



Research article

Capturing response differences of species distribution to climate and human pressures by incorporating local adaptation: Implications for the conservation of a critically endangered species

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ABSTRACT

Considering local adaptation has been increasingly involved in forecasting species distributions under climate change and the management of species conservation. Herein, we take the critically endangered Chinese giant salamander (*Andrias davidianus*) that has both a low dispersal ability and distinct population divergence in different regions as an example. Basin-scale models that represent different populations in the Huanghe River Basin (HRB), the Yangtze River Basin (YRB), and the Pearl River Basin (PRB) were established using ensemble species distribution models. The species ranges under the future human population density (HPD) and climate change were predicted, and the range loss was evaluated for local basins in 2050 and 2070. Our results showed that the predominant factors affecting species distributions differed among basins, and the responses of the species occurrence to HPD and climate factors were distinctly different from northern to southern basins. Future HPD changes would be the most influential factor that engenders negative impacts on the species distribution in all three basins, especially in the HRB. Climate change will likely be less prominent in decreasing the species range, excluding in the YRB and PRB under the highest-emissions scenario in 2050. Overall, the high-emissions scenario would more significantly aggravate the negative impacts produced by HPD change in both 2050 and 2070, with maximum losses of species ranges in the HRB, YRB, and PRB of 83.4%, 60.0%, and 53.5%, respectively, under the scenarios of the combined impacts of HPD and climate changes. We proposed adapted conservation policies to effectively protect the habitat of this critically endangered animal in different basins based on the outcomes. Our research addresses the importance of incorporating local adaptation into species distribution modeling to inform conservation and management decisions.

1. Introduction

Determining where and how species will respond to climate change is currently a pivotal topic in biogeography and conservation biology research, which can provide great knowledge to help formulate conservation and management strategies to mitigate the extinction risks of endangered species (Chardon et al., 2019). Species distribution models (SDMs) are commonly employed approaches that explore how the distribution of a species of concern will shift in space and time with a changing climate (Pacifiçi et al., 2015). Such models correlate species

occurrences with bioclimatic factors to predict the relative probability of occurrence by assuming that species track alongside the changing climatic conditions (Elith and Leathwick 2009; Booth et al., 2014). Given their simplicity and flexibility (Thuiller et al., 2009), as well as the easy accessibility of species occurrence records and climate datasets, SDMs are widely utilized to predict species' range shifts across the globe and guide the conservation management of species in all earth spheres (García-Alegre et al., 2014; Gobeyn and Goethals 2019; Pecchi et al., 2019).

Despite their widespread use, SDMs have been criticized for

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involving assumptions that ignore many ecologically relevant factors (Araújo and Peterson 2012). One of the potential sources of model error that has been of increasing concern is the assumption that species across populations are ecologically uniform in their climatic tolerances within their range (Wiens et al., 2009). Typically, SDMs treat a species as a single entity (Busby 1988) and are developed utilizing all the occurrence data of a species in the whole area to project its potential distribution (Merow et al., 2013). Substantial evidence has shown that the distribution limits of many species vary among populations and that climate tolerances differ among distribution areas due to adaptation to local climate conditions (Sheth and Angert 2014; Lee-Yaw et al., 2016). Despite this, most models assume that species' tolerances to climate changes do not differ across distributional ranges (Valladares et al., 2014). Uncertainties and errors in geographic distribution predictions can be produced by not considering local adaptation (Pearman et al., 2010; Peterson et al., 2019), which preclude the analysis of genetic variation in ecologically important traits (Marcer et al., 2016).

Local adaptation most likely exists within species whose distribution, dispersal, and population dynamics are affected by natural barriers, including physical and biological barriers (Cozzi et al., 2013). Relevant physical barriers may include geographical and topographical events that result in discontinuous habitats (Aliaga-Samanez et al., 2020) and biological barriers that may include interspecific competition and changes in the trophic habitat (Hallfors et al., 2016; Aliaga-Samanez et al., 2020). Very recent research indicated that a growing number of studies are emphasizing the importance of incorporating different forms of local adaptation or intraspecific variation in climate responses (Chardon et al., 2019; Peterson et al., 2019). When modeling range shifts under climate change with the incorporation of local adaptation, individuals within species were divided into groups with different climate responses based on taxonomic units, populations, geographic regions, phenotypes or genetic groups (Pearman et al., 2010; Kapeller et al., 2012; Marcer et al., 2016; Schwalm et al., 2016; Meynard et al., 2017; Peterson et al., 2019). Among the existing studies that incorporated local adaptation, few examined the adaptation patterns of non-climatic variables that could characterize the environmental tolerances of a species (Peterson et al., 2019). At least three studies have considered adaptations to local environmental conditions other than climate factors (Wang et al., 2010; Schwalm et al., 2016; Hu et al., 2017); however, all of them assumed the nonclimatic variables to remain static over time when predicting future conditions. Therefore, how differences in local adaptation to human-related pressures could affect future predicted range shifts remains poorly documented.

Since SDMs are widely used to support conservation or management decisions, not taking local adaptation into account may lead to inaccurate descriptions of species responses to environmental changes across their geographic ranges and, therefore, misplaced conservation efforts, especially for critically endangered species (Hamann and Aitken 2013). Amphibians represent the most threatened vertebrates around the world (Zhang et al., 2019), especially salamanders, which are highly sensitive to climate change because of their low vagility and restrictive physiological demands (Barrett and Guyer 2008). Unlike species that can track varying climates, salamanders will suffer range shrinkage when the climate condition in their distribution areas become unsuitable to sustain their populations (Araújo et al., 2006). Therefore, salamanders are likely to have distinct local adaptations because of their strong climatic requirements, and their wild populations are varied in community structure and ecosystem function in different biogeographic regions (Kozak and Wiens 2006; Ficetola et al., 2016). Human pressures from anthropic activities serve as yet another threat to salamanders' wild population and are likely to aggravate existing stresses (Hof et al., 2011). Therefore, it is fundamental to figure out how the salamanders' ranges will respond to future disturbances from exacerbated human pressures and future climate change to ensure efficient management and conservation.

In the present study, we addressed intraspecific variation in

responses to climate and human-related factors in distribution models to explore how it will affect conservation management. We take the critically endangered Chinese giant salamander (CGS; *Andrias davidianus* (Blanchard, 1871)) as a case. It is known to be historically distributed in most of mainland China. Its wild populations and habitat have been declining due to habitat destruction and hunting for use in medicinal herbs and foods, and the species is currently critically endangered (Yan et al., 2018). We separated the region into three basins, i.e. the Huang River (Yellow River) basin and its adjacent Hai River Basin, the Yangtze River basin, and the Pearl River basin. Basin-scale SDMs were constructed by considering the effects of both climate and human-related factors on the range shifts. This study aims to: (1) test whether basin-scale models describing separate populations are reliable in species distribution modeling; (2) describe whether the species responses to climate and human-related variables varied among geographical regions; (3) quantify the species range shifts impacted by human pressures and climate change in separate areas; and (4) to help guide management and conservation efforts for the CGS based on these outcomes.

2. Methods

2.1. Species occurrence and data grouping

The CGS is recognized as the world's largest amphibian. It is one of the three extant giant salamanders that are Cryptobranchidae living in aquatic habitats (Zhang et al., 2019). Due to habitat loss and human consumption, their population has sharply declined over the past decades. The species has been classified as a critically endangered animal by the Chinese government, included in Appendix I listed species of CITIES and listed as "CR" in the IUCN Red List of Threatened Species (Yan et al., 2018). The occurrence data of CGS were collected from the literature (Wen 2015; Turvey et al., 2018), the Global Biodiversity Information Facility (GBIF; <http://www.data.gbif.org/>), and the geodatabase of the natural reserves (<https://www.osgeo.cn/data/>). The period covered by these data was from the late 20th century to the early part of this century. The occurrence data were located mainly in the Huang River (Yellow River) basin (HRB), the Yangtze River basin (YRB), and the Pearl River basin (PRB), as well as adjacent rivers and basins (Fig. 1). We retained 259 occurrence records after discarding erroneous

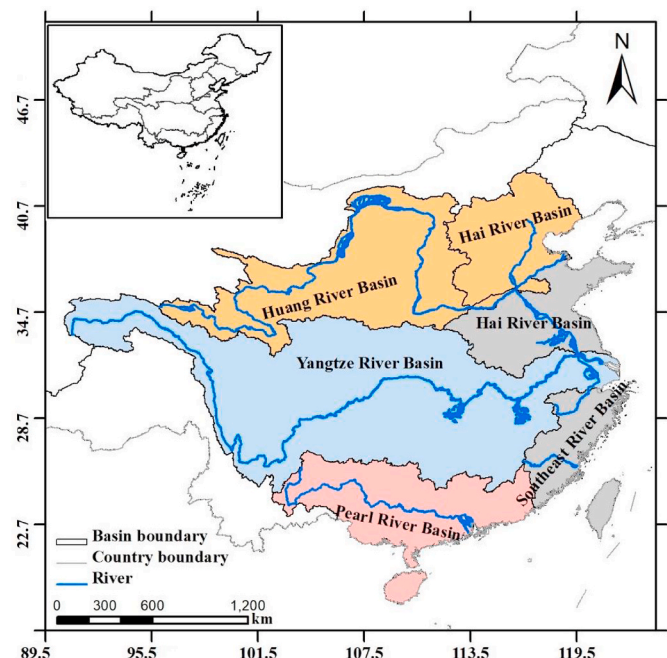


Fig. 1. Location of the study basins.

(e.g., records far from waters) and duplicate records. We selected only one record in each model grid to diminish the spatial autocorrelation of presence records (i.e., more than one presence record in one environmental grid cell with a 30 arc-second spatial resolution, ca. 1.0 km² at the equator) through a spatial thinning method provided by Boria et al. (2014), and 253 occurrences datasets finally remained for model construction.

Due to its limited ability to disperse, particularly between river systems, the CGS distributions were geographically partitioned and confined in neighboring regions (Liang et al., 2019). Considerable studies have found genetic diversity and variability among the CGS populations across the whole distribution area based on molecular analysis (Liang et al., 2019). For instance, Tao et al. (2005) discovered significant genetic differentiation between populations in the PRB and the YRB and between populations in the YRB and the PRB by applying mitochondrial DNA sequencing. Yang et al. (2011) used AFLP makers and found significant genetic diversity from northern to southern China. The high population differentiation likely originated in association with their lower dispersal ability and geographical barriers (including mountains and drainages), as well as their specific habitat requirements (Liang et al., 2019). Based on these studies, we divided all the occurrences into three populations from north to south. The northern population involved the occurrence located in the HRB and its adjacent Hai River Basin (n = 33); the central population included the occurrence located in the YRB (n = 172), and the southern population contained the occurrence located in the PRB (n = 28). Other occurrences located in Huai River Basin (HuRB, n = 8) and South-eastern River Basin (SRB, n = 12) were classified as unknown populations. We developed a model at the species level with all the occurrences for the whole area (model name “M_Whole”) and three separate basin-scale models for the populations in the HRB and Hai River Basin, the YRB, and the PRB (model names: “M_HRB”, “M_YRB” and “M_PRB”). The basin-scale models were used to test the spatial transferability to other basins and compared with the model including the whole occurrence dataset.

2.2. Model establishment

We applied the ensemble modeling technique to develop SDMs of the CGS by considering their reliability in reducing the uncertainties from a single modeling algorithm and providing robust projections of species distribution (Grenouillet et al., 2011). We used four model algorithms, i.e. the generalized linear model (GLM), generalized boosting model (GBM), random forest (RF), and multiple adaptive regression splines (MARS) model, which have been frequently employed in SDMs to develop the ensemble models (Zhang et al., 2020a). All the model algorithms and the ensemble model were implemented by the biomod2 package in the software R 3.6.1 (Thuiller et al., 2009). Since we used presence-absence algorithms and reliable absence data are not available, pseudo-absence records with the same number of presence records within the local basin for each model scenario were generated using a random method that can exclude pixels in the presence locations (Barbet-Massin et al., 2012). Afterward, all the presence and pseudo-absence records were combined and shuffled for ultimate use in model construction (Senay et al., 2013). For each model algorithms, 70% of all records were randomly chosen for model calibration, and the remaining 30% was used to assess the algorithm performance. Each model algorithm was run 10 times to avoid bias from the splitting of the total records. The predictive abilities of each model were evaluated using the true skill statistic (TSS) and the area under the receiver operating characteristic curve (AUC) (Swets 1988). To ensure the optimal predictive ability, algorithms with a TSS score greater than 0.6 and AUC score greater than 0.8 (Allouche et al., 2006) were selected to develop ensemble models by the committee-averaged method. We also determined the relative importance of the selected predictors using an inbuilt randomization procedure (Thuiller et al., 2016) and the response curves of species occurrence for each algorithm using the evaluation strip

method (Elith et al., 2005).

2.3. Predictor selection

The selection of predictors in SDMs can strongly affect the reliability of the predicted niche and spatiotemporal transferability (Peterson et al., 2007). Recent research tested 19 bioclimatic variables and 11 nonclimatic variables, including eight human-related variables, to predict the species distribution of the CGS for the whole potential distribution area in China (Zhang et al., 2020a). Through analysis of the variable collinearity, contribution, and reasonability, four climate variables, and three nonclimatic variables were finally selected as important predictors and showed a good performance in distribution modeling and prediction of the species in that study. In the present study, however, as only about forty occurrence data points were used for model calibration for the HRB and PRB (70% of the whole presence and pseudoabsence data), we selected the four most important variables from the seven variables (see Table 1 in Zhang et al. (2020a) to meet the empirical rule of the use of a maximum of one predictor for ten data points to avoid overparameterization of the models (Harrell et al., 1984; Petitpierre et al., 2017). The four predictors included three bioclimatic variables, i.e., the temperature seasonality (TS), the mean temperature of the coldest quarter (MTCQ), and the precipitation of the warmest quarter (PWQ) accessed from the WorldClim data website (<https://www.worldclim.org/data/index.html>), and the human population density (HPD) from SEDAC (<http://sedac.ciesin.columbia.edu>). Despite the small number of predictors, these four variables were regarded as the most relevant factors affecting the distribution of the CGS, as the contributions of the other three variables to species occurrence were all less than 5% (Zhang et al., 2020a). We used the four selected variables in the four basal model algorithms and ensemble models to predict current and future species distributions at the basin-scale and over the whole area.

2.4. Model prediction and evaluation

The CGS distributions under the current (1950–2000) and future (2050 and 2070) climate conditions with and without the impact of future HPD change for three separate basins and the whole area were projected. We considered two representative concentration pathways (RCPs) for climate change, the optimistic scenario with stringent mitigation (RCP 2.6) and the pessimistic scenario (RCP 8.5). Future climate data were derived from three global circulation models (GCMs) (MIR-OCESM-CHEM, CCSM4, and BCC-CSM1-1) that are widely used in Asia. To reduce uncertainties in the prediction of the species occurrence probability, the averaged outputs of the three GCMs were used as future climates. We obtained future HPD data at a spatial resolution of 1 km for 2050 and 2070 from the global population dataset of the Socioeconomic Data and Applications Center (SEDAC) (Jones and O'Neill 2016).

For real application and model evaluation, species presence and absence maps are required and obtained through transforming the continuous suitability predictions produced by SDMs to binary outputs using threshold values. We applied the mean of the predicted probabilities of species occurrences that can objectively maximize the agreement between observed and predicted distributions (Cramer 2003; Liu et al., 2005), as the threshold to determine the species range (Zhang et al., 2020a). This method was suggested to be reliable in transforming SDM results from presence probabilities to presences/absences binary maps (Liu 2005; Liu et al., 2013; França and Cabral 2019). For each basin-scale model, the threshold was calculated separately, and range sizes under current and future conditions were quantified based on the presence/absence map. The changes of the range size in the scenarios of HPD and climate changes relative to the current condition were calculated and compared among the three basins.

3. Results

3.1. Model performance

For each basin-scale model, most model algorithms performed well when assessed with AUC and TSS, with their median values being greater than 0.8 and 0.6, respectively (Supplementary Fig. S1). Of the four model algorithms, RF always performed better compared to others for all basin-scale models. Among the 40 basal models, 31, 36, and 29 basal models were respectively selected to develop the ensemble SDMs for the HRB, YRB, and PRB (Table 1). For the model with all the occurrences for the whole area, it is not surprising that all basal models performed better compared to those in the basin-scale models, and all the basal models were retained to establish the ensemble models. However, the ensemble model for each basin-scale model also showed high accuracy, with $AUC \geq 0.94$ and $TSS \geq 0.80$ for all the basins, indicating that basin-scale ensemble models could be reliable in species distribution modeling. In terms of predicted mean probabilities (MP) of species occurrence (Table 1), the whole-area model performed slightly better for the YRB (0.93) than the YRB model (0.90). The predicted MP values for the HRB and PRB (0.75 and 0.79), however, were lower than those by the local basin models (0.83 and 0.88), indicating the improved capabilities of basin-scale models in modeling the local distribution of the CGS.

3.2. Variable importance and response curves

For the whole-area model, the importance of all four predictors was greater than 10%, with the MTCQ ($32.6 \pm 2.5\%$) and HPD ($26.8 \pm 1.9\%$) being more important than the other two (Table 2). However, the allocation of the variable importance considerably changed for the basin-scale models. For the HRB model, the most important variable was the HPD (mean of 40.7%), while the MTCQ played a less pivotal role (mean of 7.8%). The second-most important variable was the PWQ, and the contribution of TS became less. The variable importance pattern produced by the YRB model was similar to that of the whole-area model, despite a significant decrease in the HPD (mean of 11.0%). The MTCQ was the most crucial factor for the species occurrence in the YRB (mean of 37.8%), surpassing all other variables. The most important predictor for the PRB was the PWQ (mean of 35.3%), while the HPD and MTCQ were less important (both mean values were less than 8%). These results revealed that the importance of each variable in the whole-area model seemed balanced by the occurrences in different basins from north to south. The findings from basin-scale models indicated that the environmental conditions affecting the distribution and survival of populations in different basins were likely to greatly differ from each other.

For each predictor, the response curves among different algorithms were similar in all basin-scale models and the whole-area model (Supplementary Fig. S2). A comparison of the response curves produced by the ensemble models showed that the species occurrence exhibited a unimodal response to three climate factors for all basins, but the responses were different among basins for each variable (Fig. 2). This demonstrated that the curves of both the MTCQ and PWQ moved from the left to the right of the horizontal axis from the HRB to the YRB and

the PRB, indicating that the requirements for these two variables were gradually enhanced for populations from north to south. The requirements for the TS of different populations, however, decreased from northern to southern basins. This revealed the response curves of the climate variables produced by the whole-area model failed to reflect the peak occurrence probabilities of different basins despite their wider range of high occurrence probabilities. The optimal ranges for the climate variables were distinctly different from each other, although they slightly overlapped between connected basins (Table 2). The optimal range increased for the MTCQ and PWQ and decreased for the TS from northern to southern basins. The optimal MTCQ for the HRB was less than the freezing temperature ($-10.8 \sim -1.1$ °C), while it was greater than 9 °C for the PRB (9.6–12.1 °C). The optimal range of the MTCQ, the most important variable for species in the YRB, was above and below 0 °C for this basin ($-1.5 \sim 9.1$ °C). As the most important variable for species in the PRB, the optimal PWQ (557.5–911.6 mm) was significantly greater than those in the other two basins. It should be noted that the whole-area model did not produce an optimal range covering those in HRB and PRB. For all basins, the occurrence probability decreased with the increase of the HPD (Fig. 2), suggesting that the species is inclined to occur in regions where the HPD is less than 450 people in one square kilometer (Table 2). The requirement for human interference of the species occurrence in the PRB is stricter, as HPD was less than 75 people per km² when its occurrence probability was above 0.6. Generally, the requirements of the species distribution varied distinctly in different basins, especially for climate factors, and these differences could only be detected by separate basin-scale species distribution models.

3.3. Current distribution

The species occurrence probabilities predicted by the basin-scale models and the whole-area model under current conditions were compared (Fig. 3). Generally, the species distribution areas predicted by the basin-scale model were constrained to local basins, despite some areas with medium species occurrence probability transferred around basin boundaries. Fig. 4 shows that the range of the climate predictors clearly varied from northern to southern basins, which could have resulted in confined projections in local areas, considering the distinct responses of the species occurrence to climate factors (Fig. 2). Comparisons showed consistent species distributions in the YRB predicted by the whole-area and YRB models (Fig. 3b and d), but this was not observed in the basin-scale models in the HRB and PRB (Fig. 3a and c). The mean occurrence probability of the species occurrence data predicted by the whole-area model was less than 0.8 (Table 1, 0.75 and 0.79 for the HRB and PRB, respectively), while it was 0.93 for the YRB, indicating that the whole-area model had a better performance for the YRB but a poor performance in predicting species occurrence for the HRB and PRB. As a result, compared with the local basin models, the whole-area model significantly underestimated the species distribution area by 93.4% and 80.3% for the HRB and PRB, respectively. Therefore, these results implied that the basin-scale model could be locally adapted and would be better in projecting the CGS distributions in different basins.

Table 1

Statistics of model performance, the number of models used in ensemble modeling (NME), and the predicted mean probabilities (MP) of species occurrence. MP_Basin: MP of local species occurrence in each basin-scale model; MP_Whole: MP of species occurrence in each basin in the whole-area model; MP_HuRB: MP of species occurrence in the Huai River Basin in Basin-scale and whole-area models; MP_SRB: MP of species occurrence in the Southeastern River Basin in the basin-scale and whole-area models.

Models	AUC	TSS	NME	MP_Basin	MP_Whole	MP_HuRB	MP_SRB
M_HRB	0.952	0.812	31	0.83	0.75	0.73	0.40
M_YRB	0.975	0.833	36	0.90	0.93	0.84	0.83
M_PRB	0.944	0.804	29	0.88	0.79	0.62	0.82
M_Whole	0.983	0.862	40	0.89	0.89	0.92	0.93

Table 2

Variable importance (%) and the optimal range of the variables (species presence probability > 0.8) produced by different models. The units for the range of the TS, MTCQ, PWQ, and HPD are Celsius, Celsius, millimeters, and people per km², respectively.

	Predictors	M_HRB	M_YRB	M_PRB	M_Whole
Variable importance	TS	3.3 ± 0.8	12.1 ± 1.1	10.6 ± 1.3	10.9 ± 1
	MTCQ	7.8 ± 0.9	37.8 ± 2	6.2 ± 0.9	32.6 ± 2.5
	PWQ	18.8 ± 2.1	8.0 ± 0.6	35.3 ± 4.3	15.2 ± 0.4
	HPD	40.7 ± 3	11.0 ± 0.9	7.6 ± 0.5	26.8 ± 1.9
Optimal range	TS	[8.6, 11.9]	[6.6, 8.4]	[6.2, 7.5]	[6.1, 10.1]
	MTCQ	[-10.8, -1.1]	[-1.5, 9.1]	[9.6, 12.1]	[-3.9, 9.7]
	PWQ	[134.8, 447.7]	[346.5, 576.2]	[557.5, 911.6]	[239.7, 721.2]
	HPD	<441.7	<437.6	–	<414.6

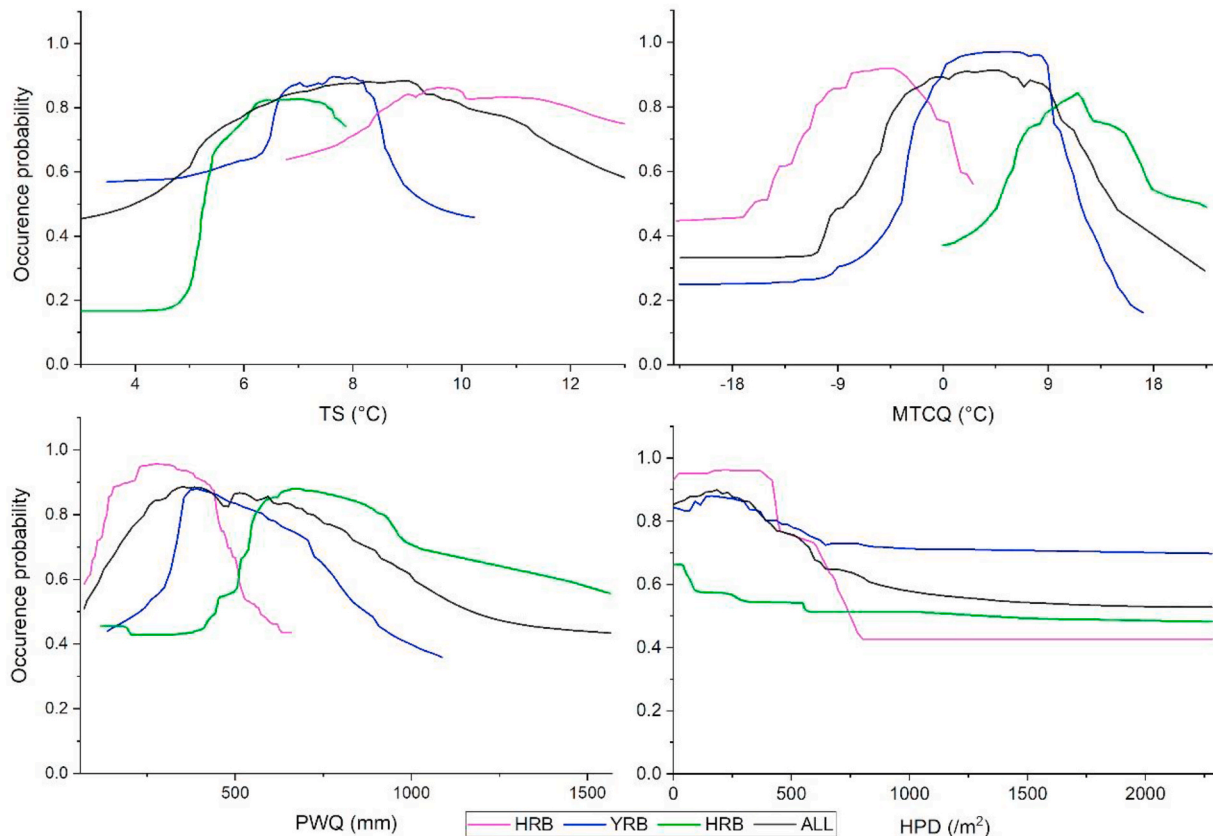


Fig. 2. Response curves of predictor variables for separate and whole populations.

3.4. Species range shifts

Future species distributions were predicted for separate basins using basin-scale models (Supplementary Fig. S3), and species range shifts were compared (Fig. 5). HPD change caused similar impacts on species distribution for the three basins in both 2050 and 2070 (Fig. 5a and b) and evidently decreased the species range by over 26% (Table 3), especially in the HRB (range loss of 55.8% and 61.3% in 2050 and 2070, respectively). Compared with the current status (Fig. 3), future HPD changes would fragment the habitat in all the basins. The species range extended westward, and new habitat was gained in the YRB due to the impact of HPD change (Fig. 5a and b). The species range was not obviously altered in the HRB and YRB due to the impact of climate change (Fig. 5c-f), and the species ranges were slightly decreased or even slightly increased (due to climate change with RCP2.6 in 2050, Table 3), excluding an obvious range loss of 11.0% in the YRB under climate change with RCP8.5 in 2050. The species range loss was obvious in the northern PRB, while the species ranges expanded southward to the coastal area of the PRB in the climate-change scenarios. The overall

range loss in the PRB, however, was more significant in 2050 than in the 2070s in both RCP scenarios (Table 3). When overlapping the impacts from HPD and climate changes, the range loss was aggravated in RCP 8.5 scenarios for all basins (Fig. 5i and j), especially in 2070 with stable habitat nearly disappearing in the HRB and only remaining in the west and the south coast, respectively, in the YRB and PRB (Fig. 5j). The maximum losses of species ranges in the HRB, YRB, and PRB were 83.4%, 60.0%, 53.5%, respectively, indicating a significant negative impact of the combined effect of HPD and climate changes on the species distributions. Despite this, slight offset effects induced by climate change with RCP 2.6 were identified in the HRB and YRB (Table 3). Generally, the effects of HPD and climate changes on species ranges varied among watersheds and periods. HPD variation was likely the most influential factor that engendered negative impacts on species distributions in all three basins, especially in the HRB. Climate change was probably less prominent in decreasing the species range, excluding the YRB and PRB in high emission scenario in 2050. Overall, the high-emissions scenario would more significantly aggravate the negative impacts produced by HPD change under the superimposed impacts of

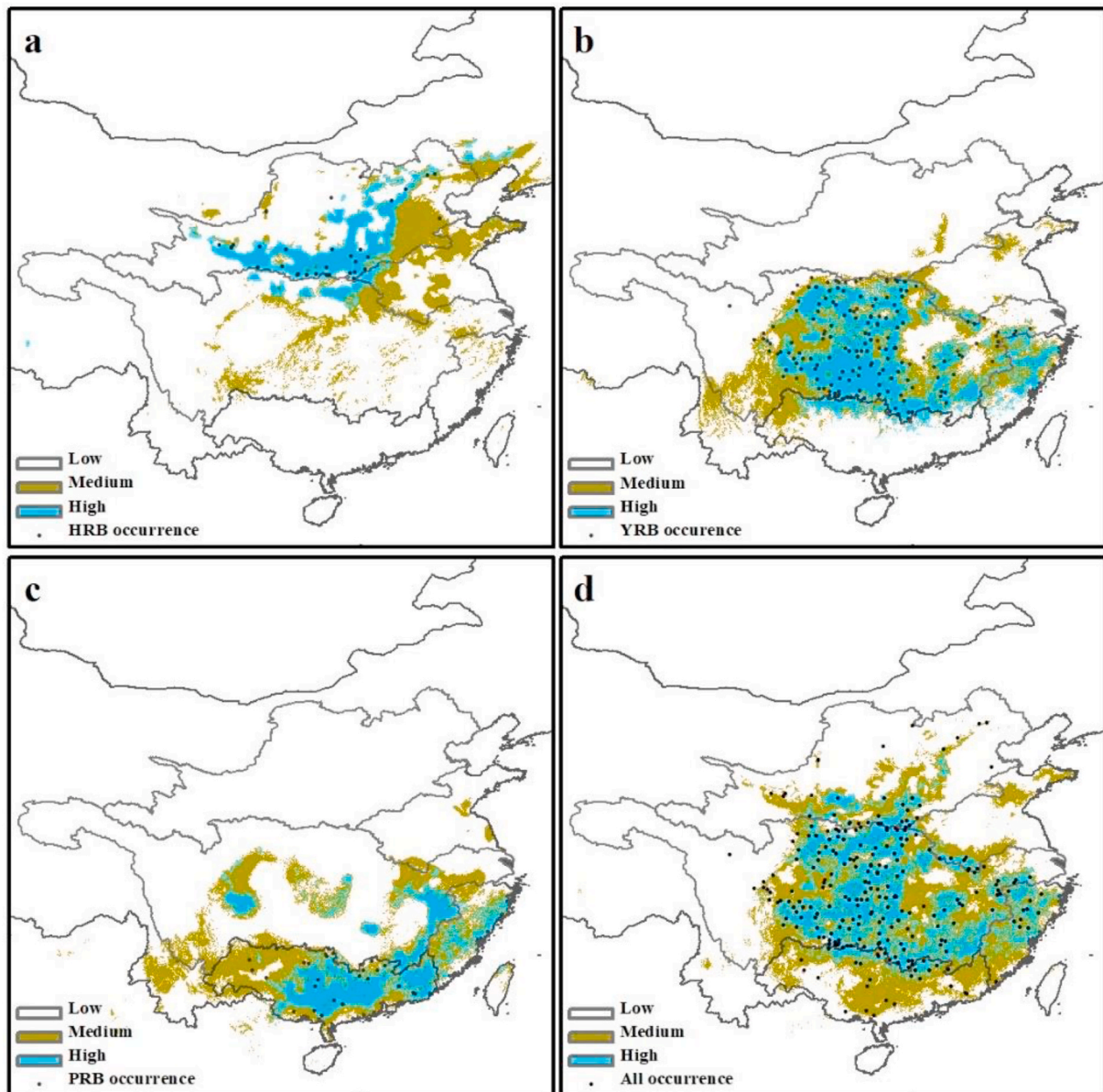


Fig. 3. Comparison of projected current occurrence probabilities for the basin-scale models and whole-area model, with a, b, c, and d representing the modeling results of the HRB, YRB, HRB and the whole basin, respectively. Low: occurrence probability below 0.6; Medium: occurrence probability from 0.6 to MH in Table 1 (MH_Basin); High: occurrence probability from MH to 1.

future climate changes and human pressures.

4. Discussion

4.1. Model comparison and consideration

In the present study, we selected the most important variables based on the model that used all species occurrence records across the whole study area. We used the same variables in the basin-scale models to make the models in separate basins comparable. Only four variables were used to avoid overparameterization because of the relatively limited occurrence records in the HRB and YRB. Although we acknowledge that the species occurrence size in these two basins was tiny and that the inference ability of the SDM could be subsequently influenced, previous studies indicated that SDMs based on small samples size can also produce useful predictions (Hernandez et al., 2006; Wisz et al., 2008; Zhang et al., 2020b). Given the assumed niche transferability of SDMs, projections in space could be useful in identifying

potential distributions in other geographical regions (Randin et al., 2006; Wenger and Olden 2012). However, the differences of environmental conditions among different study regions can be distinct in species' range, thus, the regional model can result in a generally low transferability across regions. It should be noted that the aim of this study was not to explore the model transferability of different regional models but to probe local differences in species distribution responses to environmental changes, specifically for the CGS that have a limited dispersal ability and distinct population divergence among basins. We found distinctly different responses of species occurrence to climate conditions and similar responses to HPD among the three basins (Fig. 2), which could be an adaptation to local environments (Fig. 4). Additionally, our results showed that species distribution area from the whole-area model did not completely cover the species occurrences in the HRB and YRB (Fig. 3d), while their occurrence probability was corrected to be higher by the local basin models, indicating that the local model could outperform the whole-area model. Considering the additional finding that basin-scale models could provide more detail about

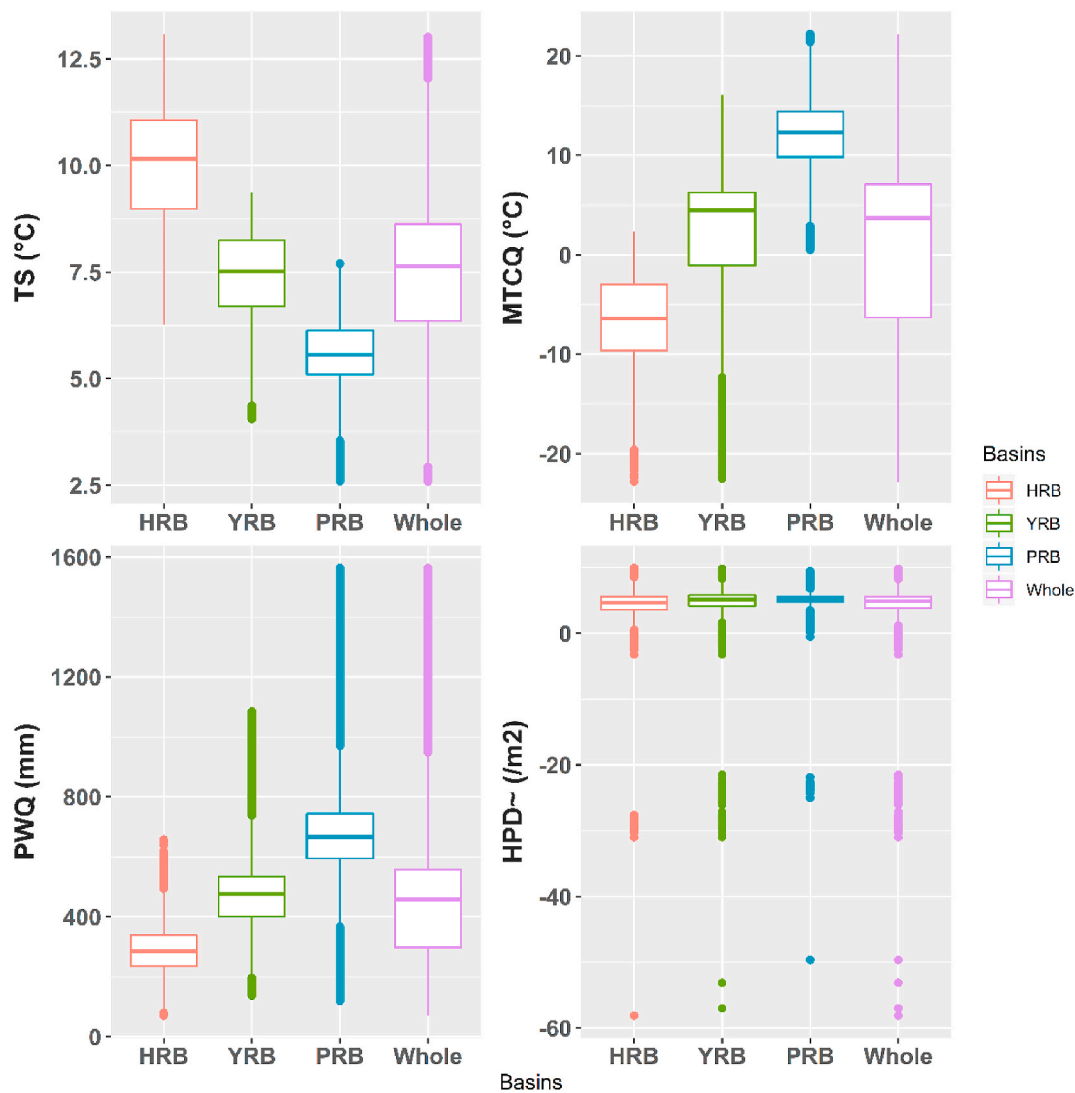


Fig. 4. Range comparison of the four predictors among the three basins and the whole area.

species distribution, basin-scale models that incorporated local adaption were suggested as more reasonable model strategies. However, to improve or validate the ability of the model to predict species distribution, independent geographically or temporally separated data should be collected (Bahn and McGill 2013). Considering the difficulty and high cost of field investigation, the emerging environmental DNA method can be employed to determine the presence in the potential distribution area of the CGS predicted by our study and incorporate the data into future SDM work.

Selecting a model-specific threshold to transform model outputs into binary presence/absence maps has been essential in various aspects of conservation applications and management (Guisan et al., 2013). Maximizing the sum of sensitivity and specificity (*MaxSSS*) is regarded as an efficient method for threshold selection for presence-only SDMs when compared with various other existing methods (Liu et al., 2013), and this method is also commonly used in real applications. However, it is stated that specificity and commission error cannot be calculated without true absence data when using the *MaxSSS* method to select the threshold (Braunisch and Suchant 2010). In this study, we tested the *MaxSSS* method to generate the binary map for all three separate basins and the whole area and found the resulted presence area of the CGS continuously spread over almost all of the basins. The predicted distribution distinctly deviated from the real distribution of this species that is limited in dispersal ability and has a habitat highly impacted and

isolated by human modification of the environment. It is indicated that the predicted distribution generated by *MaxSSS* could not characterize the potential distribution if information about the biotic and anthropogenic factors that affect the distribution of specific species is not incorporated in the SDM (Liu et al., 2013). For a given species with populations that are geographically confined due to dispersal limitation or species interactions, the occupied geographic range will be smaller than its full potential distribution (Leathwick 1998; Svenning and Skov 2004; Soberon and Arroyo-Pena 2017). Furthermore, limited climate availability is also expected to reduce the fundamental niche to a smaller realized niche (Soberón and Nakamura 2009). Although no direct biotic and human factors were considered in our model, we constrained the model area in the separate basin for this species with a limited dispersal ability and included the human population as an important predictor in the model. Therefore, we hypothesized that our model-estimated distribution was closer to the realized distribution, which is more consistent with the actual distribution of the CGS. To achieve this, we used a more rigorous threshold, which was the predicted mean probability of the occurrence data, for the studied critically endangered species. Satisfactory agreements between occurrence sites and the predicted high occurrence probabilities were also achieved with this method (Fig. 3, Table 1). The predicted current species distribution was also generally consistent with the results from the county-scale habitat model produced by Chen et al. (2018). Further work is still needed to test and

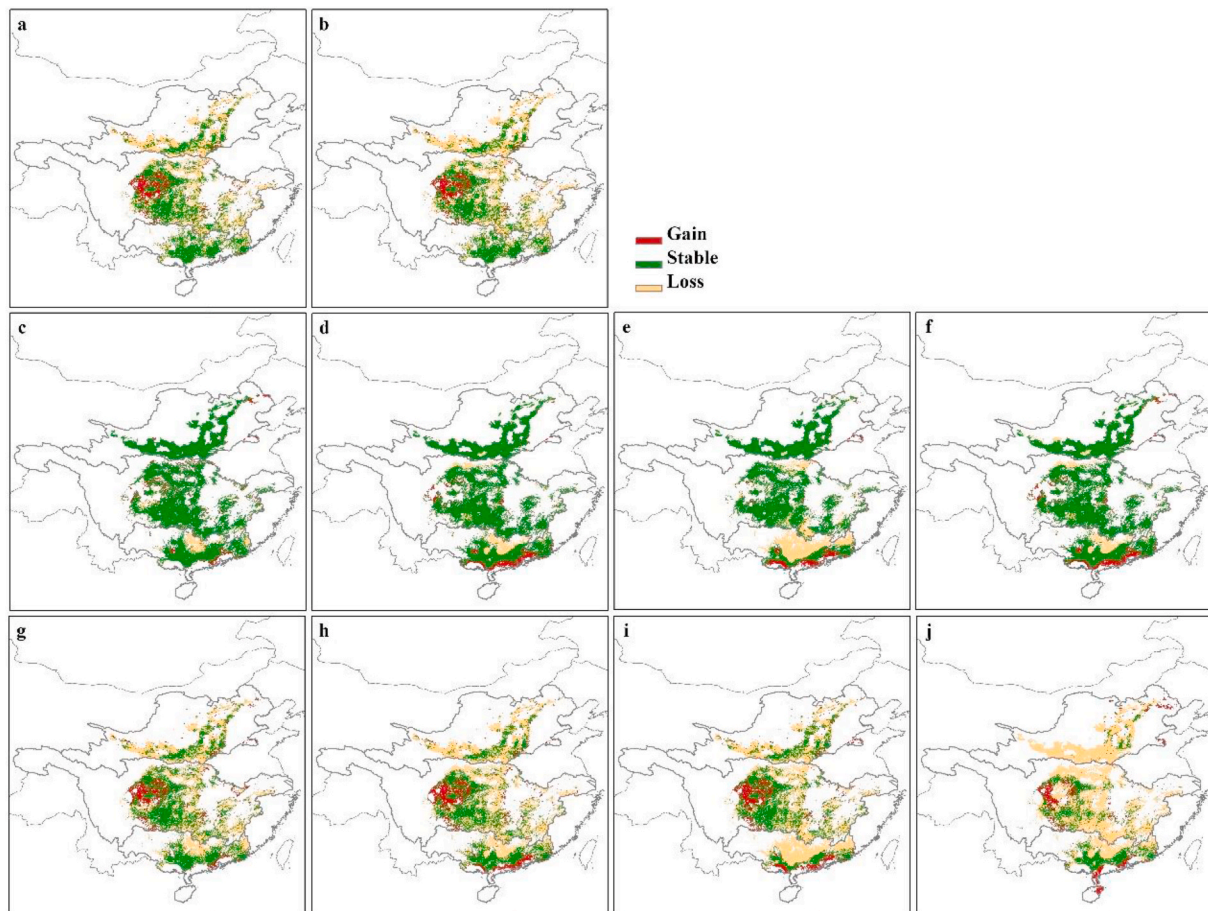


Fig. 5. Species distribution shifts predicted by the basin-scale models in different scenarios, in which (a) and (b) are HPD change scenarios in 2050 and 2070, respectively; (c) and (d) are climate change scenarios with RCP 2.6 in 2050 and 2070, respectively; (e) and (f) are climate change scenarios with RCP 8.5 in 2050 and 2070, respectively; (g) and (h) are HPD and climate changes with RCP 2.6 in 2050 and 2070, respectively; and (i) and (j) are HPD and climate changes with RCP 8.5 in 2050 and 2070, respectively.

Table 3

The relative losses of species ranges (%) for the three basins in different scenarios. CC: climate change; HPD + CC: climate change with HPD change.

Scenarios	Models	RCP2.6		RCP8.5	
		2050	2070	2050	2070
HPD	HRB	-55.8	-61.3		
	YRB	-28.1	-33.0		
	PRB	-26.9	-27.9		
CC	HRB	3.9	-0.7	-3.5	-1.7
	YRB	1.9	-1.2	-11.0	-3.2
	PRB	-13.3	-2.1	-41.8	-2.1
HPD + CC	HRB	-53.7	-60.9	-56.1	-83.4
	YRB	-26.5	-32.5	-30.8	-60.0
	PRB	-34.6	-30.3	-53.5	-37.2
Difference ^a	HRB	2.1	0.4	-0.3	-22.1
	YRB	1.6	0.5	-2.7	-27.0
	PRB	-7.7	-2.4	-26.6	-9.3

^a The difference is the range loss in scenarios HPD + CC minus that in scenario HPD. A positive value indicates offset effects by climate change, while a negative value means aggravated negative impacts due to climate change.

compare other threshold methods (e.g. kappa maximization and prevalence approaches) (Liu 2005) to select the optimal thresholds for different basins to better support model evaluation and application.

4.2. Difference among populations in local basins

Our research revealed a distinct response variation of species occurrence to climate factors from northern to southern basins. As the basins changed from temperate areas to subtropical monsoon regions, the preferred MTCQ and PWQ of the CGS were found to increase (Fig. 2) with increases in the air temperature and precipitation from north to south. As the HRB is a mountainous region with complex landforms and is partly controlled by a continental dry climate, its annual temperature differences are very large (Lu et al., 2014). This may explain why the preferred TS of the CGS in the HRB was higher than those in the other two basins. For the studied ancient animal with poor dispersal potential, mountains and rivers blocked its migration with the formation and evolution of geographic structures, which has led to a rather high level of population differentiation in different geographic regions (Liang et al., 2019). At the same time, the distributions of the species could have adapted to local climate conditions, as indicated by our research. Such local adaptation evidence was also shown in the difference in the contributions of climate factors to species occurrence (Table 2). The most important climate factor in the HRB and PRB was the PWQ, while it was the MTCQ in the YRB. Like most amphibians, the CGS needs to hibernate in cold months to reduce energy consumption and protect them from the frozen period. Unlike the HRB and PRB, where the preferred MTCQ of CGS occurrence is either below-zero temperatures or higher-than-zero temperatures (Fig. 2), the optimal range of the MTCQ in the YRB is around the freezing temperature (Table 2), revealing that the CGS in the YRB could be more sensitive to the variation of winter

temperatures required for hibernating. As the breeding month of the CGS is mainly in wet June and July and the quantity of precipitation is a dominant factor influencing the biomass and health of aquatic ecosystems (Grimm et al., 2013), a suitable PWQ could afford a suitable habitat and enough food for CGS reproduction in the HRB and PRB. Although the TS was found to be relatively less important to CGS occurrence in the three basins, studies revealed that the seasonal variation of climatic conditions may influence the phenology and spatial distributions of salamanders (Kirk et al., 2019).

As the life attributes of ectothermic animals are highly linked to the climate, climate change may cause profound impacts on salamanders (Bartelt et al., 2010). However, as indicated in this study, future HPD variations were primarily accountable for the loss of the species' range, especially for the HRB, where HPD played an important role in the occurrence of the species. Future increasing human populations may advance the harvesting rate of the CGS, where it is popularly believed that they are nutrient-rich foods. As salamanders have low dispersal abilities and rigorous habitat requirements, they are susceptible to human-induced environmental changes (e.g., urbanization and river reconstruction) (Price et al., 2011). The obvious range loss of the CGS resulting from future HPD changes will probably be caused by the booming expansion of urban areas in China in the future. As the CGS prefers to live in habitats with clean and fast-flowing waters (Chen et al., 2018), urbanization can destroy suitable habitats by changing the land cover, altering catchment hydrology, and contaminating river water (Price et al., 2011). Additionally, our study revealed distinct habitat fragmentation caused by HPD change, which would decrease the genetic diversity of populations by obstructing movement among species ranges (Marsh et al., 2005) and ultimately increase the risk of species extinction (Noël et al., 2006).

4.3. Insights for conservation and management

The endangered CGS has attracted considerable conservation attention, while the baseline data on its distribution status is often limited for identifying conservation activities and management policies (Fellowes et al., 2009). The spatiotemporal species distribution produced by our study could provide helpful guidance to surveys of the species' presence and could detect key habitats and populations throughout its ranges. Setting up nature reserves has been acknowledged as an effective strategy for protecting natural populations of the CGS (Liang et al., 2013). However, effective management to prohibit human access to habitats has been lacking in some of the protected areas (Pan et al., 2015). Our research elucidated that future HPD change would result in a significant range loss of the CGS, which is basically following the accepted view that their population decline in the wild is primarily attributed to human-induced habitat destruction and overexploitation. Therefore, tighter measures that prevent human interference should be addressed, especially for the existing nature reserves of the CGS. To do this, public education campaigns should be enhanced to provide better information about the survival status of the CGS and the importance of conserving their habitat. The government should implement severer penalties and regulations to prohibit hunting wild CGS. We recognize that climate change would induce relatively fewer negative impacts on the CGS distribution; however, it is likely to evidently aggravate the adverse impacts from human pressure in the future, as indicated in our study. Therefore, climate factors that heavily influence the habitat and survival of the CGS should not be neglected when formulating conservation measures.

We revealed local differences in climate variable importance and range shift responses to HPD and climate changes among the three basins using basin-scale models. Therefore, we suggest that local adaptive management strategies should be employed for populations in different regions in the future. For the HRB, it is especially important to eliminate the impact of human activities on the habitat of the CGS, as the variation of the used human-related factor would cause distinct range loss. For

this relatively dry basin, we reported that precipitation in the wet season is a dominant climate factor since it may affect its breeding activities. Water replenishment to the key habitat streams and rivers in the reproduction season could be an effective measure. If no urgent conservation measures are implemented, the suitable habitats would be devastated by HPD and climate changes (Fig. 5j). For the YRB, we advocate strengthening the conservation of existing nature reserves, as most of them are in this basin, and new reserves could be established in the west of the range since the habitat there is more stable; thus, new habitats would be colonized in this region with the changes of HPD and the climate (Fig. 5). Mitigating the environmental temperature in the winter is needed for the reserves, as the temperature is crucial in influencing the hibernation of the CGS. For the PRB, compared to the impact of human pressure, climate change would seriously reduce the species range in the northern part of the basin, although new habitat could be gained in the south (Fig. 5c-f). This would force the habitat and populations in the PRB to be more isolated from those on the north side. As precipitation in the wet season was found to be notably more important for species occurrence compared to other climate factors and the human factor, similar measures in the HRB should be particularly enforced to support the successful breeding of the species. As the species ranges of the three basins would distinctly be detached from each other in the future (Fig. 5g-j), specific mitigation strategies at the population level should be further addressed in future studies, and our findings concerning the local adaptation differences of species ranges provide beneficial information.

It is worth mentioning that the release of farmed salamanders has been increasingly approved as a conservation measure for the CGS in recent years. Although it could help restore its populations, the introduction of non-native individuals might induce severe genetic homogenization in local populations (Liang et al., 2019). Therefore, we suggest that environmental tolerance and genetic lineage should be tested before releasing farmed individuals into the wild. In any case, our study highlights the importance of local adaptation in generating more robust management and conservation plans for this critically endangered species of special interest.

Credit author statement

Zhang Peng: Conceptualization, Methodology, Writing - Original Draft. Grenouillet Gaël : Writing - Review & Editing, Supervision. Dong Xianghong: Software, Investigation. Zheng Yichen: Investigation, Visualization. Lek Sovan: Supervision, Validation. Chang Jianbo: Supervision, Project administration.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jenvman.2021.111998>.

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