Ecological correlates of extinction risk in Chinese amphibians

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Abstract
Aim: China is one of the countries with the richest amphibian biodiversity in the world. Among the 408 Chinese amphibians, 174 species are considered threatened according to the China Biodiversity Red List in 2015. However, to date, which species traits or extrinsic factors are correlated with extinction risk in Chinese amphibians is rarely examined. The aims of this study were thus to identify the patterns and correlates of extinction risk in Chinese amphibians and to determine whether patterns and processes are similar between species with either small or large geographic distributions.

Location: China.

Methods: We obtained twelve species traits and four extrinsic factors that have been commonly linked to the extinction risk of amphibians. After phylogenetic correction, these factors were tested separately and in combination to identify their correlations with extinction risk in all Chinese amphibians, and in small‐ranged and large‐ranged species.

Results: Geographic range size and elevational range were the most important predictors of extinction risk in all Chinese amphibians. Although extinction risk in small‐ranged amphibians was predominantly determined by small elevational range, in large‐ranged amphibians it was driven by geographic and elevational ranges, body size, human exploitation index and adult microhabitat. Small‐ranged amphibians had a higher percentage of threatened species than large‐ranged species. However, the body size distributions were not statistically different between these two amphibian subgroups.

Main conclusions: Our findings suggest that conservation priority should be given to species with small geographic and elevational ranges. Small‐ranged and large‐ranged amphibians should be conserved with different strategies because the factors influencing extinction risk differ between these two groups. In specific, the reduction of habitat loss should be a primary focus of management efforts because species with small geographic and elevational ranges are particularly vulnerable to habitat loss. Conservation efforts should also focus on protecting large‐bodied species and preventing human overexploitation for the effective conservation of large‐ranged amphibians.

Keywords
body size, Chinese amphibians, elevational range, geographic range size, human overexploitation, human threat, Red List
1 | INTRODUCTION

Amphibian species are declining worldwide at an alarming rate (Alroy, 2015; Wake & Vredenburg, 2008). Globally, almost one-third of amphibians are threatened by extinction, which is highest among all vertebrate groups (Hoffmann et al., 2010; Stuart et al., 2004). Accumulating evidence indicates that the extinction risk within amphibians is taxonomically non-random and varies depending on biological, environmental and anthropogenic factors (Bielby, Cunningham, & Purvis, 2006; Corey & Waite, 2008). Identifying key factors that predispose species to extinction is therefore an important prerequisite for minimizing the future loss of amphibians and maximizing conservation efforts (Murray, Rosauer, McCallum, & Skerratt, 2011).

Theory predicts that amphibian species with particular traits are more prone to extinction than others (Cooper, Bielby, Thomas, & Purvis, 2008). For example, species with large body size, restricted geographic and elevational ranges, low fecundity or high habitat specificity are frequently predicted to have higher extinction risk (Bielby, Cooper, Cunningham, Garner, & Purvis, 2008; Botts, Erasmus, & Alexander, 2013; Lips, Reeve, & Witters, 2003; Murray & Hose, 2005; Murray et al., 2011). The extinction risk of species is also strongly determined by environmental factors, such as temperature and precipitation (Bielby et al., 2008; Lawler, Shafer, Bancroft, & Blaustein, 2010). Furthermore, threats from land use change, human over-harvesting and pathogens could also exacerbate the extinction risk in amphibians (Ficetola, Rondinini, Bonaridi, Baisero, & Padoa-Schioppa, 2015; Hof, Araújo, Jetz, & Rahbek, 2012; Lips, 2016; Nowakowski et al., 2017; Ruland & Jeschke, 2017; Todd, Blomquist, Harper, & Osbourn, 2014). In general, the declines or extinctions in amphibians are phylogenetically dependent, so that closely related species may share similar proneness to extinction (Corey & Waite, 2008; Sodhi et al., 2008). However, to date, few studies have explicitly modelled species traits and extrinsic factors together to understand extinction risk in amphibians (Cooper et al., 2008; Nowakowski et al., 2017; Sodhi et al., 2008).

Geographic range size is often the most consistent correlate of extinction risk in amphibians (Botts et al., 2013; Murray & Hose, 2005; Sodhi et al., 2008). Amphibians with small geographic range size (hereafter small-ranged species) are generally less abundant, less mobile, poorer competitors and have narrower habitat breadths than large-ranged species (Botts et al., 2013; Cooper et al., 2008; Hero, Williams, & Magnusson, 2005; Murray & Hose, 2005). Therefore, small-ranged amphibians are more likely to decline, become threatened and eventually suffer extinction (Botts et al., 2013; Murray & House, 2005; Murray et al., 2011). By contrast, large-ranged species often face a wide variety of conditions, and those occupying human accessible ranges may also have high extinction risk (Cardillo, Mace, Gittleman, & Purvis, 2006; Di Marco & Santini, 2015). Nevertheless, range-based criteria are primarily used to estimate the extinction risk of amphibians, which further strengthens the overwhelming influence of small geographic range size in correlative studies (Botts et al., 2013; Cooper et al., 2008).

China harbours the fifth highest amphibian species richness in the world, with 408 known species recorded in the officially released China Biodiversity Red List in 2015 (MEP & CAS, 2015). Among them, 174 species are assessed as threatened (Vulnerable, Endangered and Critically Endangered) (Jiang et al., 2016; MEP & CAS, 2015). However, the knowledge of main causes (species traits and extrinsic factors) underlying declines in Chinese amphibians is still unclear and largely descriptive (Chan, Shoemaker, & Karraker, 2014; Hu, Li, Xie, & Jiang, 2012; Li & Pimm, 2016; Xie et al., 2007; Yuan et al., 2018), and lags far behind other regional studies (Hero et al., 2005; Lips et al., 2003; Menéndez-Guerrero & Graham, 2013; Murray & Hose, 2005; Murray et al., 2011). To fill knowledge and conservation gaps, there is urgent need to understand how species traits interact with environmental factors and threats to imperil Chinese amphibians.

Here, we conducted the first comparative analyses of extinction risk in Chinese amphibians by considering both species traits and extrinsic factors. We addressed the following two questions. First, which species traits and extrinsic factors are correlated with extinction risk in Chinese amphibians? Second, do small-ranged amphibians show similar patterns and processes of extinction and threat compared to that of large-ranged species? Identifying key correlates of extinction risk in Chinese amphibians is important for their proactive conservation and can be used to direct management policy.

2 | METHODS

2.1 | Data collection

We derived the species list and extinction risk of Chinese amphibians from the published China Biodiversity Red List (MEP & CAS, 2015). The information used in this Red List was mainly collected from specimens, literature and experts. It includes details on species distribution, population and habitat status, ecology, conservation and resource utilization (Jiang et al., 2016). This Red List evaluated the extinction risk of Chinese amphibians based on the criteria of IUCN Red List Categories and Criteria (Version 3.1) (IUCN, 2012a) and Guidelines for Application of IUCN Red List Criteria at Regional and National Levels (Version 4.0) (IUCN, 2012b). In total, the status of 408 amphibian species in China was comprehensively evaluated for the first time (MEP & CAS, 2015).

We used the China Biodiversity Red List because it has several advantages over the IUCN Red List. First, the China Biodiversity Red List includes the status of 53 new species and new records in China compared to the IUCN Red List (Jiang et al., 2016). Second, since the first assessment in 2004, the IUCN Red List has only updated the extinction status of 15.9% of Chinese amphibians (Table S1). Moreover, as the majority of Chinese amphibians are endemic species, the China Red List gives more precise scale and population status (Jiang et al., 2016; Milner-Gulland et al., 2006). Finally,
given better data quality and availability at the national level, the China Red List gives a more precise representation of the status of Chinese amphibians and thus is more practical for species conservation (Jiang et al., 2016).

Based on the China Biodiversity Red List categories, we converted the extinction risk of Chinese amphibians to an ordinal index of Least Concern (LC) = 0, Near Threatened (NT) = 1, Vulnerable (VU) = 2, Endangered (EN) = 3, Critically Endangered (CR) = 4 and Extinct (EX) or Regionally Extinct (RE) = 5, following Purvis, Gittleman, Cowlishaw, and Mace (2000). We excluded two types of species from analyses: (a) 52 Data Deficient (DD) species (MEP & CAS, 2015); (b) seven species that were viewed as subspecies or synonymies (e.g., *Tylototriton pulcherina*) by AmphibiaWeb 2018 (http://amphibiaweb.org). Accordingly, a total of 349 amphibian species were retained in the following analyses (Table S1). We then built a phylogenetic tree for these 349 amphibian species based on the latest global amphibian phylogeny (Jetz & Pyron, 2018). For the four species (*Nanorana sichuanensis*, *Odorrana rotodora*, *Rhadophorus leucofasciatus* and *Thelodera albopunctatum*) that were not present in the global amphibian phylogeny, we substituted them by using the branch length of their closest congener, as done in other studies (e.g., Murray & Hose, 2005).

We collected data on twelve life-history and ecological traits for each species (Table S1). Since body size can vary considerably between the sexes of amphibians, we investigated the performance of different body size variables (maximum body size of males and females and their maximum-value averages for each species) on extinction risk. Given that results did not change materially among these different variables, we retained only averaged maximum snout-vent length (SVL, in mm) to represent body size (Murray & Hose, 2005). Egg size was the mean diameter of eggs of each species (mm) (Murray & Hose, 2005). Following Hero et al. (2005), Development mode was classified as either terrestrial eggs and aquatic larvae (0) or aquatic eggs and larvae (1). Breeding site and Adult microhabitat were quantified as aquatic (1), semi-aquatic (2), terrestrial (3) and arboreal (4) (Hero et al., 2005). Primary larval habitat was classified as isolated ponds (1), stream or connected ponds (2) (Hero et al., 2005). Following Sodhi et al. (2008), reproductive cycle was classified as seasonal (0) or un-seasonal (1). Parent care was classified as either absence (0) or presence (1). Fertilization type was coded as internal (0) or external fertilization (1). We calculated geographic range size (km²) of species within China by extracting the extent-of-occurrence of each species from recently published species range maps (Fei, Ye, & Jiang, 2012) using ARCGIS v10.2 (ESRI, 2016). We applied the habitats classification scheme of the IUCN Red List assessments to classify amphibians’ habitats. We then calculated habitat specificity as the number of habitat types occupied by each species (Wang, Thornton, Ge, Wang, & Ding, 2015). To obtain elevational range of each species, we calculated the difference between the maximum and minimum elevation distribution from reported elevational ranges sourced from IUCN information, Fei et al. (2012) or Li and Pimm (2016).

We derived all the above species traits from Chinese literature (e.g., Fei, Hu, Ye, & Huang, 2006, 2009a, 2009b), which ensures that they correspond with the scale of the China Biodiversity Red List. These traits were selected based on two main considerations. First, these traits were commonly hypothesized to influence extinction vulnerability of amphibians in previous empirical and theoretical studies (Table 1; Hero et al., 2005; Lips et al., 2003; Murray & Hose, 2005; Sodhi et al., 2008). In addition, the data for these traits were available for almost all Chinese amphibians with exception for body size (1 species) and egg size (30 species). For these unavailable values, we used the estimates of each trait based on the mean values of their congeners (Wang et al., 2018). When traits were given with a range instead of mean values, we used the arithmetic mean of the limits (Wang, Zhang, Feeley, Jiang, & Ding, 2009).

We also obtained four extrinsic predictors based on hypotheses of published literature (Table 1; Collins, 2010; Sodhi et al., 2008). We extracted mean annual temperature, mean annual precipitation and mean human population density (HPD, people km⁻²) using the maps of species ranges (Fei et al., 2012) and regional/global environmental/population layers (Lee & Jetz, 2011). Mean annual temperature and precipitation are generally used as proxies of climate conditions and also reflect the primary environmental productivity (Böhm et al., 2016). The climate variables were extracted from the ESRI Arc and calculated at 0.5°× 0.5° resolution level in GRID software (ESRI, 2016). Mean HPD is viewed as a direct threat to species and likely represents the level of human impacts (Sodhi et al., 2008). HPD was calculated based on the Gridded Population of the World (CIESIN, 2000) at 0.5°× 0.5° resolution level in GRID. Moreover, amphibians are often harvested by humans in many ways, such as for research, medicine, pet trade and food purpose (Ruland & Jeschke, 2017). To quantify the effects of human exploitation on amphibian extinction risk, we derived a human exploitation index (HEI) by using existing summary reports of threats to Chinese amphibians (e.g., IUCN data; Fei et al., 2012; Li & Pimm, 2016). Overall, the index of each species was classified as rarely or never exploited (0), occasionally exploited (1) and frequently exploited or over-collected (2) based on the frequency of species’ exploitation reports (see Table S1 for details).

### 2.2 Statistical analyses

To test whether spatial autocorrelation exists in the data, we fitted exponential spatial covariance structures with the latitudinal and longitudinal centroids of species ranges using the package *nlme* (Pinheiro, Bates, DebRoy, & Sarkar, 2007) in R 3.5.2 (R Core Team, 2018). The removal of spatial effects, however, did not change the fitted values materially through visual inspection (Cooper et al., 2008). We thus only report these results in Table S4.

We employed phylogenetic generalized least square (PGLS) analyses and an information-theoretical approach to determine the relative influences of species traits and extrinsic factors on
TABLE 1 Species traits and extrinsic variables used to analyse extinction risk in Chinese amphibians. For each variable, the expected mechanism is listed, and species with given trait or under certain extrinsic condition are more or less likely to go extinct than others.

| Predictor variables | Expected mechanisms |
|---------------------|---------------------|
| **Intrinsic variables** | |
| Body size | Large body size is related to low population density, large home range, slow reproductive and recover rates (Bielby et al., 2006; Murray & Hose, 2005; Murray et al., 2011) |
| Development mode | Aquatic eggs are generally unprotected in water and thus vulnerable to regular or stochastic perturbations (Hero et al., 2005) |
| Breeding site | Species that breed in aquatic habitats are susceptible to regular or stochastic perturbations (Hero et al., 2005) |
| Egg size | Species with large egg size may have small clutch size and high egg predation risk (Murray & Hose, 2005) |
| Adult microhabitat | Species that live in aquatic habitats are susceptible to predators and regular or stochastic perturbations (Hero et al., 2005) |
| Primary larval habitat | Larvae that live in aquatic habitats are usually unprotected and susceptible to regular or stochastic perturbations (Hero et al., 2005) |
| Reproductive cycle | Species that are breeding seasonally are vulnerable to regular or stochastic perturbations in their habitats (Sodhi et al., 2008) |
| Parent care | Parental care can enhance offspring survivorship (Sodhi et al., 2008) |
| Fertilization type | Internal fertilization can increase reproductive success (Sodhi et al., 2008) |
| Geographic range size | Small‐ranged species tend to have narrow niches and may be more sensitive to local habitat modification than widespread species (Böhm et al., 2016; Cooper et al., 2008) |
| Habitat specificity | Habitat specialists are at higher extinction risk (Böhm et al., 2016) |
| Elevation range | Small elevational ranges suggest fewer refuges and less food resources (Lips et al., 2003; Murray & Hose, 2005) |
| **Extrinsic variables** | |
| Mean annual temperature | Ectotherms in lower temperature areas have slower life histories and lower reproduction (Böhm et al., 2016; Sodhi et al., 2008) |
| Mean annual precipitation | Areas with high levels of precipitation have higher productivity and potentially higher human disturbance (Böhm et al., 2016; Sodhi et al., 2008) |
| Mean human population density | Higher levels of human disturbance, resource use and increased habitat damage (Böhm et al., 2016; Sodhi et al., 2008) |
| Human exploitation index | Higher human exploitation index suggests potentially higher human disturbance and impacts, such as for research, medicine, pet trade and food purpose (Ruland & Jeschke, 2017) |

Extinction risk (Burnham & Anderson, 2002). We did not use the traditional stepwise multiple regression because it focuses inappropriately on a single best model, chooses inconsistently among model selection algorithms and is inherently flawed in parameter estimation (Whittingham, Stephens, Bradbury, & Freckleton, 2006). To avoid the statistical phylogenetic non-independence of related species, we applied the PGLS analyses (“pgls” function, package caper) to the data based on the Brownian motion (BM) model of evolution (Orme, 2013). The Ornstein–Uhlenbeck (OU) model, which is modified from the BM model, has also been widely used in previous studies (Blomberg, Garland, & Ives, 2003; Corey, 2010; Diniz-Filho, 2001). However, some studies recommended not using OU models for trees with less than 200 tips due to high type I error rates (e.g., Cooper, Thomas, Venditti, Meade, & Freckleton, 2016). Since no more than 175 species were included in the amphibian subgroups, we assumed that the BM model was more suitable for our data (Appendix S4).

To include only relevant variables in our models and to improve model fit, we built a set of relevant PGLS models in the following steps. First, we conducted univariate PGLS analyses to examine the significance of each of the twelve species traits and four extrinsic factors as predictors of extinction risk separately (Chen et al., 2019; Purvis et al., 2000). Second, because strongly correlated factors are likely to indicate similar underlying processes, we tested for collinearity between predictor variables with \( p < 0.1 \) in the first step, and only retained relevant variables with low correlations (Spearman’s \( p < 0.60 \); Mertler & Vannatta, 2002). We then built all possible combinations of models for the retained relevant variables and compared model fit and ranked candidate models using the Akaikes information criterion corrected for small sample size (AICc) (Burnham & Anderson, 2002). We calculated Akaikes weights \( (w_i) \) by comparing the difference in AICc values \( (\Delta AICc) \) between models. Finally, we ranked the predictors according to their relative importance by summing the \( w_i \) from all model combinations where that predictor occurred (Burnham & Anderson, 2002). Since our analyses frequently resulted in multiple competing models \( (\Delta AICc \leq 2) \), we used the model-average method to account for model selection uncertainty (Burnham & Anderson, 2002). We calculated weighted
estimates of regression coefficients (b) and unconditional standard errors for the models in the 95% confidence set using the MuMIn package (Barton, 2014).

Small geographic range size is used as two of the five criteria to assess extinction risk (criteria B and D2; IUCN, 2012a), so any correlation between geographic range size and extinction risk could be circular (Böhm et al., 2016). To avoid this issue, previous studies commonly excluded the species that were classified under the range-based criteria (Cooper et al., 2008; Jones, Purvis, & Gittleman, 2003; Wang et al., 2018). However, in our study, 79.0% of the 174 threatened amphibians are assessed based on restricted geographic range (MEP & CAS, 2015). We thus carried out two additional analyses to disentangle the influence of geographic range size on extinction risk. First, we simply excluded the range-based threatened species from the analyses to test whether geographic range size was still important in determining the extinction risk in Chinese amphibians (Appendix S2). Second, we excluded the variable of geographic range size from the models to determine whether its exclusion would overwhelm other variables in model selection (Appendix S3). We then calculated adjusted R² values of the two best models that included and excluded geographic range size to assess its performance.

Cardillo and Bromham (2001) treated body size as a categorical variable by using the median body weight of Australian mammals. Similarly, we used the median geographic range size of Chinese amphibians (8,499.5 km²) to distinguish between small- and large-ranged amphibians (the mid-point of the range of geographic range sizes (log-transformed) gave similar results, Table S5). We then reanalysed the patterns of extinction risk separately for these two amphibian subgroups. We also compared the values of body size between these two subgroups using the Kruskal–Wallis rank sum test and compared the value distributions of human exploitation index and adult microhabitat using Pearson’s chi-squared test when the assumption of normal distribution was not met. Prior to analyses, all continuous variables were logarithmically transformed to normalize values. All the variables were retained for the analyses because none of these variables were highly correlated (Spearman’s ρ < 0.50) in our study (Table S2).

3 | RESULTS

3.1 | The pattern of extinction risk in Chinese amphibians

As recorded in the China Biodiversity Red List in 2015, 115 species of Chinese amphibians were Vulnerable, 46 were Endangered, 13 were Critically Endangered, and 2 species were Extinct or Regionally Extinct (Table S1, Figure 1). Therefore, 176 (50.4%) of the 349 non-data-deficient Chinese amphibians were listed as threatened or extinct (Figure 1). Moreover, 175 of the 349 amphibians were classified as small-ranged amphibians, with geographic range sizes spanning from 9.9 to 8,499.5 km² (Figure 2a). Among all amphibians, 130 of the 175 (74.3%) small-ranged amphibians were threatened or extinct, which was about three times higher than that of large-ranged species (46 of 174, 26.4%).

3.2 | Correlates of extinction risk in Chinese amphibians

The univariate PGLS analyses showed that extinction risk in Chinese amphibians was significantly associated with seasonal reproductive cycle, high annual temperature, small geographic and elevational ranges, and high habitat specificity (Table 2). The best multivariate model for all amphibians accounted for 31.31% of total variation (Table 3), suggesting that amphibians have a higher risk of extinction if they have small geographic and elevational ranges. However, there were four models with ΔAICc ≤ 2 (Tables 3, Table S3), which suggests substantial model selection uncertainty. The relative variable importance (wv) indicated that geographic range size and elevational range were also important in the 95% confidence set (Table 4). In contrast, mean annual temperature, habitat specificity and reproductive cycle showed considerably less support (Table 4).

For small-ranged amphibians, geographic and elevational ranges, and human exploitation index were important predictors of extinction risk in univariate PGLS analyses (Table 2). By contrast, the extinction risk of large-ranged species was related to geographic and elevational ranges, body size, adult microhabitat, primary larval habitat and human exploitation index (Table 2). The best multivariable models for small- and large-ranged amphibians accounted for 7.17% and 31.71% of total variations, respectively (Table 3, Table S3). The relative variable importance (wv) indicated that elevational range was substantially important for small-ranged species, while the variables of geographic and elevational ranges, body size, human exploitation index and adult microhabitat were important for large-ranged species in the 95% confidence sets (Table 4).

3.3 | Effects of geographic range size on extinction risk

When excluding species assessed as threatened on the basis of their small geographic range size, the traits of geographic range size (wv = 1) and elevational range (wv = 0.84) were still substantially important in the 95% confidence set for the remaining Chinese amphibians (Table S9 in Appendix S2). Moreover, when the variable of geographic range size was excluded, model selection based on AICc identified the model incorporating elevational range, mean annual temperature and habitat specificity as the best for all amphibians (Table 3). Nevertheless, only 19.87% of the variance was explained by this model compared with 31.31% when geographic range size was included (Table 3). For large-ranged amphibians, the model including elevational range, body size, human exploitation index, adult microhabitat and primary larval habitat was the best when geographic range size was excluded (Table 3). The best model accounted for 22.06% of the variation in extinction risk, which was
much lower than 31.71% when geographic range size was included (Table 3). By contrast, geographic range size received considerably less support for small‐ranged amphibians (Table 4).

Compared with small‐ranged amphibians, large‐ranged amphibians had a comparatively higher number of human exploited species (Pearson's chi‐squared test, $\chi^2 = 17.96, df = 2, p < 0.001$; Figure 2c).
FIGURE 2  The value distribution of geographic range size and body size, and the percentage of species within each category of human exploitation index and adult microhabitat for small-ranged (red colour) and large-ranged (blue colour) amphibians. In subplots a and b, the boxplots show the median (centre bar in the box), the interquartile range (box) and the distribution of values (black dots). In subplots c and d, the total number of species in each category is given in the heading of each bar. \( \chi^2 \) and p-values were obtained from Kruskal–Wallis rank sum test in subplot b, and from Pearson's chi-squared test in subplots c and d.

| Variable                        | All amphibians | Small-ranged amphibians | Large-ranged amphibians |
|---------------------------------|----------------|-------------------------|-------------------------|
|                                 | Slope (t (p))  | Slope (t (p))           | Slope (t (p))           |
| Body size                       | 0.05 (0.32)    | -0.25 (-1.38)           | 0.75 (0.75)             |
| Egg size                        | 0.37 (1.31)    | 0.02 (0.08)             | 0.44 (0.96)             |
| Development mode                | -0.07 (-0.36)  | -0.20 (-0.86)           | -0.09 (-0.36)           |
| Breeding site                   | -0.05 (-0.58)  | -0.07 (-0.67)           | -0.08 (-0.25)           |
| Adult microhabitat              | 0.12 (1.37)    | 0.12 (1.10)             | -0.17 (-1.77)           |
| Primary larval habitat          | 0.07 (0.51)    | -0.14 (-0.79)           | 0.39 (2.65)             |
| Reproductive cycle              | -0.30 (-2.08**)| -0.02 (-0.08)           | -0.11 (-0.71)           |
| Parent care                     | 0.13 (0.60)    | -0.03 (-0.11)           | 0.26 (0.84)             |
| Fertilization type              | 0.30 (0.43)    | 0.12 (0.23)             | 0.55 (0.61)             |
| Geographic range size           | -0.24 (-11.51****) | -0.12 (-2.28**)       | -0.24 (-5.46****)       |
| Habitat specificity             | -0.16 (-3.51****) | -0.05 (-0.62)       | -0.06 (-1.43)           |
| Elevationary range              | -0.48 (-8.82****)| -0.27 (-3.80****)   | -0.36 (-4.11****)       |
| Mean annual temperature         | 0.02 (2.32**)  | 0.01 (0.33)             | 0.01 (1.44)             |
| Mean annual precipitation       | 0.03 (0.22)    | -0.22 (-1.31)           | -0.19 (-1.26)           |
| Mean population density         | 0.01 (0.34)    | 0.06 (1.29)             | 0.02 (0.38)             |
| Human exploitation index        | -0.05 (-0.70)  | -0.20 (-1.88*)          | 0.29 (3.57****)         |

Significant results were marked in bold.

* \( p < 0.1; \)

** \( p < 0.05; \)

*** \( p < 0.01; \)

**** \( p < 0.001; \)

TABLE 2  Results of univariate PGLS models predicting extinction risk in all Chinese amphibians, small-ranged and large-ranged species.
TABLE 3  The performance of PGLS models predicting the extinction risk of all Chinese amphibians, small-ranged and large-ranged species. The table shows models with ΔAICc ≤ 4, model rank, change in AICc from the top model (ΔAICc), model weight (wi) and adjusted R². The two best models that included and excluded geographic range size were marked in bold. All candidate models were listed in Table S3.

| All amphibians | K | AICc | ΔAICc | wi  | R²  |
|----------------|---|------|-------|-----|-----|
| RS + ER        | 3 | 893.23 | 0 | 0.2648 | 0.3131 |
| RS + ER + MAT  | 4 | 893.65 | 0.41 | 0.2154 | 0.3143 |
| RS + ER + MAT + RC | 5 | 894.75 | 1.51 | 0.1243 | 0.3142 |
| RS + ER + RC   | 4 | 894.75 | 1.51 | 0.1243 | 0.3122 |
| RS + ER + HS   | 4 | 895.28 | 2.05 | 0.0952 | 0.3111 |
| RS + ER + HS + MAT | 5 | 895.62 | 2.39 | 0.0802 | 0.3125 |
| RS + ER + HS + MAT + RC | 6 | 896.54 | 3.30 | 0.0507 | 0.3129 |
| RS + ER + HS + RC | 5 | 896.78 | 3.55 | 0.0450 | 0.3102 |
| ER + HS + MAT  | 4 | 948.17 | 54.94 | 3.12 × 10⁻¹³ | 0.0793 |

| Small-ranged amphibians | K | AICc | ΔAICc | wi  | R²  |
|-------------------------|---|------|-------|-----|-----|
| ER                      | 2 | 472.2 | 0 | 0.2914 | 0.0717 |
| ER + HEI                | 3 | 472.34 | 0.14 | 0.2718 | 0.0767 |
| ER + RS                 | 3 | 472.79 | 0.58 | 0.2177 | 0.0740 |
| ER + RS + HEI           | 4 | 472.89 | 0.69 | 0.2063 | 0.0793 |

| Large-ranged amphibians | K | AICc | ΔAICc | wi  | R²  |
|-------------------------|---|------|-------|-----|-----|
| RS + ER + BS + HEI + AM | 6 | 381.55 | 0 | 0.4527 | 0.3171 |
| RS + ER + BS + HEI      | 5 | 382.98 | 1.43 | 0.2216 | 0.3017 |
| RS + ER + BS + HEI + AM + LH | 7 | 383.33 | 1.77 | 0.1864 | 0.3144 |
| RS + ER + BS + HEI + LH | 6 | 384.66 | 3.11 | 0.0958 | 0.2995 |
| ER + BS + HEI + AM + LH | 6 | 405.13 | 23.58 | 3.43 × 10⁻⁶ | 0.2206 |

Abbreviations: AM, adult microhabitat; BS, body size; ER, elevational range; HEI, human exploitation index; HS, habitat specificity; LH, primary larval habitat; MAT, mean annual temperature; RC, reproductive cycle; RS, geographic range size.

TABLE 4  Model-averaged parameter estimates (θ), unconditional standard errors (SE) and relative variable importance (wᵢ) for each variable in the 95% confidence set for all amphibians, small-ranged and large-ranged species in China.

| All amphibians | wᵢ | θ   | SE  | z Value | p    |
|----------------|-----|-----|-----|---------|------|
| Intercept      | /   | 5.007 | 0.513 | 9.761   | <0.001 |
| Geographic range size | 1 | -0.190 | 0.024 | 7.938   | <0.001 |
| Elevational range | 1 | -0.259 | 0.057 | 4.541   | <0.001 |
| Mean annual temperature | 0.46 | 0.011 | 0.008 | 1.327   | 0.184  |
| Reproductive cycle | 0.27 | -0.107 | 0.126 | 0.847   | 0.397  |
| Habitat specificity | 0.19 | 0.006 | 0.041 | 0.144   | 0.885  |

| Small-ranged amphibians | wᵢ | θ   | SE  | z Value | p    |
|-------------------------|-----|-----|-----|---------|------|
| Intercept      | /   | 3.854 | 0.582 | 6.62    | <0.001 |
| Elevational range | 1 | -0.260 | 0.074 | 3.507   | <0.001 |
| Human exploitation index | 0.35 | -0.142 | 0.103 | 1.382   | 0.167  |
| Geographic range size | 0.28 | -0.067 | 0.055 | 1.213   | 0.225  |

| Large-ranged amphibians | wᵢ | θ   | SE  | z Value | p    |
|-------------------------|-----|-----|-----|---------|------|
| Intercept      | /   | 2.941 | 1.006 | 2.924   | <0.01  |
| Geographic range size | 1 | -0.217 | 0.042 | 5.158   | <0.001 |
| Elevational range | 1 | -0.254 | 0.079 | 3.195   | <0.001 |
| Body size      | 1   | 0.562 | 0.169 | 3.333   | <0.001 |
| Human exploitation index | 1 | 0.245 | 0.074 | 3.324   | <0.001 |
| Adult microhabitat | 0.74 | -0.154 | 0.080 | 1.914   | 0.056  |
| Primary larval habitat | 0.22 | 0.082 | 0.133 | 0.618   | 0.536  |
and water-associated species ($\chi^2 = 7.59, df = 3, p = 0.055$; Figure 2d). However, the body size distributions were not statistically different between these two amphibian subgroups (Kruskal–Wallis rank sum test, $p = 0.792$; Figure 2b).

## 4. DISCUSSION

Our study is the first to systematically investigate the patterns and processes of extinction and threat in Chinese amphibians, as well as in small-ranged versus large-ranged amphibians. We found that among the 50.4% threatened Chinese amphibian species included in our data set, species at greatest risk of extinction had small geographic and elevational range sizes. However, a more detailed analysis showed that the species traits and extrinsic factors influencing extinction risk differed between small- and large-ranged species.

### 4.1. Correlates of extinction risk in Chinese amphibians

We found that small geographic range size was significantly and negatively associated with extinction risk in Chinese amphibians. Geographic range size also explained a large variance of extinction risk in all Chinese amphibians and in large-ranged species compared to other variables, which further indicates a strong effect of geographic range size on extinction risk. In general, small geographic range size is the most important predictor of extinction risk in many taxa, including amphibians, birds, reptiles and mammals (Böhm et al., 2016; Botts et al., 2013; Crooks et al., 2017; Jones et al., 2003; Purvis et al., 2000). Small-ranged species are often habitat or environmental specialists, and such specialization may make a species highly susceptible to environmental changes or climatic fluctuations (Bott et al., 2013; Cooper et al., 2008; Murray & Hose, 2005). Restricted geographic range is also likely to increase the vulnerability of species to serious demographic stochasticity and inbreeding, and overall promotes the extinction risk (Cooper et al., 2008; Crooks et al., 2017; Jones et al., 2003).

Aside from geographic range size, small elevational range was the most consistent ecological predictor of extinction risk in Chinese amphibians. The influence of elevational range on extinction risk in amphibians has been frequently described in previous studies (Hero et al., 2005; Lip et al., 2003; Murray & Hose, 2005). As summarized by Tobias and Seddon (2009), elevational range can be a surrogate for both ecological plasticity and adaptability to different habitats and diets, and ecological generalism as their ability to exploit different environments simultaneously. Therefore, species with restricted elevational ranges may have fewer refuges, less food resources, lower population densities and fail to recolonize suitable habitats, thereby have increased extinction risk (Gaston, 1994; Li & Pimm, 2016; Purvis et al., 2000; White & Bennett, 2015). Our finding also showed that elevational range is complementary to geographic range size in predicting extinction risk. These two measures of range size are thus related as they both represent the habitat breadth/width that a species can utilize and potentially overlap in their effects on extinction risk of Chinese amphibians (Cooper et al., 2008; Hu et al., 2012).

Moreover, body size and human exploitation index were important variables in predicting the extinction risk of large-ranged amphibians, but not of small-ranged ones. In general, large-bodied animals are highly likely to have low population densities, slow reproductive and recovery rates, and all of which may increase their extinction risk (Bielby et al., 2006; Henle, Davies, Kleyer, Margules, & Settele, 2004). Large-bodied species are also more likely to be found and then harvested, as has been widely demonstrated for amphibians, birds and mammals (Cowlishaw & Dunbar, 2000; Isaac & Cowlishaw, 2004; Keane, Brooke, & McGowan, 2005; Ruland & Jeschke, 2017; Weaver, Paquet, & Ruggiero, 1996). An interesting finding was that body size received considerably less support for small-ranged species, while the body size distributions were not different between these two amphibian subgroups. This may relate to the fact that the vast majority of small-ranged species were assessed under range-based criteria, rather than the more demographically related criteria (Cooper et al., 2008). Moreover, body size was positively associated with human exploitation probability of large-ranged species and there were comparatively more human exploited species in large-ranged amphibians (Figure 2c), which all reflect the fact that the extensive harvest of amphibians in Asia is mainly directed towards the large-bodied and large-ranged species (e.g., Ranidae: Stuart et al., 2004).

We also found that large-ranged amphibians that were highly dependent on aquatic and riparian habitats over their life cycles were more threatened than forest-associated species (Hero & Morrison, 2004; Lips et al., 2003). With wide geographic distributions and a large number of water-associated species, large-ranged amphibians are more likely to suffer from threats of extreme climate, dam construction and water pollution (reviewed by Hughes, 2017). Some of these threats may kill riparian amphibians directly (e.g., pollution), or indirectly by reducing growth or disrupting reproduction (e.g., damming), and overall make water-associated species highly susceptible to extinction (Becker, Fonseca, Haddad, Batista, & Prado, 2007; Blaustein et al., 2001; Hughes, 2017). In addition, amphibian fungal disease caused by *Batrachochytrium* species is also likely to lead to higher extinction vulnerability in water-associated amphibians than in terrestrial amphibians (Bielby et al., 2008; Kriger & Hero, 2007; Lips et al., 2003). Although we did not consider fungal infection due to poor regional sampling (Bai, Liu, Fisher, Garner, & Li, 2012; Batalle et al., 2013; O’hanlon et al., 2018), it may play a role in imperilling large-ranged amphibians, because water-associated amphibians had a strikingly higher percentage of threatened species than terrestrial amphibians (Table S6).

### 4.2. Effects of geographic range size on extinction risk

Range-based criteria are predominantly used to estimate extinction risk of amphibians because of less information on population...
status (Böhm et al., 2016; Mace et al., 2008). Our finding that most of the variation in extinction risk is explained by geographic range size is therefore a possible reflection of the Red List assessment process (Böhm et al., 2016). However, when species listed as threatened on the basis of small geographic range size were excluded from the analyses, geographic range size was still the most important predictor of extinction risk. Therefore, endangered species generally have smaller geographic range sizes compared to less-threatened ones (Cardillo et al., 2005; Crooks et al., 2017; Koh, Sodhi, & Brook, 2004).

While our overall results suggested that Chinese amphibians with small geographic range sizes are the most threatened, the partition of species into small- and large-ranged species provided additional insights into the causes of their high extinction risk. For Chinese and global amphibians, habitat degradation is commonly assessed as the biggest threat (Cushman, 2006; Stuart et al., 2004; Xie et al., 2007). Thus, declines in amphibians with small geographic and elevational ranges in highly transformed regions are likely to be prevalent (Harris & Pimm, 2008; Li & Pimm, 2016). Small-ranged species are probably most affected because any loss of their favoured habitats will result in population declines (Botts et al., 2013; Stuart et al., 2004). Moreover, large-ranged species also face a high probability of being harvested, because their extinction risk was strongly related to large body size and high human exploitation index (Ruland & Jeschke, 2017). Therefore, we expect that human overexploitation acts in conjunction with habitat degradation in driving the extinction of large-ranged amphibians. Overall, our study showed that grouping amphibians based on the geographic range size can reduce its overwhelming influence on extinction risk and hence contributes to a better understanding of patterns of extinction risk and the underlying drivers.

4.3 | Conservation implications

Since most conservation policies and actions are made within national boundaries, identifying amphibian species with high conservation need in China is of crucial importance for making successful conservation decisions. Our findings have several important implications with regard to management practices in Chinese amphibians. First, we suggest that a basic conservation strategy should try to maximize the preservation of species with small geographic range sizes (Cooper et al., 2008; Stuart et al., 2004). In particular, small-ranged amphibians should be conserved in priority because the proportion of threatened small-ranged species was almost three times higher than that of large-ranged amphibians. Thus, special wildlife refuges need to be established and well maintained to protect the endangered Chinese amphibians with very small geographic range sizes, such as Chinhai spiny newt (Echinotriton chinhaiensis) and Chinese Giant Salamander (Andrias davidianus) (Stuart et al., 2008). Moreover, small-ranged and large-ranged amphibians should be conserved with different strategies because the factors influencing extinction risk differ between these two groups. In specific, Chinese species with small geographic and elevational ranges are particular vulnerable to habitat loss and degradation. To effectively conserve these threatened species, the reduction of habitat degradation and restoration of their habitats should be a primary focus of management efforts (Stuart et al., 2004). On the other hand, large-ranged species with large body size and high exploitation probability have high extinction vulnerability (Ruland & Jeschke, 2017). Therefore, the reduction of anthropogenic threats, such as human overexploitation, is also critically important for the conservation of large-ranged species.

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DATA ACCESSIBILITY

The data used for this research will be archived in dryad/figshare upon acceptance.

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