, L. A., V. Santos, T. Ribeiro, M. Guimaraes & L. Verrastro (2019): Are Lizards sensitive to anomalous seasonal temperatures? Long-term thermobiological variability in subtropical species. – PLoS ONE, **14**: e0226399.

Vu, N. T., Q. T. Nguyen, L. L. Grismer & T. Ziegler (2006): First record of the Chinese leopard gecko, *Goniurosaurus luii* (Reptilia: Eublepharidae) from Vietnam. – Current Herpetology, **25**: 93–95.

Weiskopf, R. S., M. A. Rubenstein, L. G. Crozier, S. Gaichas, R. Griffis, J. E. Halofsky, K. J.W. Hyde, T. L. Morelli, J. T. Morisette, R. C. Muñoz, A. J. Pershing, D. L. Peterson, R. Poudel, M. D. Staudinger, A. E. Sutton-Grier, L. Thompson, J. Vose, J. F. Weltzin & K. P. Whyte (2020): Climate change effects on biodiversity, ecosystems, ecosystem services, and natural resource management in the United States. – Science of the Total Environment, **733**: 137782.

Wu, T., L. Song, W. Li et al. (2014): An overview of BCC climate system model development and application for climate change studies. – Journal of Meteorological Research, **28**: 34–56.

Zhang, Y., C. Chen, L. Li, C. Zhao, W. Chen & Y. Huang (2014): Insights from ecological niche modeling on the taxonomic distinction and niche differentiation between the black-spotted and red-spotted tokay geckoes (*Gekko gecko*). – Ecology and Evolution, **4**: 3383–3394.

Ziegler, T., T. Q. Nguyen, A. Schmitz, R. Stenke & H. Rösler (2008): A new species of *Goniurosaurus* from Cat Ba Island, Hai Phong, Northern Vietnam (Squamata: Eublepharidae). – Zootaxa, **1771**: 16–30.

Supplementary data

The following data are available online:

Supplementary Figure S1. Schematic of the Ensemble Small Models (ESM) for each selected modelling technique.

Supplementary Figure S2. Performance of seven Ensemble of Small Models of climate according to adjustment indices of TSS, AUC and Somers'D.

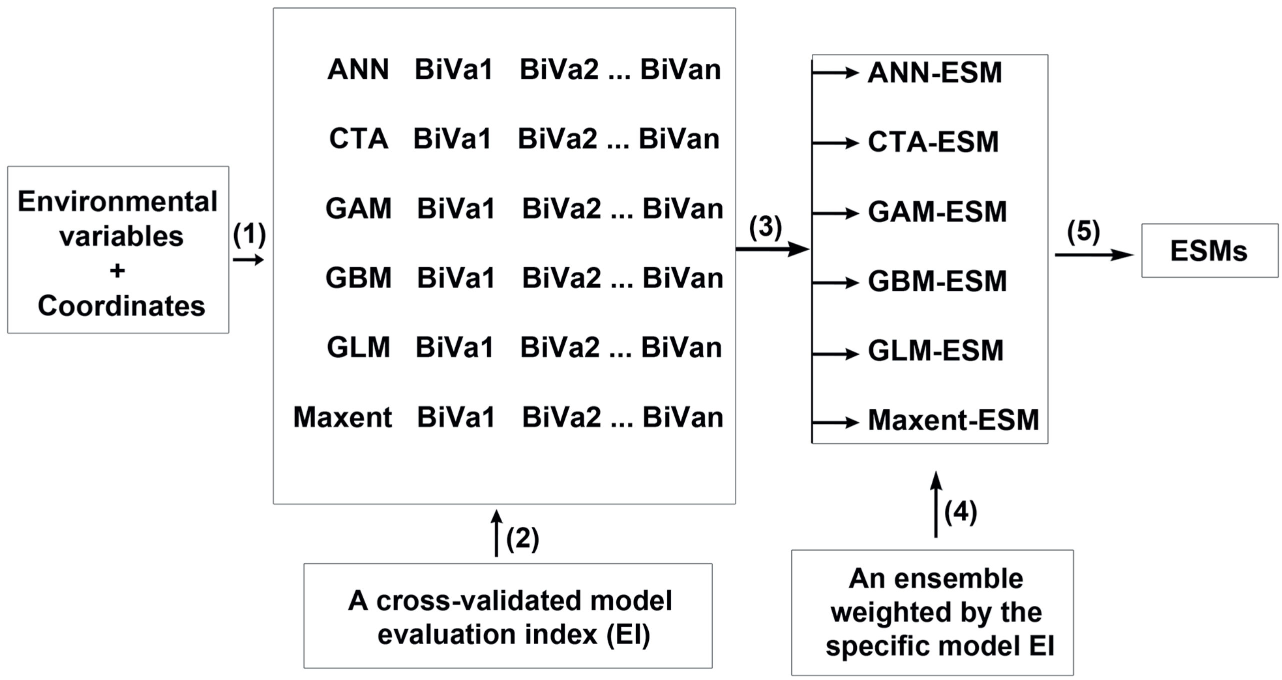
Supplementary Figure S3. Performance of seven Ensemble of Small Models of vegetation according to adjustment indices of TSS, AUC and Somers'D

Supplementary Figure S4. Multi-Environment Similarity Surface (MESS) map of the novel habitat following future circulation models.

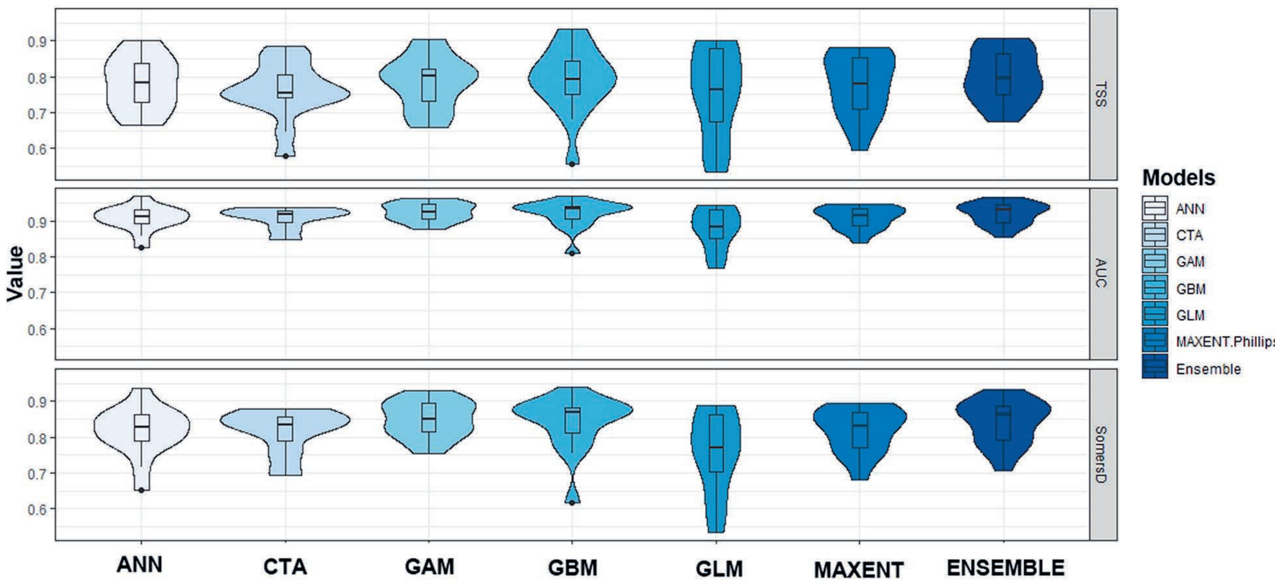
Supplementary Figure S5. Predicted areas of novel habitats as per MESS analyses under different conditions of current and future scenarios.

Supplementary Table S1. Relative contributions (percentages) of climatic variables for ESMs.

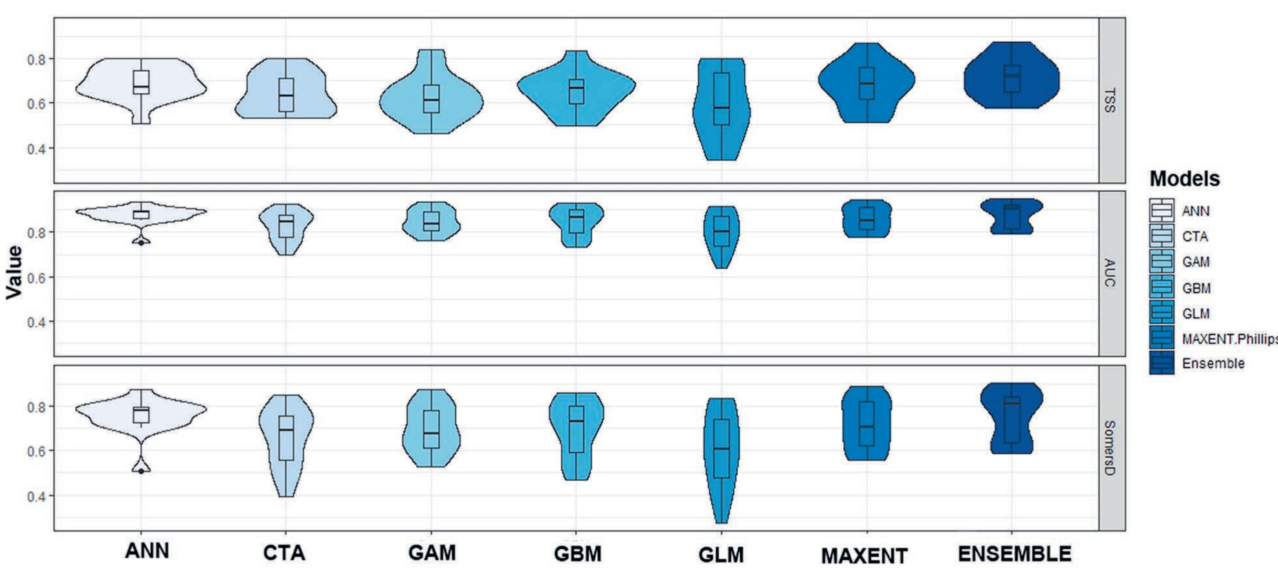
Supplementary Table S2. Relative contributions (percentages) of vegetation variables for ESMs.



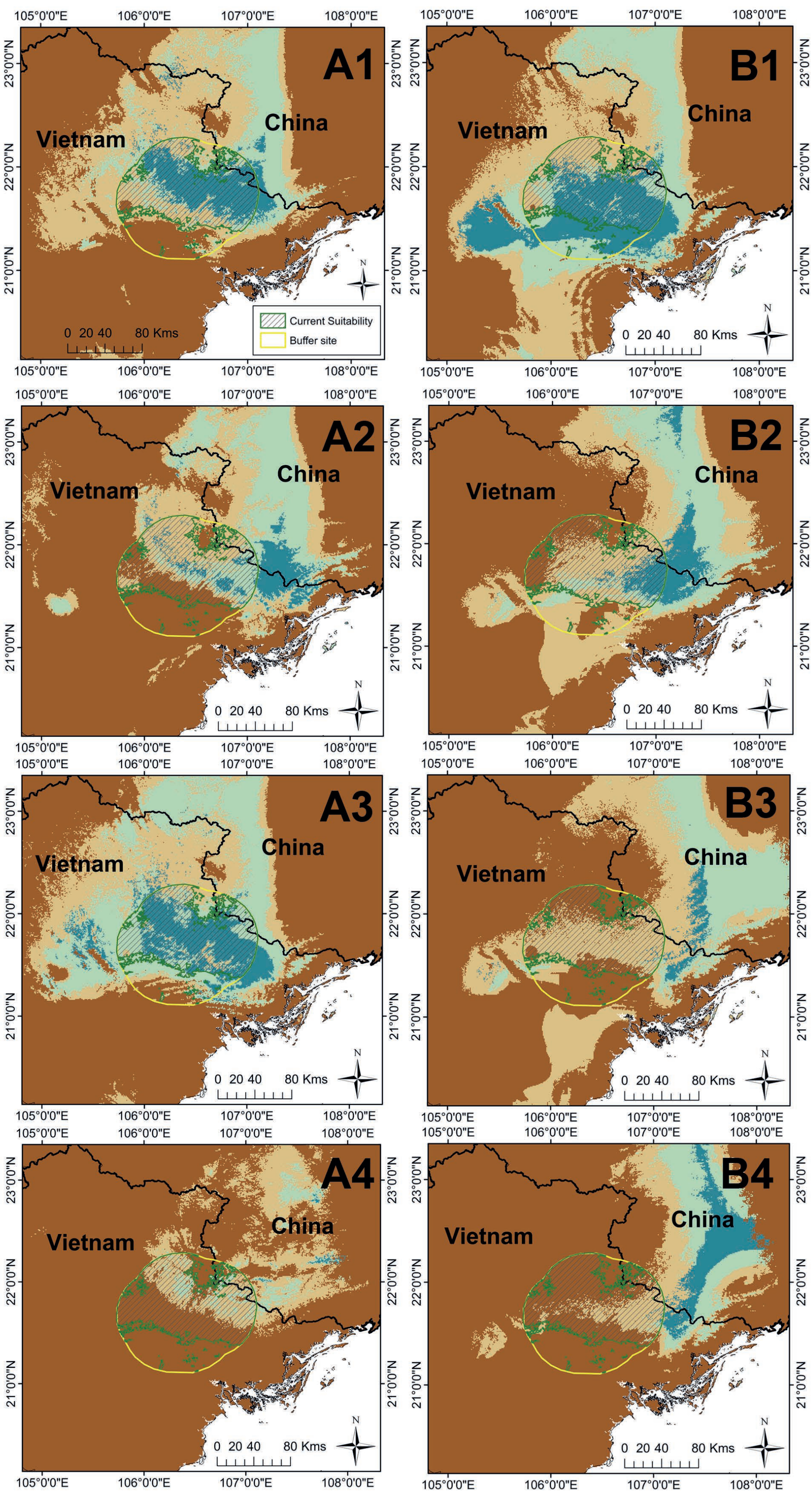
Supplementary Figure S1. Schematic Ensemble Small Models (ESM) for each selected modelling technique with all bivariate models (BiVan, with 06 climate (n = 15) and 05 vegetation predictors (n = 10)) that were calibrated and evaluated (Steps 1 and 2) and averaged to a single ESM per technique (Step 3). ESMs were finally evaluated and averaged again to a single ensemble prediction (Steps 4 and 5).



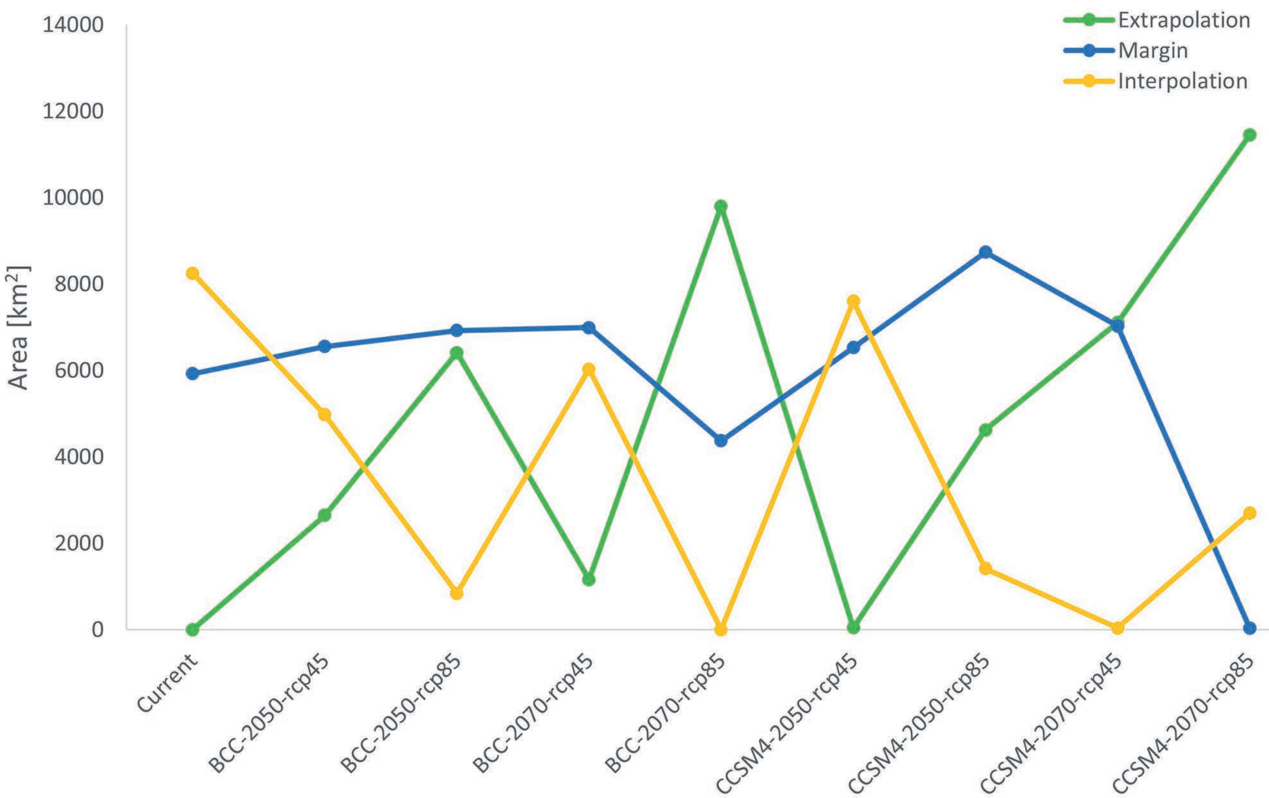
Supplementary Figure S2. Performance of seven Ensemble of Small Models of climate according to adjustment indices of TSS, AUC and Somers'D, evaluated with the testing data from the fifteen-fold spatially segregated dataset. Higher values indicate better-performing models.



Supplementary Figure S3. Performance of seven Ensemble of Small Models of vegetation according to adjustment indices of TSS, AUC and Somers'D, evaluated with the testing data from the fifteen-fold spatially segregated dataset. Higher values indicate better-performing models.



Supplementary Figure S4. Multi-Environment Similarity Surface (MESS) map of the novel habitat following future circulation models of BCC_CSM-1-1: (A1) RCP-4.5 by 2050s; (A2) RCP-4.5 by 2070s; (A3) RCP-8.5 by 2050s; (A4) RCP-8.5 by 2070s; and CCSM4: (B1) RCP-4.5 by 2050s; (B2) RCP-4.5 by 2070s; (B3) RCP-8.5 by 2050s; and (B4) RCP-8.5 by 2070s (teal colour represents high interpolation habitat, aqua colour – low interpolation, coral colour – low extrapolation, brown colour – high extrapolation).



Supplementary Figure S5. Predicted areas of novel habitats in the Multi-Environment Similarity Surface (MESS) analyses under different conditions of current and future scenarios (green line represents Extrapolation; orange line Interpolation; blue line Margin).

Supplementary Table S1. Relative contributions (percentages) of climatic variables for ESMs (Bio-2: Mean Day Temperature (Temp) Range, Bio-3: Isothermality, Bio-9: Mean Temp of Driest Quarter, Bio-15: Precipitation Seasonality, Bio-18: Precipitation of Warmest Quarter, Bio-19: Precipitation of Coldest Quarter).

	ANN	CTA	GAM	GBM	GLM	MAXENT.Phillips	ENSEMBLE
Bio-2	18.3	19.2	22.1	18.0	22.4	18.9	19.8
Bio-3	14.7	16.4	0.0	16.0	19.6	16.3	13.7
Bio-9	15.0	12.9	16.1	14.1	13.2	14.2	14.3
Bio-15	20.8	17.1	19.7	17.4	15.0	17.3	17.9
Bio-18	15.0	18.4	21.6	17.6	14.7	17.7	17.6
Bio-19	16.1	16.0	20.4	16.9	15.2	15.6	16.7

Supplementary Table S2. Relative contributions (percentages) of vegetation variables for ESMs (NDVI-1: Mean Coldest Quarter NDVI, NDVI-2: Minimum Coldest Quarter NDVI, NDVI-3: Minimum Warmest Quarter NDVI, NDVI-4: STD of NDVI and EVI: Range EVI)

	ANN	CTA	GAM	GBM	GLM	MAXENT.Phillips	ENSEMBLE
NDVI-1	23.6	22.9	21.5	22.3	25.0	22.9	23.0
NDVI-2	22.7	23.3	21.7	20.9	19.0	20.2	21.3
NDVI-3	18.8	14.6	18.6	17.6	10.3	17.1	16.4
NDVI-4	19.3	20.3	20.3	20.1	26.3	21.4	21.2
EVI	15.6	18.9	17.8	19.1	19.3	18.5	18.1