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1 **Capturing response differences of species distribution to climate and human**  
2 **pressures by incorporating local adaptation: implications for the conservation of**  
3 **a critically endangered species**

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16

17 **Abstract:** Considering local adaptation has been increasingly involved in forecasting  
18 species distributions under climate change and the management of species  
19 conservation. Herein, we take the critically endangered Chinese giant salamander  
20 (*Andrias davidianus*) that has both a low dispersal ability and distinct population  
21 divergence in different regions as an example. Basin-scale models that represent  
22 different populations in the Huanghe River Basin (HRB), the Yangtze River Basin  
23 (YRB), and the Pearl River Basin (PRB) were established using ensemble species

24 distribution models. The species ranges under the future human population density  
25 (HPD) and climate change were predicted, and the range loss was evaluated for local  
26 basins in 2050 and 2070. Our results showed that the predominant factors affecting  
27 species distributions differed among basins, and the responses of the species  
28 occurrence to HPD and climate factors were distinctly different from northern to  
29 southern basins. Future HPD changes would be the most influential factor that  
30 engenders negative impacts on the species distribution in all three basins, especially in  
31 the HRB. Climate change will likely be less prominent in decreasing the species range,  
32 excluding in the YRB and PRB under the highest-emissions scenario in 2050. Overall,  
33 the high-emissions scenario would more significantly aggravate the negative impacts  
34 produced by HPD change in both 2050 and 2070, with maximum losses of species  
35 ranges in the HRB, YRB, and PRB of 83.4%, 60.0%, and 53.5%, respectively, under  
36 the scenarios of the combined impacts of HPD and climate changes. We proposed  
37 adapted conservation policies to effectively protect the habitat of this critically  
38 endangered animal in different basins based on the outcomes. Our research addresses  
39 the importance of incorporating local adaptation into species distribution modeling to  
40 inform conservation and management decisions.

41 **Keywords:** local adaptation; Chinese giant salamander; species distribution models;  
42 human population density; climate change; range loss

## 43 **1 Introduction**

44 Determining where and how species will respond to climate change is currently

45 a pivotal topic in biogeography and conservation biology research, which can provide  
46 great knowledge to help formulate conservation and management strategies to  
47 mitigate the extinction risks of endangered species (Chardon et al. 2019). Species  
48 distribution models (SDMs) are commonly employed approaches that explore how the  
49 distribution of a species of concern will shift in space and time with a changing  
50 climate (Pacifiçi et al. 2015). Such models correlate species occurrences with  
51 bioclimatic factors to predict the relative probability of occurrence by assuming that  
52 species track alongside the changing climatic conditions (Elith and Leathwick 2009,  
53 Booth et al. 2014). Given their simplicity and flexibility (Thuiller et al. 2009), as well  
54 as the easy accessibility of species occurrence records and climate datasets, SDMs are  
55 widely utilized to predict species' range shifts across the globe and guide the  
56 conservation management of species in all earth spheres (García-Alegre et al. 2014,  
57 Gobeyn and Goethals 2019, Pecchi et al. 2019).

58 Despite their widespread use, SDMs have been criticized for involving  
59 assumptions that ignore many ecologically relevant factors (Araújo and Peterson  
60 2012). One of the potential sources of model error that has been of increasing concern  
61 is the assumption that species across populations are ecologically uniform in their  
62 climatic tolerances within their range (Wiens et al. 2009). Typically, SDMs treat a  
63 species as a single entity (Busby 1988) and are developed utilizing all the occurrence  
64 data of a species in the whole area to project its potential distribution (Merow et al.  
65 2013). Substantial evidence has shown that the distribution limits of many species  
66 vary among populations and that climate tolerances differ among distribution areas

67 due to adaptation to local climate conditions (Sheth and Angert 2014, Lee - Yaw et al.  
68 2016). Despite this, most models assume that species' tolerances  
69 to climate changes do not differ across distributional ranges (Valladares et al. 2014).  
70 Uncertainties and errors in geographic distribution predictions can be produced by not  
71 considering local adaptation (Pearman et al. 2010, Peterson et al. 2019), which  
72 preclude the analysis of genetic variation in ecologically important traits (Marcer et al.  
73 2016).

74 Local adaptation most likely exists within species whose distribution, dispersal,  
75 and population dynamics are affected by natural barriers, including physical and  
76 biological barriers (Cozzi et al. 2013). Relevant physical barriers may include  
77 geographical and topographical events that result in discontinuous habitats (Aliaga -  
78 Samanez et al. 2020) and biological barriers that may include interspecific  
79 competition and changes in the trophic habitat (Hallfors et al. 2016, Aliaga - Samanez  
80 et al. 2019). Very recent research indicated that a growing number of studies are  
81 emphasizing the importance of incorporating different forms of local adaptation or  
82 intraspecific variation in climate responses (Chardon et al. 2019, Peterson et al. 2019).  
83 When modeling range shifts under climate change with the incorporation of local  
84 adaptation, individuals within species were divided into groups with different climate  
85 responses based on taxonomic units, populations, geographic regions, phenotypes or  
86 genetic groups (Pearman et al. 2010, Kapeller et al. 2012, Marcer et al. 2016,  
87 Schwalm et al. 2016, Meynard et al. 2017, Peterson et al. 2019). Among the existing  
88 studies that incorporated local adaptation, few examined the adaptation patterns of

89 nonclimatic variables that could characterize the environmental tolerances of a  
90 species(Peterson et al. 2019). At least three studies have considered adaptations to  
91 local environmental conditions other than climate factors (Wang et al. 2010, Schwalm  
92 et al. 2016, Hu et al. 2017); however, all of them assumed the nonclimatic variables to  
93 remain static over time when predicting future conditions. Therefore, how differences  
94 in local adaptation to human-related pressures could affect future predicted range  
95 shifts remains poorly documented.

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

111 ([Hof et al. 2011](#)). Therefore, it is fundamental to figure out how the salamanders'  
112 ranges will respond to future disturbances from exacerbated human pressures and  
113 future climate change to ensure efficient management and conservation.

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

## 130 **2 Methods**

### 131 **2.1 Species occurrence and data grouping**

132 The CGS is recognized as the world's largest amphibian. It is one of the three  
133 extant giant salamanders that are Cryptobranchidae living in aquatic habitats (Zhang  
134 et al. 2019). Due to habitat loss and human consumption, their population has sharply  
135 declined over the past decades. The species has been classified as a critically  
136 endangered animal by the Chinese government, included in the Appendix I listed  
137 species of CITES and listed as "CR" in the IUCN Red List of Threatened Species  
138 (Yan et al. 2018). The occurrence data of CGS were collected from the literature (Wen  
139 2015, Turvey et al. 2018), the Global Biodiversity Information Facility (GBIF;  
140 <http://www.data.gbif.org/>), and the geodatabase of the natural reserves  
141 (<https://www.osgeo.cn/data/>). The period covered by these data was from the late 20th  
142 century to the early part of this century. The occurrence data were located mainly in  
143 the Huang River (Yellow River) basin (HRB), the Yangtze River basin (YRB), and the  
144 Pearl River basin (PRB), as well as adjacent rivers and basins (Figure 1). We retained  
145 259 occurrence records after discarding erroneous (e.g., records far from waters) and  
146 duplicate records. We selected only one record in each model grid to diminish the  
147 spatial autocorrelation of presence records (i.e., more than one presence record in one  
148 environmental grid cell with a 30 arc-second spatial resolution, ca. 1.0 km<sup>2</sup> at the  
149 equator) through a spatial thinning method provided by Boria et al. (2014), and 253  
150 occurrences datasets finally remained for model construction.

151 Due to its limited ability to disperse, particularly between river systems, the CGS



152 distributions were geographically partitioned and confined in neighboring regions  
153 (Liang et al. 2019). Considerable studies have found genetic diversity and variability  
154 among the CGS populations across the whole distribution area based on molecular  
155 analysis (Liang et al. 2019). For instance, Tao et al. (2005) discovered significant  
156 genetic differentiation between populations in the PRB and the YRB and between  
157 populations in the YRB and the PRB by applying mitochondrial DNA sequencing.  
158 Yang et al. (2011) used AFLP makers and found significant genetic diversity from  
159 northern to southern China. The high population differentiation likely originated in  
160 association with their lower dispersal ability and geographical barriers (including  
161 mountains and drainages), as well as their specific habitat requirements (Liang et al.  
162 2019). Based on these studies, we divided all the occurrences into three populations  
163 from north to south. The northern population involved the occurrence located in the  
164 HRB and its adjacent Hai River Basin (n=33); the central population included the  
165 occurrence located in the YRB (n=172), and the southern population contained the  
166 occurrence located in the PRB (n=28). Other occurrences located in Huai River Basin  
167 (HuRB, n=8) and South-eastern River Basin (SRB, n=12) were classified as unknown  
168 populations. We developed a model at the species level with all the occurrences for  
169 the whole area (model name “M\_Whole”) and three separate basin-scale models for  
170 the populations in the HRB and Hai River Basin, the YRB, and the PRB (model  
171 names: “M\_HRB”, “M\_YRB” and “M\_PRB”). The basin-scale models were used to  
172 test the spatial transferability to other basins and compared with the model including  
173 the whole occurrence dataset.

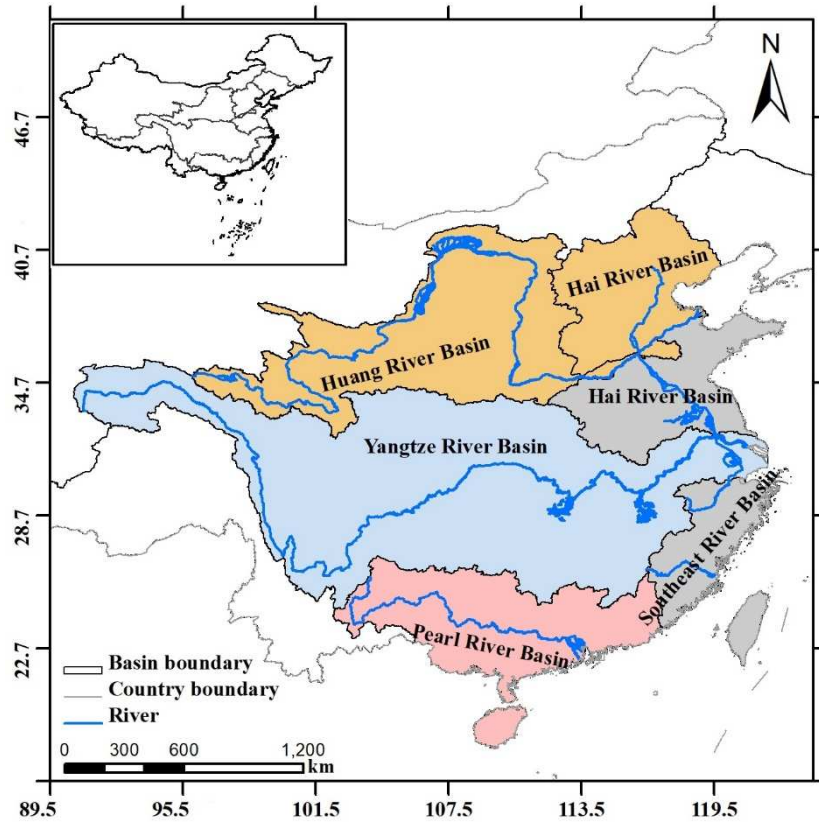


Figure 1. Location of the study basins

### 2.3 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

187 absence data are not available, pseudo-absence records with the same number of  
188 presence records within the local basin for each model scenario were generated using  
189 a random method that can exclude pixels in the presence locations ([Barbet-Massin et](#)  
190 [al. 2012](#)). Afterward, all the presence and pseudo-absence records were combined and  
191 shuffled for ultimate use in model construction ([Senay et al. 2013](#)). For each model  
192 algorithms, 70% of all records were randomly chosen for model calibration, and the  
193 remaining 30% was used to assess the algorithm performance. Each model algorithm  
194 was run 10 times to avoid bias from the splitting of the total records. The predictive  
195 abilities of each model were evaluated using the true skill statistic (TSS) and the area  
196 under the receiver operating characteristic curve (AUC) (Swets 1988). To ensure the  
197 optimal predictive ability, algorithms with a TSS score greater than 0.6 and AUC  
198 score greater than 0.8 ([Allouche et al. 2006](#)) were selected to develop ensemble  
199 models by the committee-averaged method. We also determined the relative  
200 importance of the selected predictors using an inbuilt randomization procedure  
201 ([Thuiller et al. 2016](#)) and the response curves of species occurrence for each algorithm  
202 using the evaluation strip method ([Elith et al. 2005](#)).

203

## 204 **2.2 Predictor selection**

205 The selection of predictors in SDMs can strongly affect the reliability of the  
206 predicted niche and spatiotemporal transferability ([Peterson et al. 2007](#)). Recent  
207 research tested 19 bioclimatic variables and 11 nonclimatic variables, including eight  
208 human-related variables, to predict the species distribution of the CGS for the whole

209 potential distribution area in China (Zhang et al. 2020a). Through analysis of the  
210 variable collinearity, contribution, and reasonability, four climate variables, and three  
211 nonclimatic variables were finally selected as important predictors and showed a good  
212 performance in distribution modeling and prediction of the species in that study. In the  
213 present study, however, as only about forty occurrence data points were used for  
214 model calibration for the HRB and PRB (70% of the whole presence and  
215 pseudoabsence data), we selected the four most important variables from the seven  
216 variables (see Table 1 in Zhang et al. (2020)) to meet the empirical rule of the use of a  
217 maximum of one predictor for ten data points to avoid overparameterization of the  
218 models(Harrell Jr et al. 1984, Petitpierre et al. 2017). The four predictors included  
219 three bioclimatic variables, i.e., the temperature seasonality (TS), the mean  
220 temperature of the coldest quarter (MTCQ), and the precipitation of the warmest  
221 quarter (PWQ) accessed from the WorldClim data website  
222 (<https://www.worldclim.org/data/index.html>), and the human population density  
223 (HPD) from SEDAC (<http://sedac.ciesin.columbia.edu>). Despite the small number of  
224 predictors, these four variables were regarded as the most relevant factors affecting  
225 the distribution of the CGS, as the contributions of the other three variables to  
226 species occurrence were all less than 5% (Zhang et al. 2020a). We used the four  
227 selected variables in the four basal model algorithms and ensemble models to predict  
228 current and future species distributions at the basin-scale and over the whole area.

229

## 230 **2.4 Model prediction and evaluation**

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

243 For real application and model evaluation, species presence and absence maps  
244 are required and obtained through transforming the continuous suitability predictions  
245 produced by SDMs to binary outputs using threshold values. We applied the mean of  
246 the predicted probabilities of species occurrences that can objectively maximize the  
247 agreement between observed and predicted distributions (Cramer 2003, Liu et al.  
248 2005), as the threshold to determine the species range (Zhang et al. 2020a). This  
249 method was suggested to be reliable in transforming SDM results from presence  
250 probabilities to presences/absences binary maps (Liu 2005, Liu et al. 2013, França  
251 and Cabral 2019). For each basin-scale model, the threshold was calculated separately,

252 and range sizes under current and future conditions were quantified based on the  
253 presence/absence map. The changes of the range size in the scenarios of HPD and  
254 climate changes relative to the current condition were calculated and compared  
255 among the three basins.

## 256 **3 Results**

### 257 **3.1 Model performance**

258 For each basin-scale model, most model algorithms performed well when  
259 assessed with AUC and TSS, with their median values being greater than 0.8 and 0.6,  
260 respectively (Supplementary Figure S1). Of the four model algorithms, RF always  
261 performed better compared to others for all basin-scale models. Among the 40 basal  
262 models, 31, 36, and 29 basal models were respectively selected to develop the  
263 ensemble SDMs for the HRB, YRB, and PRB (Table 1). For the model with all the  
264 occurrences for the whole area, it is not surprising that all basal models performed  
265 better compared to those in the basin-scale models, and all the basal models were  
266 retained to establish the ensemble models. However, the ensemble model for each  
267 basin-scale model also showed high accuracy, with  $AUC \geq 0.94$  and  $TSS \geq 0.80$  for  
268 all the basins, indicating that basin-scale ensemble models could be reliable in species  
269 distribution modeling. In terms of predicted mean probabilities (MP) of species  
270 occurrence (Table 1), the whole-area model performed slightly better for the YRB  
271 (0.93) than the YRB model (0.90). The predicted MP values for the HRB and PRB  
272 (0.75 and 0.79), however, were lower than those by the local basin models (0.83 and

273 0.88), indicating the improved capabilities of basin-scale models in modeling the local  
 274 distribution of the CGS.

275

276

277

278 **Table 1 Statistics of model performance, the number of models used in ensemble modeling**  
 279 **(NME), and the predicted mean probabilities (MP) of species occurrence. MP\_Basin: MP of**  
 280 **local species occurrence in each basin-scale model; MP\_Whole: MP of species occurrence in**  
 281 **each basin in the whole-area model; MP\_HuRB: MP of species occurrence in the Huai River**  
 282 **Basin in Basin-scale and whole-area models; MP\_SRB: MP of species occurrence in the**  
 283 **Southeastern River Basin in the basin-scale and whole-area models**

Models	AUC	TSS	NME	MP_Whole			
				MP_Basin	e	MP_HuRB	MP_SRB
	0.95	0.81					
M_HRB	2	2	31	0.83	0.75	0.73	0.40
	0.97	0.83					
M_YRB	5	3	36	0.90	0.93	0.84	0.83
	0.94	0.80					
M_PRB	4	4	29	0.88	0.79	0.62	0.82
M_Whole	0.98	0.86					
e	3	2	40	0.89	0.89	0.92	0.93

284

### 285 3.2 Variable importance and response curves

286 For the whole-area model, the importance of all four predictors was greater than  
 287 10%, with the MTCQ (32.6±2.5%) and HPD (26.8±1.9%) being more important than  
 288 the other two (Table 2). However, the allocation of the variable importance  
 289 considerably changed for the basin-scale models. For the HRB model, the most  
 290 important variable was the HPD (mean of 40.7%), while the MTCQ played a less  
 291 pivotal role (mean of 7.8%). The second-most important variable was the PWQ, and

292 the contribution of TS became less. The variable importance pattern produced by the  
 293 YRB model was similar to that of the whole-area model, despite a significant decrease  
 294 in the HPD (mean of 11.0%). The MTCQ was the most crucial factor for the species  
 295 occurrence in the YRB (mean of 37.8%), surpassing all other variables. The most  
 296 important predictor for the PRB was the PWQ (mean of 35.3%), while the HPD and  
 297 MTCQ were less important (both mean values were less than 8%). These results  
 298 revealed that the importance of each variable in the whole-area model seemed  
 299 balanced by the occurrences in different basins from north to south. The findings from  
 300 basin-scale models indicated that the environmental conditions affecting the  
 301 distribution and survival of populations in different basins were likely to greatly differ  
 302 from each other.

303 **Table 2 Variable importance (%) and the optimal range of the variables (species presence**  
 304 **probability>0.8) produced by different models. The units for the range of the TS, MTCQ,**  
 305 **PWQ, and HPD are Celsius, Celsius, millimeters, and people per km<sup>2</sup>, 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

306

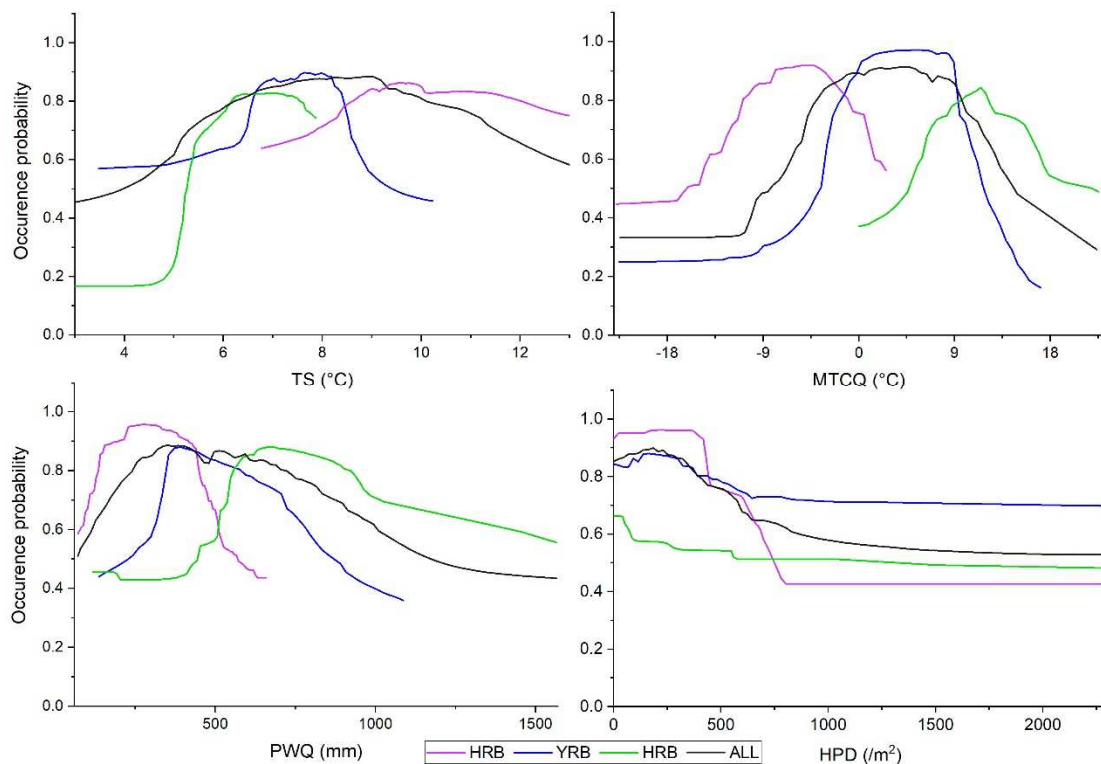
307 For each predictor, the response curves among different algorithms were similar  
 308 in all basin-scale models and the whole-area model ([Supplementary Figure S2](#)). A  
 309 comparison of the response curves produced by the ensemble models showed that the



310 species occurrence exhibited a unimodal response to three climate factors for all  
311 basins, but the responses were different among basins for each variable (Figure 2).  
312 This demonstrated that the curves of both the MTCQ and PWQ moved from the left  
313 to the right of the horizontal axis from the HRB to the YRB and the PRB, indicating  
314 that the requirements for these two variables were gradually enhanced for populations  
315 from north to south. The requirements for the TS of different populations, however,  
316 decreased from northern to southern basins. This revealed the response curves of the  
317 climate variables produced by the whole-area model failed to reflect the peak  
318 occurrence probabilities of different basins despite their wider range of high  
319 occurrence probabilities. The optimal ranges for the climate variables were distinctly  
320 different from each other, although they slightly overlapped between connected basins  
321 (Table 2). The optimal range increased for the MTCQ and PWQ and decreased for the  
322 TS from northern to southern basins. The optimal MTCQ for the HRB was less than  
323 the freezing temperature (-10.8~-1.1°C), while it was greater than 9°C for the PRB  
324 (9.6~12.1°C). The optimal range of the MTCQ, the most important variable for  
325 species in the YRB, was above and below 0°C for this basin (-1.5~9.1°C). As the most  
326 important variable for species in the PRB, the optimal PWQ (557.5~911.6 mm) was  
327 significantly greater than those in the other two basins. It should be noted that the  
328 whole-area model did not produce an optimal range covering those in HRB and PRB.  
329 For all basins, the occurrence probability decreased with the increase of the HPD  
330 (Figure 2), suggesting that the species is inclined to occur in regions where the HPD is  
331 less than 450 people in one square kilometer (Table 2). The requirement for human

332 interference of the species occurrence in the PRB is stricter, as HPD was less than 75  
 333 people per km<sup>2</sup> when its occurrence probability was above 0.6. Generally, the  
 334 requirements of the species distribution varied distinctly in different basins, especially  
 335 for climate factors, and these differences could only be detected by separate  
 336 basin-scale species distribution models.

337



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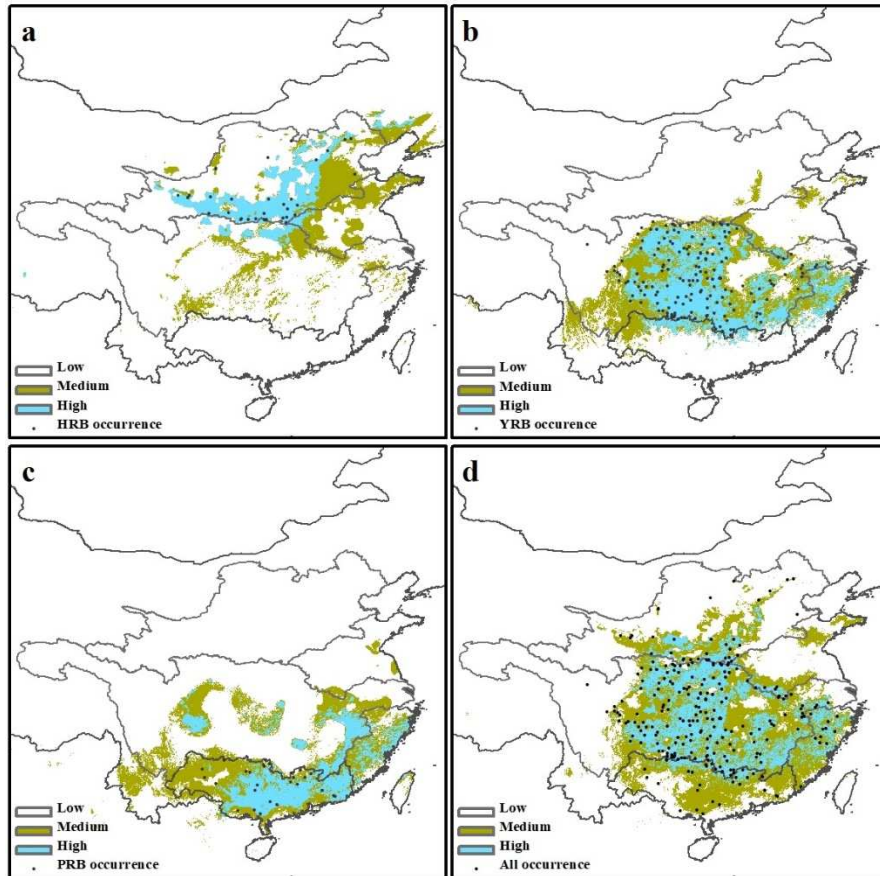
339 **Figure 2. Response curves of predictor variables for separate and whole populations**

340

### 341 **3.3 Current distribution**

342 The species occurrence probabilities predicted by the basin-scale models and the  
 343 whole-area model under current conditions were compared (Figure 3). Generally, the  
 344 species distribution areas predicted by the basin-scale model were constrained to local  
 345 basins, despite some areas with medium species occurrence probability transferred

346 around basin boundaries. Figure 4 shows that the range of the climate predictors  
347 clearly varied from northern to southern basins, which could have resulted in confined  
348 projections in local areas, considering the distinct responses of the species occurrence  
349 to climate factors (Figure 2). Comparisons showed consistent species distributions in  
350 the YRB predicted by the whole-area and YRB models (Figure 3b and 3d), but this  
351 was not observed in the basin-scale models in the HRB and PRB (Figure 3a and 3c).  
352 The mean occurrence probability of the species occurrence data predicted by the  
353 whole-area model was less than 0.8 (Table 1, 0.75 and 0.79 for the HRB and PRB,  
354 respectively), while it was 0.93 for the YRB, indicating that the whole-area model had  
355 a better performance for the YRB but a poor performance in predicting species  
356 occurrence for the HRB and PRB. As a result, compared with the local basin models,  
357 the whole-area model significantly underestimated the species distribution area by  
358 93.4% and 80.3% for the HRB and PRR, respectively. Therefore, these results implied  
359 that the basin-scale model could be locally adapted and would be better in projecting  
360 the CGS distributions in different basins.



361

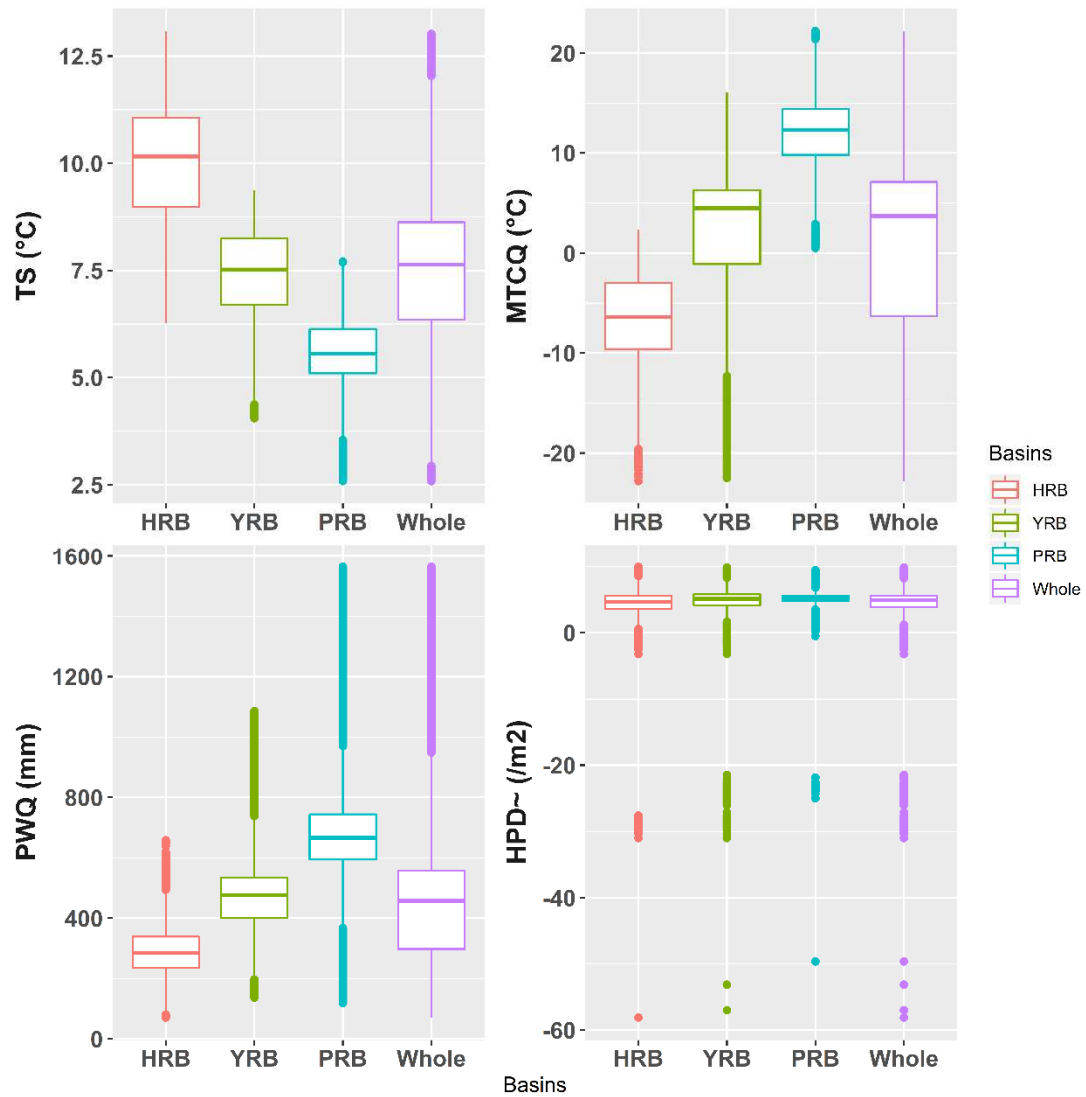
362 **Figure 3. Comparison of projected current occurrence probabilities for the basin-scale**

363 **models and whole-area model, with a, b, c, and d representing the modeling results of**

364 **the HRB, YRB, HRB and the whole basin, respectively. Low: occurrence probability**

365 **below 0.6; Medium: occurrence probability from 0.6 to MH in Table 1 (MH\_Basin);**

366 **High: occurrence probability from MH to 1.**



367

368 **Figure 4. Range comparison of the four predictors among the three basins and the whole**

369

**area**

370

### 371 **3.4 Species range shifts**

372 Future species distributions were predicted for separate basins using basin-scale

373 models ([Supplementary Figure S3](#)), and species range shifts were compared ([Figure](#)

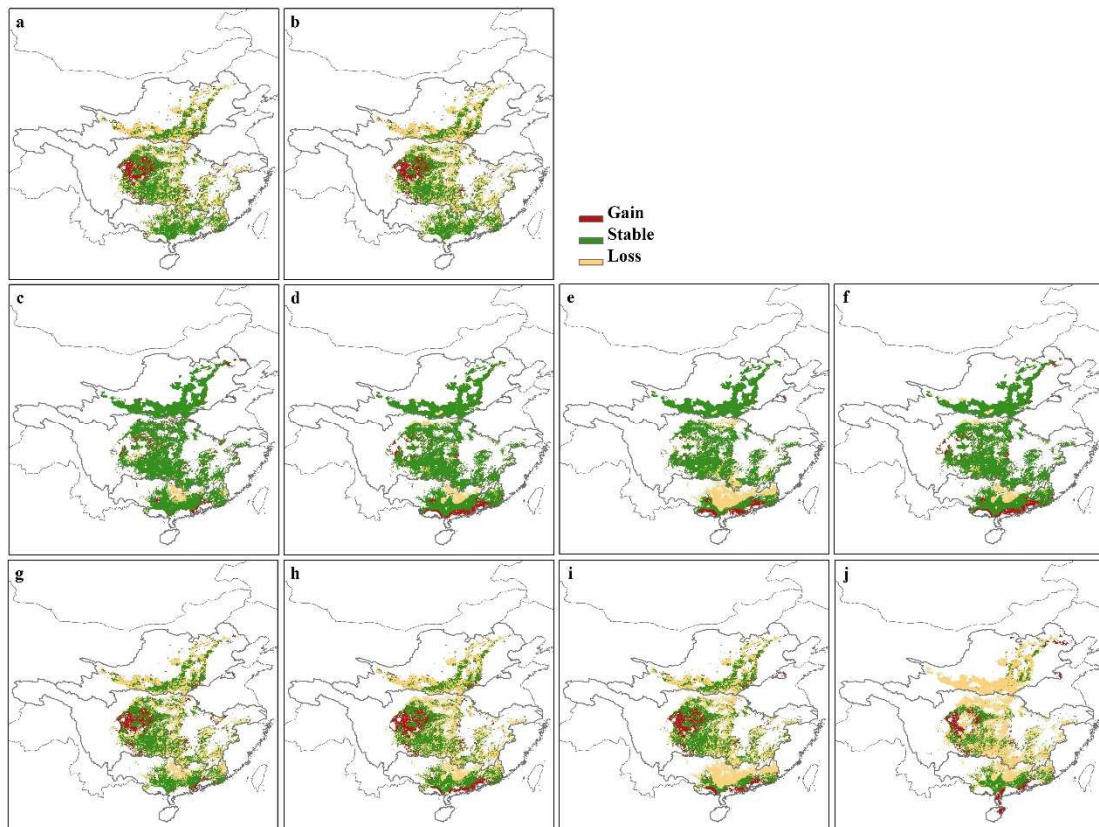
374 [5](#)). HPD change caused similar impacts on species distribution for the three basins in

375 both 2050 and 2070 ([Figure 5a, 5b](#)) and evidently decreased the species range by over

376 26% ([Table 3](#)), especially in the HRB (range loss of 55.8% and 61.3% in 2050 and

377 2070, respectively). Compared with the current status (Figure 3), future HPD changes  
378 would fragment the habitat in all the basins. The species range extended westward,  
379 and new habitat was gained in the YRB due to the impact of HPD change (Figures 5a  
380 and 5b). The species range was not obviously altered in the HRB and YRB due to the  
381 impact of climate change (Figures 5c-5f), and the species ranges were slightly  
382 decreased or even slightly increased (due to climate change with RCP2.6 in 2050,  
383 Table 3), excluding an obvious range loss of 11.0% in the YRB under climate change  
384 with RCP8.5 in 2050. The species range loss was obvious in the northern PRB, while  
385 the species ranges expanded southward to the coastal area of the PRB in the  
386 climate-change scenarios. The overall range loss in the PRB, however, was more  
387 significant in 2050 than in the 2070s in both RCP scenarios (Table 3). When  
388 overlapping the impacts from HPD and climate changes, the range loss was  
389 aggravated in RCP 8.5 scenarios for all basins (Figure 5i, 5j), especially in 2070 with  
390 stable habitat nearly disappearing in the HRB and only remaining in the west and the  
391 south coast, respectively, in the YRB and PRB (Figure 5j). The maximum losses of  
392 species ranges in the HRB, YRB, and PRB were 83.4%, 60.0%, 53.5%, respectively,  
393 indicating a significant negative impact of the combined effect of HPD and climate  
394 changes on the species distributions. Despite this, slight offset effects induced by  
395 climate change with RCP 2.6 were identified in the HRB and YRB (Table 3).  
396 Generally, the effects of HPD and climate changes on species ranges varied among  
397 watersheds and periods. HPD variation was likely the most influential factor that  
398 engendered negative impacts on species distributions in all three basins, especially in

399 the HRB. Climate change was probably less prominent in decreasing the species  
400 range, excluding the YRB and PRB in high emission scenario in 2050. Overall, the  
401 high-emissions scenario would more significantly aggravate the negative impacts  
402 produced by HPD change under the superimposed impacts of future climate changes  
403 and human pressures.



404

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

411

412 **Table 3. The relative losses of species ranges (%) for the three basins in different scenarios.**

413 **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*	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

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

## 417 **4 Discussion**

### 418 **4.1 Model comparison and consideration**

419 In the present study, we selected the most important variables based on the model  
 420 that used all species occurrence records across the whole study area. We used the  
 421 same variables in the basin-scale models to make the models in separate basins  
 422 comparable. Only four variables were used to avoid overparameterization because of  
 423 the relatively limited occurrence records in the HRB and YRB. Although we  
 424 acknowledge that the species occurrence size in these two basins was tiny and that the  
 425 inference ability of the SDM could be subsequently influenced, previous studies



426 indicated that SDMs based on small samples size can also produce useful predictions  
427 (Hernandez et al. 2006, Wisz et al. 2008, Zhang et al. 2020b). Given the assumed  
428 niche transferability of SDMs, projections in space could be useful in identifying  
429 potential distributions in other geographical regions (Randin et al. 2006, Wenger and  
430 Olden 2012). However, the differences of environmental conditions among different  
431 study regions can be distinct in species' range, thus, the regional model can result in a  
432 generally low transferability across regions. It should be noted that the aim of this  
433 study was not to explore the model transferability of different regional models but to  
434 probe local differences in species distribution responses to environmental changes,  
435 specifically for the CGS that have a limited dispersal ability and distinct population  
436 divergence among basins. We found distinctly different responses of species  
437 occurrence to climate conditions and similar responses to HPD among the three basins  
438 (Figure 2), which could be an adaptation to local environments (Figure 4).  
439 Additionally, our results showed that species distribution area from the whole-area  
440 model did not completely cover the species occurrences in the HRB and YRB (Figure  
441 3d), while their occurrence probability was corrected to be higher by the local basin  
442 models, indicating that the local model could outperform the whole-area model.  
443 Considering the additional finding that basin-scale models could provide more detail  
444 about species distribution, basin-scale models that incorporated local adaption were  
445 suggested as more reasonable model strategies. However, to improve or validate the  
446 ability of the model to predict species distribution, independent geographically or  
447 temporally separated data should be collected (Bahn and McGill 2013). Considering

448 the difficulty and high cost of field investigation, the emerging environmental DNA  
449 method can be employed to determine the presence in the potential distribution area  
450 of the CGS predicted by our study and incorporate the data into future SDM work.

451         Selecting a model-specific threshold to transform model outputs into binary  
452 presence/absence maps has been essential in various aspects of conservation  
453 applications and management (Guisan et al. 2013). Maximizing the sum of sensitivity  
454 and specificity (*MaxSSS*) is regarded as an efficient method for threshold selection for  
455 presence-only SDMs when compared with various other existing methods (Liu et al.  
456 2013), and this method is also commonly used in real applications. However, it is  
457 stated that specificity and commission error cannot be calculated without true absence  
458 data when using the *MaxSSS* method to select the threshold (Braunisch and Suchant  
459 2010). In this study, we tested the *MaxSSS* method to generate the binary map for all  
460 three separate basins and the whole area and found the resulted presence area of the  
461 CGS continuously spread over almost all of the basins. The predicted distribution  
462 distinctly deviated from the real distribution of this species that is limited in dispersal  
463 ability and has a habitat highly impacted and isolated by human modification of the  
464 environment. It is indicated that the predicted distribution generated by *MaxSSS* could  
465 not characterize the potential distribution if information about the biotic and  
466 anthropogenic factors that affect the distribution of specific species is not  
467 incorporated in the SDM (Liu et al. 2013). For a given species with populations that  
468 are geographically confined due to dispersal limitation or species interactions,  
469 the occupied geographic range will be smaller than its full potential distribution

470 (Leathwick 1998, Svenning and Skov 2004, Soberon and Arroyo-Pena 2017).  
471 Furthermore, limited climate availability is also expected to reduce the fundamental  
472 niche to a smaller realized niche (Soberón and Nakamura 2009). Although no direct  
473 biotic and human factors were considered in our model, we constrained the model  
474 area in the separate basin for this species with a limited dispersal ability and included  
475 the human population as an important predictor in the model. Therefore, we  
476 hypothesized that our model-estimated distribution was closer to the realized  
477 distribution, which is more consistent with the actual distribution of the CGS. To  
478 achieve this, we used a more rigorous threshold, which was the predicted mean  
479 probability of the occurrence data, for the studied critically endangered species.  
480 Satisfactory agreements between occurrence sites and the predicted high occurrence  
481 probabilities were also achieved with this method (Figure 3, Table 1). The predicted  
482 current species distribution was also generally consistent with the results from the  
483 county-scale habitat model produced by Chen et al. (2018). Further work is still  
484 needed to test and compare other threshold methods (e.g. kappa maximization and  
485 prevalence approaches) (Liu 2005) to select the optimal thresholds for different basins  
486 to better support model evaluation and application.

487

#### 488 **4.2 Difference among populations in local basins**

489 Our research revealed a distinct response variation of species occurrence to  
490 climate factors from northern to southern basins. As the basins changed from  
491 temperate areas to subtropical monsoon regions, the preferred MTCQ and PWQ of the

492 CGS were found to increase (Figure 2) with increases in the air temperature and  
493 precipitation from north to south. As the HRB is a mountainous region with complex  
494 landforms and is partly controlled by a continental dry climate, its annual temperature  
495 differences are very large (Lu et al. 2014). This may explain why the preferred TS of  
496 the CGS in the HRB was higher than those in the other two basins. For the studied  
497 ancient animal with poor dispersal potential, mountains and rivers blocked its  
498 migration with the formation and evolution of geographic structures, which has led to  
499 a rather high level of population differentiation in different geographic regions (Liang  
500 et al. 2019). At the same time, the distributions of the species could have adapted to  
501 local climate conditions, as indicated by our research. Such local adaptation evidence  
502 was also shown in the difference in the contributions of climate factors to species  
503 occurrence (Table 2). The most important climate factor in the HRB and PRB was the  
504 PWQ, while it was the MTCQ in the YRB. Like most amphibians, the CGS needs to  
505 hibernate in cold months to reduce energy consumption and protect them from the  
506 frozen period. Unlike the HRB and PRB, where the preferred MTCQ of CGS  
507 occurrence is either below-zero temperatures or higher-than-zero temperatures (Figure  
508 2), the optimal range of the MTCQ in the YRB is around the freezing temperature  
509 (Table 2), revealing that the CGS in the YRB could be more sensitive to the variation  
510 of winter temperatures required for hibernating. As the breeding month of the CGS is  
511 mainly in wet June and July and the quantity of precipitation is a dominant factor  
512 influencing the biomass and health of aquatic ecosystems (Grimm et al. 2013), a  
513 suitable PWQ could afford a suitable habitat and enough food for CGS reproduction

514 in the HRB and PRB. Although the TS was found to be relatively less important to  
515 CGS occurrence in the three basins, studies revealed that the seasonal variation of  
516 climatic conditions may influence the phenology and spatial distributions of  
517 salamanders (Kirk et al. 2019).

518 As the life attributes of ectothermic animals are highly linked to the climate,  
519 climate change may cause profound impacts on salamanders (Bartelt et al. 2010).  
520 However, as indicated in this study, future HPD variations were primarily accountable  
521 for the loss of the species' range, especially for the HRB, where HPD played an  
522 important role in the occurrence of the species. Future increasing human populations  
523 may advance the harvesting rate of the CGS, where it is popularly believed that they  
524 are nutrient-rich foods. As salamanders have low dispersal abilities and rigorous  
525 habitat requirements, they are susceptible to human-induced environmental changes  
526 (e.g., urbanization and river reconstruction) (Price et al. 2011). The obvious range loss  
527 of the CGS resulting from future HPD changes will probably be caused by the  
528 booming expansion of urban areas in China in the future. As the CGS prefers to live  
529 in habitats with clean and fast-flowing waters(Chen et al. 2018), urbanization can  
530 destroy suitable habitats by changing the land cover, altering catchment hydrology,  
531 and contaminating river water (Price et al. 2011). Additionally, our study revealed  
532 distinct habitat fragmentation caused by HPD change, which would decrease the  
533 genetic diversity of populations by obstructing movement among species ranges  
534 (Marsh et al. 2005) and ultimately increase the risk of species extinction (Noël et al.  
535 2006).

536

### 537 **4.3 Insights for conservation and management**

538 The endangered CGS has attracted considerable conservation attention, while the  
539 baseline data on its distribution status is often limited for identifying conservation  
540 activities and management policies (Fellowes et al. 2009). The spatiotemporal species  
541 distribution produced by our study could provide helpful guidance to surveys of the  
542 species' presence and could detect key habitats and populations throughout its ranges.  
543 Setting up nature reserves has been acknowledged as an effective strategy for  
544 protecting natural populations of the CGS (Liang et al. 2013). However, effective  
545 management to prohibit human access to habitats has been lacking in some of the  
546 protected areas (Pan et al. 2015). Our research elucidated that future HPD change  
547 would result in a significant range loss of the CGS, which is basically following the  
548 accepted view that their population decline in the wild is primarily attributed to  
549 human-induced habitat destruction and overexploitation. Therefore, tighter measures  
550 that prevent human interference should be addressed, especially for the existing nature  
551 reserves of the CGS. To do this, public education campaigns should be enhanced to  
552 provide better information about the survival status of the CGS and the importance of  
553 conserving their habitat. The government should implement severer penalties and  
554 regulations to prohibit hunting wild CGS. We recognize that climate change would  
555 induce relatively fewer negative impacts on the CGS distribution; however, it is likely  
556 to evidently aggravate the adverse impacts from human pressure in the future.\, as  
557 indicated in our study. Therefore, climate factors that heavily influence the habitat and

558 survival of the CGS should not be neglected when formulating conservation  
559 measures.

560 We revealed local differences in climate variable importance and range shift  
561 responses to HPD and climate changes among the three basins using basin-scale  
562 models. Therefore, we suggest that local adaptive management strategies should be  
563 employed for populations in different regions in the future. For the HRB, it is  
564 especially important to eliminate the impact of human activities on the habitat of the  
565 CGS, as the variation of the used human-related factor would cause distinct range loss.  
566 For this relatively dry basin, we reported that precipitation in the wet season is a  
567 dominant climate factor since it may affect its breeding activities. Water  
568 replenishment to the key habitat streams and rivers in the reproduction season could  
569 be an effective measure. If no urgent conservation measures are implemented, the  
570 suitable habitats would be devastated by HPD and climate changes (Figure 5j). For  
571 the YRB, we advocate strengthening the conservation of existing nature reserves, as  
572 most of them are in this basin, and new reserves could be established in the west of  
573 the range since the habitat there is more stable; thus, new habitats would be colonized  
574 in this region with the changes of HPD and the climate (Figure 5). Mitigating the  
575 environmental temperature in the winter is needed for the reserves, as the temperature  
576 is crucial in influencing the hibernation of the CGS. For the PRB, compared to the  
577 impact of human pressure, climate change would seriously reduce the species range in  
578 the northern part of the basin, although new habitat could be gained in the south  
579 (Figure 5c-5f). This would force the habitat and populations in the PRB to be more

580 isolated from those on the north side. As precipitation in the wet season was found to  
581 be notably more important for species occurrence compared to other climate factors  
582 and the human factor, similar measures in the HRB should be particularly enforced to  
583 support the successful breeding of the species. As the species ranges of the three  
584 basins would distinctly be detached from each other in the future (Figure 5g-5j),  
585 specific mitigation strategies at the population level should be further addressed in  
586 future studies, and our findings concerning the local adaptation differences of species  
587 ranges provide beneficial information.

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

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