ORIGINAL ARTICLE

Future climate change will severely reduce habitat suitability of the Critically Endangered Chinese giant salamander

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Abstract

1. Being the largest extant amphibian in the world, the IUCN Critically Endangered Chinese giant salamander *Andrias davidianus* is a charismatic species with great international public interest. While threats such as commercial overexploitation and habitat degradation have been extensively documented to affect natural populations of *A. davidianus*, still no information is available about the species sensitivity to climate change.

2. Here, we develop an ensemble of species distribution models (SDMs) for *A. davidianus* and projected its habitat suitability under present-day and future climate change scenarios. We based our SDMs on bioclimatic and topographic predictors, and recent (2012–2018) field-collected occurrence data across the whole distribution range of the species.

3. The ensemble SDMs exhibited good predictive capacity and suggested that slope, maximum temperature of warmest month, precipitation of driest month, and isothermality are the most influential predictors in determining distribution patterns in this species. The projections of our models point to a pronounced impact of climate changes over *A. davidianus*, with more than two-thirds of its suitable range expected to be lost in all scenarios of future climates tested.

4. In concert with the numerous other threats that are affecting this species, climate change poses a serious hindrance to the long-term survival of *A. davidianus*. We emphasise the urgent need of undertaking strict measures to manage this species and safeguard the few remaining available suitable habitats. We suggest that adaptive management strategies including designation of new reserves should be considered to mitigate the impacts of climate change on *A. davidianus*.

KEYWORDS

Andrias davidianus, global warming, habitat contraction, species distribution model, potential distribution

1 | INTRODUCTION

As one of the most serious global environmental concerns, climate change poses multiple threats to terrestrial (Burrows et al., 2011), freshwater (Mantyka-Pringle, Martin, Moffatt, Linke, & Rhodes, 2014), marine (Burrows et al., 2011; Dulvy et al., 2008), and subterranean ecosystems (Mammola, Piano, et al., 2019), encompassing habitat change, biodiversity loss, alterations in species interactions, and shifts in species phenology (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012; Parmesan, 2006). For instance, previous

studies have demonstrated that in response to global warming, terrestrial species are shifting their distribution towards higher altitudes or latitudes (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011) and marine species are even migrating to deeper waters (Dulvy et al., 2008). For the purpose of better conserving and managing biodiversity, it is of great urgency and significance to understand how future climate change will influence species distributions. In the past 2 decades, species distribution models (SDMs) have emerged as one of the most effective techniques to investigate the impact of climate change on species habitat suitability (Elith & Leathwick, 2009; Guisan & Thuiller, 2005; Guisan, Thuiller, & Zimmermann, 2017; Guisan & Zimmermann, 2000; Phillips, Anderson, & Schapire, 2006). Accordingly, the use of SDMs in conservation biology and biodiversity assessments is ever-increasing (Araújo et al., 2019).

Amphibians represent the most threatened vertebrate group in the world (Heatwole, 2013; Stuart et al., 2004). Out of 6,771 amphibian species assessed in the IUCN Red List of Threatened Species, 2,157 are listed in one of the Endangered categories (CR, EN, VU), while 34 species are considered to be either extinct or extinct in the wild (IUCN, 2019). Many factors have been targeted as responsible for amphibian population declines, including overexploitation, pollution, habitat degradation and destruction, diseases, invasive species, and climate change (Heatwole, 2013; IUCN, 2019; Li, Cohen, & Rohr, 2013; Stuart et al., 2004). Amongst these, climate change is regarded as one of the most important drivers of amphibian extinction. Concerns over the fate of amphibian in a climate change perspective, have recently encouraged more conservation scientists to develop SDMs for estimating future shift and contractions in amphibian distributions (e.g. D'Amen et al., 2011; Duan, Kong, Huang, Varela, & Ji, 2016; Milanovich, Peterman, Nibbelink, & Maerz, 2010; Ochoa-Ochoa, Rodríguez, Mora, Flores-Villela, & Whittaker, 2012; Popescu, Rozylowicz, Cogălniceanu, Niculae, & Cucu, 2013). For instance, Duan et al. (2016) investigated possible effects of climate change on habitat suitability of 134 amphibian species in China via SDMs. Their results highlighted that future climate change will probably result in large shifts in amphibian habitat suitability, thus determining substantial change in patterns of amphibian diversity in China. Milanovich et al. (2010) developed SDMs for 41 plethodontid salamander species in the Appalachian Highlands of the eastern U.S.A., pointing out that climate change diminishes their habitat suitability in the future.

The Chinese giant salamander *Andrias davidianus* (Blanchard, 1871; Amphibia: Cryptobranchidae) is the largest extant amphibian species in the world and is mainly distributed in central and southern China (Fu, 1993). The species is entirely aquatic and normally inhabits fast-flowing streams and rivers with abundant shelters or dens such as holes, rocks, and bedrock crevices (Browne et al., 2014; Luo, Song, et al., 2018) (Figure S1). During the reproductive season, females lay eggs in their dens, and males guard eggs until they are hatched (Luo, Tong, et al., 2018). Given that this species generally breeds in caves and other underground voids, *A. davidianus* is regarded as a facultative subterranean species (Liang et al., 2019; Luo, Zhang, Liu, Chen, & Gan, 2009). *Andrias davidianus* is a Critically Endangered species (IUCN, 2019; Turvey et al., 2018) and is listed in the Appendix I of Convention on International

Trade in Endangered Species of Wild Fauna and Florax. Despite its threatened status, few studies have explored the sensitivity of *A. davidianus* to climate change (Chen et al., 2018; Chen, 2013). Chen (2013) evaluated habitat suitability of 51 amphibians, including *A. davidianus*, in southern and central China by ecological niche factor analysis. In addition, Chen et al. (2018) developed a habitat suitability model for this species and predicted its present-day potentially suitable habitat. To the best of our knowledge, no study has investigated potential impacts of future climate change on the habitat suitability for *A. davidianus* yet.

We structured our study under the hypothesis that climate change will result in range contraction of *A. davidianus*, meanwhile pushing this species to higher altitudes and/or latitudes. To explore this hypothesis, we developed SDMs for *A. davidianus* by using climatic and topographic variables to: (1) assess its environmental requirements; (2) predict its habitat suitability under current climate conditions; and (3) forecast its habitat suitability under different future climate scenarios. Being the first attempt to study climate change impacts on habitat suitability of *A. davidianus*, this study provides important guidance for future conservation strategies of this unique, charismatic, and severely threatened amphibian.

2 | METHODS

2.1 | Study area and species occurrence records

Previous studies have demonstrated that the extent of study area (accessible area) plays a critical role in the calibration of SDMs (Barve et al., 2011; VanDerWal, Shoo, Graham, & Williams, 2009). Our study area is located in central and southern China, ranging from 100 to 124°E and 23.5 to 36°N (Figure 1). We determined the extent of the accessible area by considering the known geographical distribution of *A. davidianus* (Fu, 1993; Liang et al., 2019), and the distribution predicted by a previous SDM study focusing on this species (Chen et al., 2018).

We assembled a database of recent georeferenced occurrence records of *A. davidianus* in China, based on field surveys performed between 2012 and 2018. With the aid of local management agencies of *A. davidianus*, we recorded the presence of the species in both rivers and from natural populations breeding in caves. In fact, while this is mostly a surface-dwelling species, 11 natural breeding caves of *A. davidianus* have been reported in five provinces in China over the past 15 years (Liang et al., 2019; Liang, Zhang, Wang, Wei, & Wu, 2013; Luo et al., 2009). As a result of the sampling activities, we assembled a dataset of 50 spatially unique occurrence records, scattered through 15 provinces in China (Table S1).

To minimise sampling bias effect in our dataset (Boria, Olson, Goodman, & Anderson, 2014), we randomly selected only one record per each 5 × 5 arcmin grid cell (9.2 × 9.2 km at the equator), i.e. the resolution of our environmental predictors. This resulted in 44 occurrence records being retained for model calibration. Although we acknowledge that the sample size is small and that the ultimate strength of the SDM inference may be affected as a result (e.g.
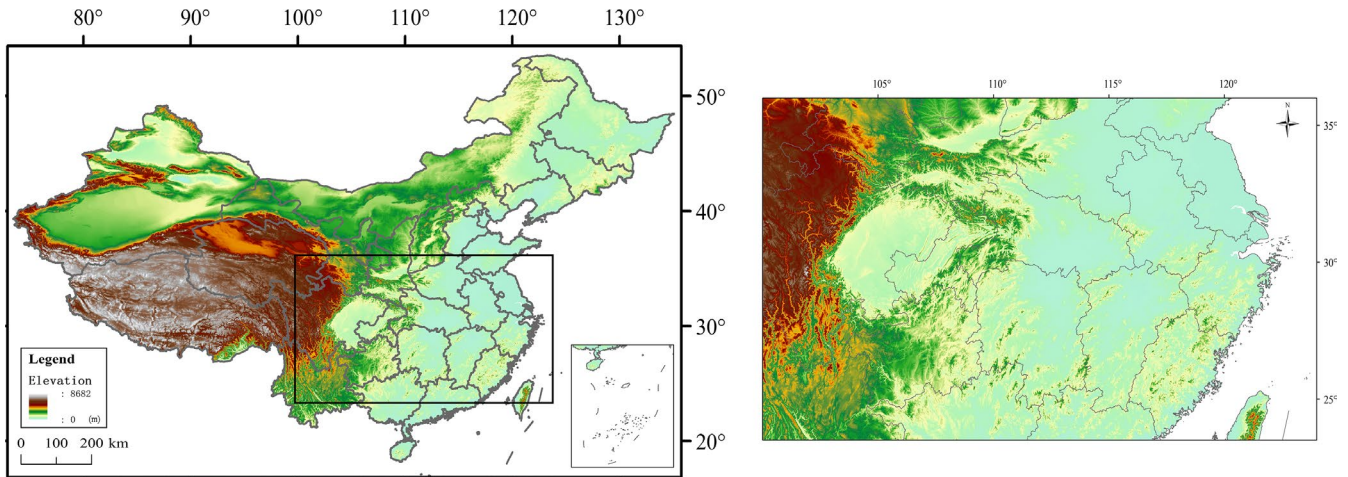
FIGURE 1 Map of the study area

Hernandez, Graham, Master, & Albert, 2006; Wisz et al., 2008), previous studies revealed that SDMs based on small sample size can also provide useful predictions (Hernandez et al., 2006; Pearson, Raxworthy, Nakamura, & Townsend Peterson, 2007).

2.2 | Environmental predictors

We downloaded the current land surface climatic data with a resolution of 30 arc-second from CHELSA (available at http://chelsa-clima te.org), which contains average values of 19 predictor variables for the time period 1979–2013 (Karger et al., 2017; Table S2). In addition, we obtained elevation and slope at 30 arc-second resolution from EarthEnv (available at http://www.earthenv.org/topography; Amatulli et al., 2018). We resampled all variables to 5 arc-minutes. For the purpose of reducing the effect of multicollinearity, we calculate pairwise Pearson's correlation coefficients r amongst the 21 predictor variables. When two or more predictors had a $|r| > 0.70$ (Dormann et al., 2013), we only included one of them in our model.

We generated projections of future climates for two periods, 2050 (average for 2041–2060) and 2070 (average for 2061–2080), under two representative concentration pathways (RCPs) scenarios (i.e. RCP 2.6 [an optimistic scenario] and RCP 8.5 [a pessimistic scenario]) from six widely used global circulation models (GCMs): BCC-CSM1-1, HadGEM2-ES, IPSL-CM5A-LR, MRI-CGCM3, MIROC-ESM-CHEM, and NorESM1-M. We retrieved all future climate projections from WorldClim (http://www.worldclim.org; Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). We assumed elevation and slope to remain constant in the considered time periods. To reduce uncertainties amongst different GCMs, we averaged projections of six GCMs as future climates to map future habitat suitability of *A. davidianus*.

2.3 | Modelling procedure

To predict current habitat suitability of *A. davidianus*, we used an ensemble modelling approach of 10 algorithms: artificial neural

networks, classification tree analysis, flexible discriminant analysis, generalised additive model, generalised boosting model, generalised linear model, multiple adaptive regression splines, maximum entropy, random forests, and surface range envelope (Thuiller, Georges, Engler, & Breiner, 2019). For algorithms requiring species absence records, we generated 10,000 pseudo-absences for the species using a common strategy of randomly selecting pseudo-absences from across the study area (Guisan et al., 2017; Merow, Smith, & Silander, 2013; Phillips et al., 2006). We evaluated predictive performances of the 10 algorithms by a five-fold cross-validation approach, in which 80% of data were randomly chosen for model construction and the remaining data were held for model test (Guisan et al., 2017; Thuiller et al., 2019). We used two performance criteria, true skill statistics (TSS) and area under the receiver operating characteristic curve (AUC), to measure the predictive performance of the 10 algorithms (Allouche, Tsoar, & Kadmon, 2006; Swets, 1988). Algorithms with TSS > 0.60 and AUC > 0.80 were considered to have good predictive performance (Allouche et al., 2006; Gallien, Douzet, Pratte, Zimmermann, & Thuiller, 2012; Swets, 1988). We used the selected algorithms to evaluate relative contributions of predictor variables in determining the distribution of *A. davidianus* and to project its habitat suitability. We determined the relative contribution of each predictor by a randomisation method (Guisan et al., 2017; Thuiller et al., 2019). Response curves of the most important predictor variables were also estimated. We predicted habitat suitability of *A. davidianus* under current and future climates by using all occurrence and pseudo-absence data. We ensembled predictions of selected individual algorithm via a committee averaging algorithm (Guisan et al., 2017; Thuiller et al., 2019). Dispersal plays an important role in determining species distribution (Guisan & Thuiller, 2005; Guisan et al., 2017). However, *A. davidianus* still remains poorly understood and we lack precise estimation of its dispersal potential. As with previous studies, we assume unlimited dispersal ability (no dispersal limitation) when estimating changes in species habitat suitability (Araújo, Thuiller, & Pearson, 2006; Boulangeat, Gravel, & Thuiller, 2012; Schweiger, Settele, Kudrna, Klotz, & Kühn, 2008). We acknowledge that this assumption may overestimate establishment of

species in new areas (Araújo et al., 2006; Boulangeat et al., 2012; Schweiger et al., 2008), but such projections are still helpful to advance our understanding of climate change impacts. For a better interpretation of model outcomes, continuous habitat suitability projections were converted into binary maps (i.e. suitable/unsuitable) by using a threshold maximising the TSS value (Guisan et al., 2017; Liu, White, & Newell, 2013).

We counted the number of raster cells classified as suitable to estimate changes in range size between present and future climate conditions (Thuiller et al., 2019). In addition, we extracted elevation of suitable raster cells and evaluated changes in altitudinal distribution of *A. davidianus* between present and futures scenarios with Mann–Whitney *U* tests. Finally, we determined centroids of present and future binary SDM projections via the *gCentroid* function in the *rgeos* R package (Bivand & Rundel, 2018). The distance and direction between present and future centroids were used to estimate how the future distribution range will shift in respect to present one.

3 | RESULTS

3.1 | Model performances and contributions of predictor variables

According to the results of multicollinearity analysis, we selected nine predictor variables to develop SDMs for *A. davidianus*: annual mean temperature, mean diurnal range, isothermality, maximum temperature of warmest month, temperature annual range, annual precipitation, precipitation of driest month, precipitation of warmest quarter, and slope (Figure S2). Predictive performances of the 10 modelling algorithms are presented in Table 1. Two modelling algorithms (generalised boosting model and maximum entropy) clearly outperformed the others in terms of predictive power (Table 1), and therefore were used for calibrating the final models. Mean (± *SE*) TSS and AUC values of ensemble models built by the two algorithms were 0.745 (±0.014) and 0.887 (±0.006), respectively, which are superior to single modelling algorithms.

Amongst the nine selected predictor variables, slope emerged as the most influential variable, followed by maximum temperature of warmest month, precipitation of driest month, and isothermality (Table 2). Annual mean temperature, mean diurnal range, and annual precipitation contributed little to the distribution of *A. davidianus* (Table 2). Response curves of the four most important predictors indicate that *A. davidianus* occurs mainly in areas with slope ranging from approximately 8.7 to 22.5°, maximum temperature of warmest month between about 24.6 and 30.1°C, precipitation of driest month between 21.3 and 40.2 mm, and isothermality <21 (Figure 2).

3.2 | Habitat suitability under current and future climates

Habitat suitability of *A. davidianus* under current climate conditions is presented in Figure 3. SDM projection suggests that the current

TABLE 1 Predictive abilities of 10 modelling algorithms used to estimate habitat suitability of the Chinese giant salamander *Andrias davidianus*

Modelling algorithm	AUC	TSS
Artificial neural network	0.743 ± 0.025	0.500 ± 0.041
Classification tree analysis	0.750 ± 0.020	0.489 ± 0.044
Flexible discriminant analysis	NA	NA
Generalised additive model	0.783 ± 0.034	0.555 ± 0.061
Generalised boosting model*	0.863 ± 0.013	0.691 ± 0.026
Generalised linear model	0.747 ± 0.033	0.549 ± 0.052
Multiple adaptive regression splines	0.692 ± 0.030	0.385 ± 0.061
Maximum entropy*	0.861 ± 0.015	0.668 ± 0.027
Random forest	0.760 ± 0.022	0.514 ± 0.042
Surface range envelope	0.721 ± 0.017	0.441 ± 0.034

Note: Algorithms marked with asterisks (*) showed good predictive performance and were selected to develop the ensemble model. Results are expressed as mean ± *SE*. NA (missing data) indicates algorithms that failed to converge.

Abbreviations: AUC, area under the receiver operating characteristic curve; TSS, true skill statistics.

TABLE 2 Relative contributions of the nine selected predictor variables in the ensemble model of habitat suitability for the Chinese giant salamander *Andrias davidianus*

Predictor variable	Contribution
Slope	0.416 ± 0.019
Maximum temperature of warmest month	0.258 ± 0.017
Precipitation of driest month	0.218 ± 0.018
Isothermality	0.198 ± 0.017
Temperature annual range	0.152 ± 0.016
Precipitation of warmest quarter	0.067 ± 0.010
Annual precipitation	0.031 ± 0.007
Mean diurnal range	0.028 ± 0.007
Annual mean temperature	0.110 ± 0.003

Note: The results are expressed in descending order of relative contributions. Data are expressed as mean ± *SE*.

suitable habitat for this species is mainly located in central China, including Chongqing City, Shaanxi, Henan, Hunan, Hubei, and Guizhou provinces (Figure 3). Besides, small areas in Anhui, Jiangxi, Zhejiang, Sichuan, Yunnan, Guangxi, and Gansu provinces are also predicted to be suitable for *A. davidianus* (Figure 3).

Despite the fact that projections of future habitat suitability for *A. davidianus* varied depending on the GCMs and RCPs used, they consistently pointed to severe range contraction under future climates (Figure 4). Model projections indicate that range contraction of this species could be from 55.1% (under MRI-CGCM3 climate model and RCP 8.5 scenario) to 83.0% (under HadGEM2-ES climate model and RCP 8.5 scenario) in 2050, and from 53.1% (under MRI-CGCM3 climate model and RCP 2.6 scenario) to 92.6% (under IPSL-CM5A-LR climate model
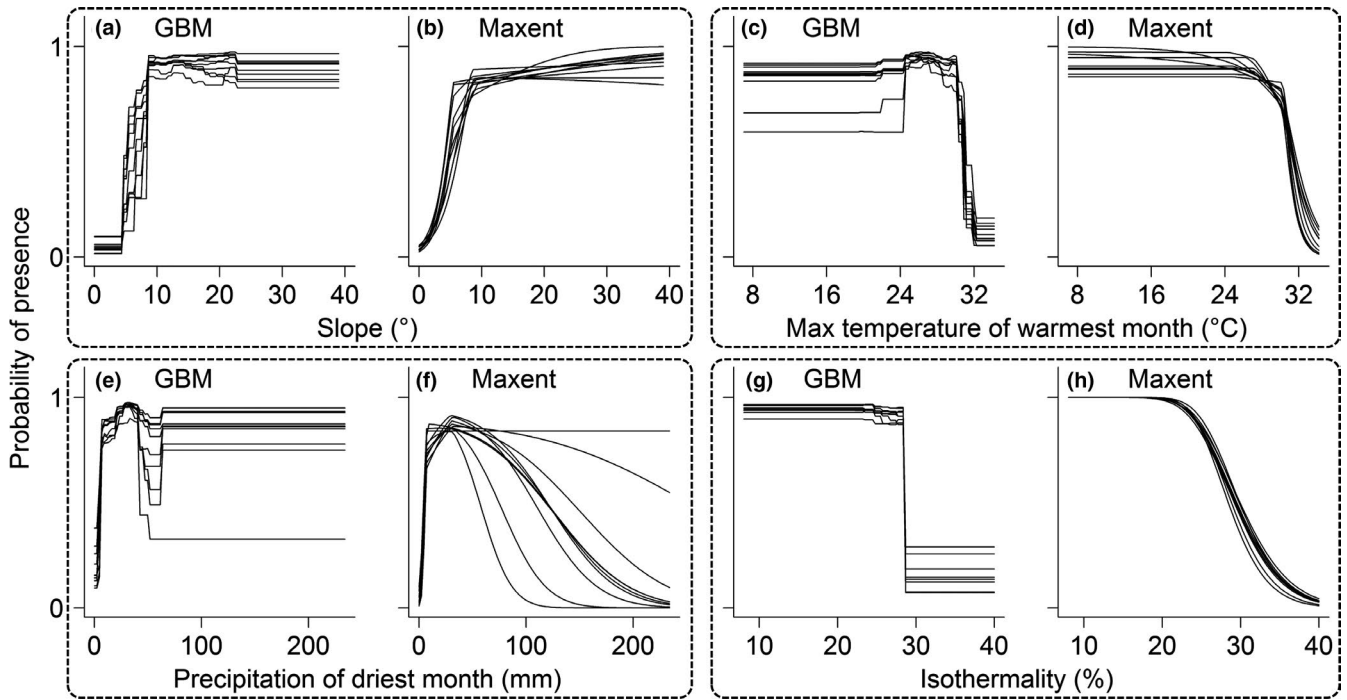
FIGURE 2 Response curves of predicted occurrence probability of *Andrias davidianus* against slope, maximum temperature of warmest month, precipitation of driest month, and isothermality. GBM, generalised boosting model; Maxent, maximum entropy
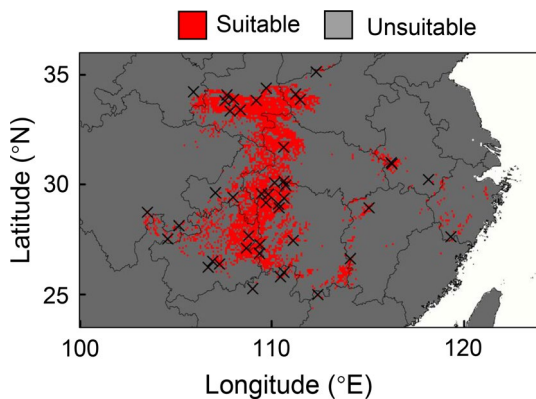

FIGURE 3 Binary output of habitat suitability of *Andrias davidianus* under current climate conditions. Red colour indicates suitable area and grey colour represents unsuitable range. Black crosses represent occurrence points used to develop species distribution model

FIGURE 4 Range size change of *Andrias davidianus* in (a) 2050 and (b) 2070. The labels on the *x*-axis represent different global circulation models. bc, BCC-CSM1-1; he, HadGEM2-ES; ip, IPSL-CM5A-LR; mg, MRI-CGCM3; mi, MIROC-ESM-CHEM; no, NorESM1-M; RCP, representative concentration pathway

and RCP 8.5 scenario) in 2070 (Figure 4). Projections of future habitat suitability forecasted by the average values of six GCMs are displayed in Figure 5. Under RCP 2.6 scenario, *A. davidianus* range is predicted to decrease by about 68.5% in both 2050 and 2070; under RCP 8.5 scenario, range of this species will contract by 74.0% and 85.9% in 2050 and 2070, respectively. Under future climate conditions, suitable range of *A. davidianus* is mainly projected in areas straddling the border of Chongqing City, Hubei, Shaanxi, and Sichuan provinces (Figure 5). Projections also indicate that a small part of Chongqing City, Hubei, Shaanxi, Gansu, and Sichuan provinces will probably become suitable for this species in the future (Figure 5). Mean elevation across suitable range under present climate conditions 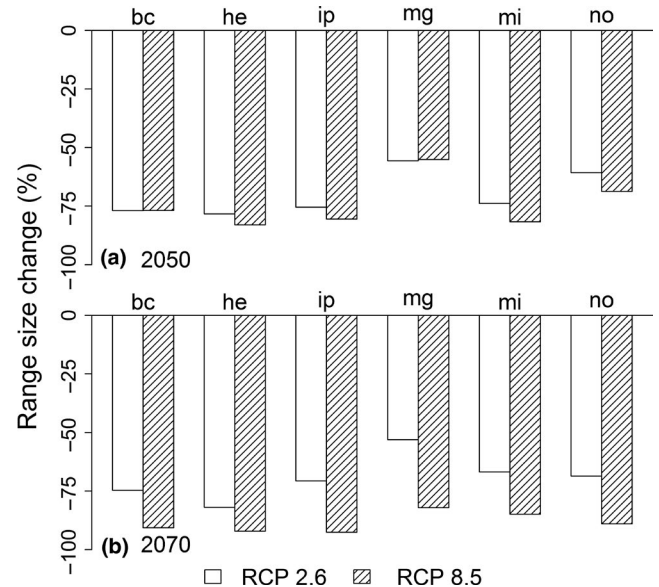(907.3 ± 6.4 m) was found to be significantly lower than those of under future climate scenarios (1,430.1 ± 11.3 m under RCP 2.6 in 2050, 1,579.9 ± 11.4 m under RCP 8.5 in 2050, 1,420.8 ± 11.2 m under RCP 2.6 in 2070, and 1755.1 ± 15.0 m under RCP 8.5 in 2070), hinting at a future increase in the elevation range extent of the species (Figures 5 and 6). In the future, centroid of potential suitable range of *A. davidianus* is projected to shift >280 km north-west (Figure 5).
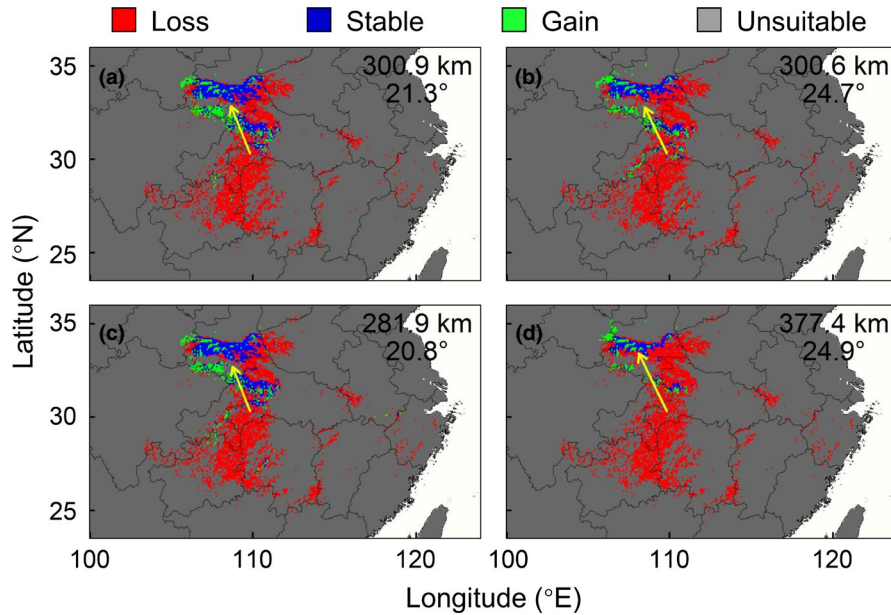
FIGURE 5 Changes in suitable ranges of *Andrias davidianus* projected by ensemble species distribution model under future changing climate conditions: (a) under RCP 2.6 scenario in 2050, (b) under RCP 8.5 scenario in 2050, (c) under RCP 2.6 scenario in 2070, and (d) under RCP 8.5 scenario in 2070. Averages of six global circulation models were used as future climates. The arrow in each inset map shows direction and distance between present and future distribution centroids. The start of arrow represents centroid of projected suitable area of *A. davidianus* under present climate conditions, while the end coincides with the position of the centroid under future climate scenarios. Direction is measured in degrees west of north
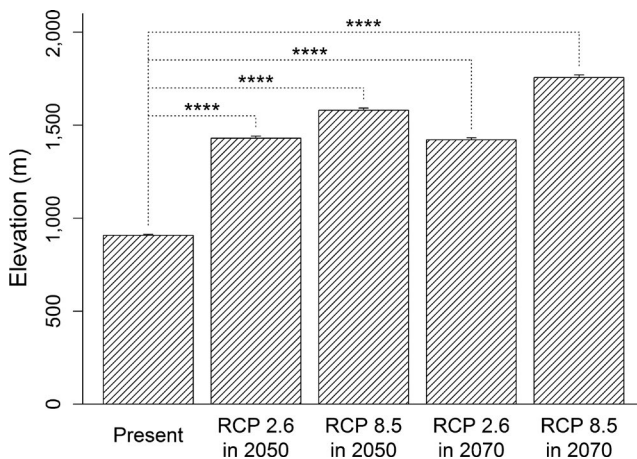

FIGURE 6 Mean (± *SE*) elevation values within suitable raster cells under present and future climate conditions. Mean (± *SE*) elevation of suitable raster cells was 907.3 ± 6.4 m under present climate conditions, 1,430.1 ± 11.3 m under RCP 2.6 in 2050, 1,579.9 ± 11.4 m under RCP 8.5 in 2050, 1,420.8 ± 11.2 m under RCP 2.6 in 2070, and 1,755.1 ± 15.0 m under RCP 8.5 in 2070. Elevation under future climate scenarios was significantly higher than that of present (Mann–Whitney *U* Test; ****$p < 2.2 \times 10^{-16}$)

4 | DISCUSSION

In this study, we developed ensemble SDMs for the Chinese giant salamander *A. davidianus* and estimated its habitat suitability under current and future climate conditions. Our SDMs, with good predictive accuracy, pointed out that climate change will probably lead to a reduction of more than two-thirds of its range and to a shift of its

range towards higher latitudes and altitudes. Our findings highlight the high sensitivity of *A. davidianus* to changing climate and thus have important implications for planning future conservation strategies.

4.1 | Important predictors and model caveats

A proper selection of predictors is critical for SDM studies (Fourcade, Besnard, & Secondi, 2018; Harris et al., 2013; Synes & Osborne, 2011). As a result of multicollinearity analysis, we selected nine predictors for modelling the distribution of *A. davidianus*. Of these, four were strongly associated with the distribution of the species. Slope emerged as the most important topographic predictor of the distribution of *A. davidianus*. Slope is correlated with several parameters measurable at the microhabitat level, such as water flow velocity and dissolved oxygen (Hynes, 1970; Platts, 1979; Skoulikidis, Karaouzas, & Gritzalis, 2009). In shallow slope areas, dissolved oxygen concentration is low as a result of the low water velocity, which is unsuitable for the survival of *A. davidianus*; in steep slope sites, the high water speed could lead to low larval retention rate. For instance, Barrett, Helms, Guyer, and Schoonover (2010) have demonstrated that high water velocities can decrease larval retention rate of the southern two-lined salamander *Eurycea cirrigera* (Green, 1818; Amphibia: Plethodontidae). This may also be true for *A. davidianus*. Variables related to extreme environmental conditions (maximum temperature of warmest month and precipitation of driest month) also emerged as important in explaining the distribution of *A. davidianus*. Precipitation is closely related to the amount of water in streams, and its velocity as well. Thus, low

precipitation events, combined with extreme high temperature, could reduce the dissolved oxygen in the environment, thus creating unsuitable conditions for the species.

In present study, we developed SDMs for *A. davidianus* by using coarse-scale climatic and topographic predictors. It should be noted that fine-scale microhabitat characteristic plays an important role in determining species distribution and could buffer species from climate changes (Ficetola et al., 2018; Lunghi, Manenti, & Ficetola, 2015; Scheffers, Edwards, Diesmos, Williams, & Evans, 2014; Varner & Dearing, 2014). For instance, Scheffers et al. (2014) measured temperature data from microhabitats and macrohabitats in primary rainforests in the Philippines. Their results clearly showed that microhabitats can greatly reduce mean temperature and the duration of extreme temperature exposure; thus, microhabitats have the potential to buffer species from climate change. We acknowledge that our SDM provides a broad picture of variation in habitat suitability for this species and may overestimate range contraction. A further caveat in model interpretation could be clade-specific variability and phenotypic plasticity. Yan et al. (2018) and Liang et al. (2019) uncovered seven divergent mitochondrial clades in *A. davidianus*. Besides, Riddell, Odom, Damm, and Sears (2018) revealed that plasticity may contribute in buffering salamander species from climate change. Models not accounting for plasticity may overestimate a species' extinction risk. Accordingly, a novel generation of hybrid SDM accounting for phenotypic plasticity is being developed (e.g. Benito Garzón, Robson, & Hampe, 2019). It is unknown whether *A. davidianus* possesses clade-specific variability and plasticity in response to changing climates. In view of above uncertainties, further field monitoring and laboratory experiments are required.

4.2 | Impacts of climate change on *A. davidianus*

Our SDM future projection indicates that suitable range of *A. davidianus* will shift towards higher altitudes and latitudes, and large areas of its currently suitable area will become progressively unsuitable. These findings are consistent with our initial working hypotheses. Climate change-induced altitudinal and/or latitudinal range shifts have been observed in a number of organisms (Chen et al., 2011; Poloczanska et al., 2013). For instance, Chen et al. (2011) reported that terrestrial species are shifting their distributions towards higher altitudes at a median rate of 11.0 m/decade and to higher latitudes at a median rate of 16.9 km/decade. Amphibians are experiencing global declines (IUCN, 2019) and, thus, a number of SDMs have been built to estimate their habitat suitability under future climate conditions (e.g. Duan et al., 2016; Milanovich et al., 2010; Popescu et al., 2013; Teixeira & Arntzen, 2002). We should consider that species dispersal capability is a critical limiting factor influencing species distribution and SDM projections can be largely divergent depending on different assumptions regarding dispersal abilities (Araújo et al., 2006; Guisan & Thuiller, 2005; Guisan et al., 2017; Schweiger et al., 2008). For instance, Araújo et al. (2006) studied potential impacts of climate change on habitat suitability of 108 European amphibian and reptile species by SDMs under two dispersal assumptions (i.e. no dispersal

and unlimited dispersal). Their results showed that more than half species were estimated to expand their ranges under unlimited dispersal scenario while the majority of studied species were projected to contract under no dispersal scenario. In present SDM study, we adopted an unlimited dispersal ability assumption and our SDM projections suggest that in addition to considerable range loss, *A. davidianus* will expand its range in some provinces. It is unclear whether *A. davidianus* has the ability to keep pace with climate change-induced range shifts and colonise new areas; we recognise that our results based on unlimited dispersal assumption could overestimate range expansion to these new areas and the range contraction should be more severe under no dispersal scenario (80.1% reduction under RCP 2.6 in 2050, 85.4% reduction under RCP 8.5 in 2050, 80.0% reduction under RCP 2.6 in 2070, and 92.4% reduction under RCP 8.5 in 2070). However, regardless of dispersal scenario, our results highlight the high vulnerability of this Critically Endangered species to climate change.

It is worth noting that climate change will also determine substantial environmental changes in the subterranean habitats that this species uses as breeding sites (Figure S1). While the effects of climate change are largely studied in surface habitats, the impacts on subterranean habitats are still poorly explored (Mammola, Cardoso, et al., 2019; Mammola, Piano, et al., 2019). *Andrias davidianus* primarily exploits habitats at the surface/subterranean interface for breeding (Liang et al., 2019; Luo et al., 2009). The temperature increment in these transitional subterranean habitats is expected to parallel the external one almost synchronically (Mammola, Piano, et al., 2019). Furthermore, climate change is expected to determine drops in relative humidity and even desiccation of subterranean habitats (Mammola, Piano, et al., 2019). Drought was highlighted as one of the potentially most critical threats for cave-dwelling species in China (Shu, Jiang, Whitten, Yang, & Chen, 2013), and should be even more so in the case of an aquatic species such as *A. davidianus*.

Climate change-induced range contraction will sum up to other threats that are currently severely affecting this species, from commercial overexploitation for human consumption to habitat degradation and disruption (Turvey et al., 2018; Yan et al., 2018). In view of our results, we strongly recommend that future adaptive management strategies should take into consideration the potential impacts of climate change on *A. davidianus*. As a Critically Endangered species with great public interest, *A. davidianus* has attracted considerable conservation attention. The Chinese government has already set up 53 nature reserves to conserve natural populations of *A. davidianus* (Liang et al., 2013). Protected areas have been considered an effective in-situ strategy for conserving biodiversity and ecosystem services, but the projected decline of suitable ranges of *A. davidianus* will possibly diminish the efficacy of these existing nature reserves. Adverse effects of climate change on protected areas of amphibians have already been elucidated (e.g. D'Amen et al., 2011; Lemes, Melo, & Loyola, 2014; Popescu et al., 2013). For instance, D'Amen et al. (2011) evaluated the efficacy of Italian reserve network for amphibians under future climate change scenarios by SDMs. Their results suggested that climate change would reduce suitable ranges of amphibians within reserves, and they recommended that new reserves

should be designed to maximise the benefits of conservation efforts. We advocate similar conservation strategies, such as establishment of new reserves, to be quickly implemented for *A. davidianus.*

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

AUTHORS' CONTRIBUTIONS

Z.Z., S.M., and Z.L. conceived the study; Z.L., Y.W., and C.W. collected the data; Z.Z. performed data analyses, with suggestions by S.M.; Z.Z., S.M., Z.L., C.C., and J.Z. led the writing of the first draft; all authors contributed to writing and approved the final manuscript.

DATA AVAILABILITY STATEMENT

Environmental data can be obtained from CHELSA (http://chelsa-climate.org), EarthEnv (http://www.earthenv.org/topography), and WorldClim (http://www.worldclim.org). Distribution data of *Andrias davidianus* are in Table S1.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.