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Effects of climate and human activity on the current distribution of amphibians in China

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Abstract

In China, as elsewhere, amphibians are highly endangered. Anthropogenic environmental change has affected the distribution and population dynamics of species, and species distributions at a broad scale are strongly driven by climate and species' ability to disperse. Yet, current knowledge remains limited on how widespread human activity affects the distribution patterns of amphibians in China and whether this effect extends beyond climate. We compiled a relatively comprehensive database on the distribution of 196 amphibian species in China from the literature, public databases, and field data. We obtained 25,826 records on almost 50% of known species in China. To test how environmental factors and human activities influence the current distribution of amphibians (1960–1990), we used range filling, which is species realized ranges relative to their potential climate distribution. We used all species occurrence records to represent realized range and niche models to predict potential distribution range. To reduce uncertainty, we used 3 regression methods (beta regression, generalized boosted regression models, and random forest) to test the associations of species range filling with human activity, climate, topography, and range size. The results of the 3 approaches were consistent. At the species level, mean annual precipitation (climate) had the most effect on spatial distribution pattern of amphibians in China, followed by range size. Human activity ranked last. At the spatial level, mean annual precipitation remained the most important factor. Regions in southeastern of China that are currently moist supported the highest amphibian diversity, but were predicted to experience a decline in precipitation under climate change scenarios. Consequently, the distributions of amphibians will likely shift to the northwest in the future, which could affect future conservation efforts.

KEYWORDS

amphibian, climate, conservation, human activity, range filling, range size, species distribution model

Resumen

En China, como en todos lados, los anfibios están gravemente en peligro. El cambio ambiental antropogénico ha afectado la distribución y dinámica poblacional de especies, y la distribución de especies a gran escala están muy influidas por el clima y la habilidad de dispersión de las especies. Sin embargo, el conocimiento actual sigue siendo limitado sobre cómo la actividad humana generalizada afecta a los patrones de distribución de anfibios en China y si este efecto se extiende más allá del clima. A partir de literatura, bases de datos públicas y datos de campo, integramos una base datos relativamente completa sobre la distribución de 196 especies de anfibios en China. Obtuvimos 25,826 registros de casi 50% de las especies conocidas en China. Para probar cómo los factores ambientales y las actividades humanas influyen en la distribución actual de anfibios (1960-1990), utilizamos la ocupación de rango, que contrasta los rangos de distribución observada de las especies en relación con su distribución climática potencial. Utilizamos los registros de ocurrencia de todas las especies para representar el rango observado y modelos de nicho para predecir el rango de distribución potencial. Para reducir la incertidumbre, utilizamos 3 métodos de regresión (regresión beta, modelos de regresión acelerada generalizada y bosque aleatorio) para probar las asociaciones de la ocupación de rango de especies con la actividad humana, clima, topografía y extensión de rango. Los resultados de los tres métodos fueron consistentes. A nivel de especie, la precipitación media anual (clima) tuvo el mayor efecto sobre el patrón de distribución de anfibios en China, seguida por la extensión del rango. La actividad humana ocupó el último lugar. A nivel espacial, la precipitación media anual siguió como el factor más importante. Las regiones en el sureste de China que aun son húmedas sostuvieron la mayor diversidad de anfibios, pero se pronosticó que la precipitación declinará bajo escenarios de cambio climático. Consecuentemente, la distribución de anfibios muy probablemente cambiará hacia el noreste, lo cual podría afectar esfuerzos futuros de conservación.

PALABRAS CLAVE

Actividad humana, anfibio, clima, conservación, extensión del rango, modelo de distribución de especies, ocupación del rango

摘要

两栖动物是陆生脊椎中最受胁的类群, 中国两栖动物的受胁状态更为严峻。人类活动导致的环境变化深刻影响着物种的分布和种群动态。传统生态学认为大尺度上的物种分布格局主要受当前气候和物种扩散能力的影响。近几百年来, 人类活动的日益加剧, 其对物种分布的影响也日益加强。中国幅员辽阔, 自然环境类型多样, 同时人口众多。然而, 目前尚不知自然因素和人类活动是如何影响着中国两栖动物当前的分布格局?人类活动的影响是否已经超出了气候等自然环境因素的影响?我们通过三种方法收集了中国两栖动物的分布数据, 包括615篇文献, 网上公开数据和野外调查数据, 最终获得中国196种两栖动物的25826个分布点。并将这些数据用于预测两栖动物当前潜在分布区, 用实际分布点代表其当前实际分布区, 实际分布区和潜在分布区的比值来代表每一物种对其潜在分布区的占据状态。为了减少不确定性, 我们使用了三种回归模型 (beta 回归、广义增强回归模型和随机森林) , 在物种尺度和地理空间尺度上分析人类活动因子 (人口密度、人类足迹、农田比例) , 气候因子 (年均温、年均降水量, 古气候变化) , 以及物种分布的海拔范围和分布区大小等因素对当前中国两栖动物分布占据的影响。三种回归方法的结果一致。在物种尺度, 降水是影响中国两栖动物空间分布格局的最重要因素, 其次是物种的分布范围。生活在湿润区域以及分布面积大的物种其占据潜在适宜栖息地的比例更高。人类活动的影响尚不明显。在地理空间尺度, 降水依然是影响中国两栖动物当前分布格局的最重要因子。分布占据高的区域在中国的东南部, 这和中国当前的降水空间分布格局一致。中国的东南部是两栖动物多样性最高的区域之一, 但预计在气候变化情景下降水量将减少。因此, 未来这些区域的两栖动物很可能向西北方向迁移, 这将影响未来的生物多样性保护。

两栖动物, 气候, 人类活动, 保护, 物种分布模型, 分布范围, 分布占据

INTRODUCTION

Among vertebrates, amphibians are at the highest risk of extinction globally (Barnosky et al., 2011; Wake & Vredenburg, 2008). It is predicted that over 41% of global amphibian species are threatened with extinction (IUCN, 2021; Wake & Vredenburg, 2008). The risk of extinction is significantly greater in China; 43.1% of amphibian species are under threat (Jiang et al., 2016). Therefore, it is important to understand the causes and processes threatening these amphibians, which requires determining the current distributions of amphibians and the primary risk factors.

Climate plays a key role in determining the potential distribution areas of species at broad spatial scales (Huettmann, 2018; Pearson & Dawson, 2003; Woodward, 1987). These potential distributions, however, are often not fully occupied, due to dispersal and physiology limitations, biotic interactions, and evolutionary change (Araújo et al., 2006; Pearson & Dawson, 2003; Soberón, 2007; Wisz et al., 2013). Besides these factors, recent human activities might also greatly affect distribution (Newbold et al., 2015; Xu et al., 2019). For example, human-induced environmental change, through land-use change and associated habitat loss for species, has resulted in the reduction of distributional ranges for many species (Ceballos & Ehrlich, 2002; Li et al., 2015; Marco & Santini, 2015). By contrast, anthropogenic changes also contribute to increased species distributions, including the spread of non-native species, due to human transportation (Kleunen et al., 2015; Lôbo et al., 2011).

Therefore, the realized (i.e., actual) ranges of species are often in disequilibrium with the current climate, with some species filling only part of their potential distribution. However, the degree of equilibrium in species ranges with natural climatic factors might be distorted by human activities. Furthermore, the ratio of realized to potential range size (hereafter range filling) of species in a given region might increase or decrease due to anthropogenic activities (Tulowiecki & Larsen, 2015; Xu et al., 2019). For instance, in 1 New York (U.S.A.) county, the distributions of tree species were associated in the "early historic era" with Native American settlements. The probability of tree species presence is greater near villages than near trails, leading to higher or lower range filling, respectively (Tulowiecki & Larsen, 2015).

In China, the realized distribution of species is affected by the huge variety of ecosystems and extensive anthropogenic pressures over millennia (Xu et al., 2019; Li et al., 2015). Because amphibians are an environmentally sensitive group, they are vulnerable to both environmental variation and human activity (Alford et al., 2007; Araújo et al., 2006; Jiang et al., 2016). However, the hierarchical ranking of parameters affecting amphibian distribution patterns across China is unclear. By elucidating the main factors influencing the distributions of amphibians, practical and reasonable conservation plans could be devised (e.g., Chen et al., 2017).

We modeled potential habitats across China for 196 amphibian species and calculated the range-filling capacity for each species at the species level. We also calculated the geographic patterns of mean range filling on a grid to represent amphibian distribution patterns at spatial levels. Variation in range filling across species and spatial extent was then modeled against frequently used indicators of human activity: human population density (HPD), human footprint (HFP), proportion of cropland (cropland), and other potential factors (e.g., topography, climate, and range size).

METHODS

Occurrence data for ecological niche models

We collected information on the occurrence of amphibians from the following sources: database of the Global Biodiversity Information Facility (GBIF) (https://www.gbif.org/), published literature, and our own field survey records. Our surveys were reviewed and approved by the Animal Ethics Committee at the Institute of Zoology, Chinese Academy of Sciences (IOZ14001).

We downloaded occurrence records for 1970–2020 based on geographic information from GBIF (accessed June 2020). We then searched the literature (published after 1970) for occurrence data containing geographic information (longitude and latitude) or location name (village or town) in CNKI (https://www.cnki.net/), Baidu Xueshu (https://xueshu.baidu.com/), and Google Scholar (https://scholar.google.com/). We then georeferenced these location names with Google Earth and specific sampling sites according to the habitat descriptions and obtained longitudinal and latitudinal information. We used occurrence data from 615 published articles and Chinese nature reserve investigation reports (Appendix S1). We also included occurrence records from our fieldwork. Then, we combined the information from the 3 data sources. To reduce record errors, we removed presence points derived from the spatial distribution map of the International Union for the Conservation of Nature (IUCN) (https://www.iucnredlist.org/ [accessed in March 2019]), following Ma et al. (2021). To reduce sampling bias, we used the CoordinateCleaner package (Zizka et al., 2019) to remove records from institutes and museums. The spThin package (Aiello-Lammens et al., 2015) was used to remove redundant occurrence records in a single grid cell (Erfanian et al., 2021). This process was conducted in R 3.6.2. Species with $\geq$5 presence records were selected for further analyses (Chen et al., 2017). After collation and screening, we used 25,826 records (of which 42.6% were from articles and 19.1% were from nature reserve reports) of 196 amphibian species throughout China. The coverages of these species were from low to high latitudes and elevations, from rural counties to urban areas, and from wetland to arid areas, which could be widely representative across China (Appendix S2).

Environmental variables for ecological niche models

We extracted current climatic data from WorldClim 1.4 (www.worldclim.org) at a resolution of ~1 × 1 km for 1960–1990. Five bioclimatic variables were used to construct ecological niche models: annual mean temperature (BIO1), maximum temperature of warmest month (BIO5), minimum temperature of coldest month (BIO6), mean annual precipitation (MAP) (BIO12), and precipitation of warmest quarter (BIO18). We chose these variables because their effects are well established, and they impose constraints on amphibian distributions based on physiological limitations (Araújo et al., 2006; Carey & Alexander, 2003). Furthermore, in case certain key factors were excluded from the 5 bioclimatic variables model, we ran models with all 19 bioclimatic variables (www.worldclim.org). We used the vif function in usdm package to reduce the number of bioclimatic variables for each species (Naimi & Araújo, 2016).

Construction of ecological niche models and evaluation

We used an ensemble approach to reduce model uncertainty (Hao et al., 2020) when forecasting potential species distributions at 1 × 1 km resolution with the sdm package in R 3.6.2. We used 4 modeling algorithms, because of their widespread popularity in predicting the potential distributional range of species: generalized linear models, generalized boosted regression models, random forest, and support vector machines (Drake et al., 2006; Elith et al., 2006; Han et al., 2018; Mi et al., 2017; Naimi & Araújo, 2016). These models were implemented following an established method (Xu et al., 2019). Within a 50-km radius around the presence records (Andrade et al., 2020), we generated pseudo absences for each species with the eRandom method (Naimi & Araújo, 2016).

Niche model performance was evaluated using 2 widely applied methods: true skill statistics (TSS) (Allouche et al., 2006) and area under the receiver operating characteristic curve (AUC) (Manel et al., 2001). We used 70% random samples of initial data as training data and evaluated them against the remaining 30% (Araújo & New, 2007). We split sampled data 5 times to account for the uncertainty associated with data partition (Thuiller, 2003). We then created an ensemble model to average all models for each species and weighted them by their TSS values (Gallardo et al., 2017; Thuiller et al., 2009). We retained only models with TSS values >0.6 (Li et al., 2016). The ensemble forecasts were classified based on presence and absence, and the threshold maximizing TSS value was used to obtain species potential range size (Liu et al., 2005). All the models were generated using the sdm package in R 3.6.2 (Naimin & Araújo, 2016). Presence records at 1 × 1 km resolution were used for the niche models. Occurrence records at 50 × 50 km resolution were used to describe observed species distributions. For comparison, the IUCN distribution map was also used to represent the observed distribution, although the habitat and elevational ranges in these maps are subject to dispute (Li & Pimm, 2015; Xu et al. 2017). However, only 134 species from the IUCN Red List (68% of species based on occurrence records) occur in China. Shapefiles of IUCN distribution maps were transformed to raster format at 1 × 1 km resolution.

Species range filling

We calculated species range filling as the ratio of observed areas to potential range sizes for each species (Tulowiecki & Larsen, 2015). This allowed us to measure range equilibrium under current climatic conditions. Potential range size was transformed from the habitat suitability map to binary distribution maps (presence or absence); the maximizing TSS value was used as a threshold. This approach has been widely used to produce species potential distribution maps (Barbet-Massin et al., 2012; Liu et al., 2005; Mi et al., 2016). Both observed and potential range sizes were measured as the number of grid cells at 1 × 1 km resolution. We overlaid the observed species distributions at 50 × 50 km resolution with the potential range sizes at 1 × 1 km resolution. In this way, all climatically suitable grid cells of 1 × 1 km in a 50 × 50 km grid cell were assumed to be occupied when a species was observed in the 50 × 50 km grid cell. To examine whether the scale of resolution of observed versus potential species range size influenced our results, we used the same methods to calculate range filling with climatically suitable grid cells of 1 × 1 km in a 5 × 5 km and a 20 × 20 km grid cell and in climatically suitable grid cells of 10 × 10 km in 20 × 20, 50 × 50, and 100 × 100 km grid cells. We also examined whether species sample size affected our results by comparing the results with those based on species with over 20 and 50 occurrences.

Geographic range filling

In addition to the species-level range filling analyses, we used an assemblage-based approach to summarize geographic (space) range filling of species in each 50 × 50 km grid cell and to explore the spatial patterns of range filling. By integrating all species range filling estimates with distribution data at 1 × 1 km resolution, we calculated the mean value of range filling of species observed in each grid cell of 50 × 50 km resolution.

Explanatory variables for range filling

We used established methods to explain variation in species range filling and geographic patterns of grid mean range filling (Wan et al., 2019; Xu et al., 2019). For climate, we used current mean annual temperature (MAT), MAP (1960–1990) (https://www.worldclim.org/), and paleoclimatic change (anomaly) to control for environmental differences across geographic extents in China. For paleoclimatic change, we used temperature anomalies recorded since the Last Glacial Maximum, which were calculated as the difference between MAT and the average of 3 estimates of MAT during the Last Glacial Maximum from 3 model simulations: CCSM4 (developed by the National Center for Atmospheric Research [Gent et al., 2011]), MIROC-ESM (developed by Japan Agency for Marine-Earth Science and Technology [Watanabe et al., 2011]), and MPI-ESM-P (developed by Max Planck Institute for Meteorology [Giorgetta et al., 2013]) based on WorldClim 1.4 (https://www.worldclim.org/). We also included 4 indicators that are universally used to represent the cumulative effects of human activities: human footprint (HFP) (Venter et al., 2016), human population density (HPD) (http://sedac.ciesin.columbia.edu), proportion of cropland (cropland) (http://sedac.ciesin.columbia.edu), and human influence index (HII) (http://sedac.ciesin.columbia.edu). However, HII was highly correlated with HFP (Pearson $r = 0.82$); thus, we retained only the first 3 factors. In addition to human impacts, range filling might be affected by topography (Tulowiecki & Larsen, 2015). We used elevation range (EleR) to represent topography, which we defined as the range of elevation within each grid cell based on elevation data at a 1-km spatial resolution (https://www.worldclim.org/data/worldclim21.html). We also used species range size (RS), which we derived from the observed range size of species. The absolute Pearson correlation coefficient of the 3 variables for human activity and other explanatory environmental variables, both at species and geographic scale, were <0.8 (calculated in ArcGIS 10.5) (Levin, 2017) (Appendices S10 & S11); thus, all variables were retained in subsequent analyses.

Analyses of range filling and explanatory variables

To reduce uncertainty, we tested for associations between species range filling and explanatory variables with beta regression, a frequentist approach in the betareg package (Cribari-Neto & Zeileis, 2010), and 2 machine learning methods, generalized boosted regression models (GBM) in gbm (Greenwell et al., 2020) and random forest (RF) in randmForest (Liaw & Wiener, 2002) in R 3.6.2. For geographic range filling, we used multiple linear regressions, GBM, and RF. The explanatory variables included human impact indicators (HFP, HPD, or cropland), EleR, Anomaly, MAT, MAP, and species range size. Environmental variables were calculated as the median value across species potential ranges generated by niche models for species range filling. The HPD and cropland were $\log_{10}$-transformed to improve the linearity and goodness of fit of models. All of the explanatory variables were standardized to compare beta regression coefficients. For GBM and RF, we used variable importance to represent the role of explanatory variables in range filling. The variable importance of GBM was presented using the relative influence, which was based on the number of times a variable was selected for splitting, and was then weighted by the squared improvement to the model as a result of each split and averaged across all trees (Friedman & Meulman, 2003). The relative influence (or contribution) of each variable was scaled so that the sum was 100; the higher the number, the stronger the influence on the response (Elith et al., 2008). In comparison, the variable importance of RF was calculated from a total decrease in node impurities from splitting the variable and was averaged across all trees. It was measured by the residual sum of squares (Liaw & Wiener, 2002).

The effect of human activities on the distribution area of species may depend on range size (e.g., Xu et al., 2019). Thus, we analyzed the patterns for amphibians with narrow and wide ranges. We also analyzed the interaction between the 2 most important variables and human impact factors with the beta regression method. If the interaction was not significant, it was excluded from the final model. The 2 machine learning regression methods included the interaction between variables (Denisko & Hoffman, 2018). All statistical analyses were performed using R 3.6.2 (R Core Team, 2013). Asia North Albers Equal Area projection was used to calculate species range size and to generate the spatial figures.

RESULTS

The performance of niche models for all species was reasonable (TSS 0.767 [SD 0.088]; AUC 0.899 [SD 0.041]) (Appendix S9). The results obtained with occurrence records (Appendices S12–S14) versus IUCN maps (Appendices S15–S18), different sets of bioclimate variables (Appendices S19–S22), different resolution settings (observed and climate distribution [Appendices S23–S42), and different sample sizes were consistent (Appendices S43–S50). Therefore, we only present results of all species with climatically suitable grid cells (predicted by 5 bioclimate variable models) of 1 × 1 km in 50 × 50 km grid cells. The interaction between human activity and the 2 most important variables in the beta regression method was small (Appendices S53–S58); thus, they were excluded from the subsequent analyses.

TABLE 1 Results of beta regression, variable importance of generalized boosted regression models (GBM), and Random Forest for amphibian species range filling relative to explanatory variables

Variable	Estimate[a]	SE	*Z*	*p*	GBM	RF
HPD	0.139	0.204	2.50	0.012	0.04	0.54
EleR	−0.031	0.000	−0.67	0.501	10.83	1.34
Anomaly	0.368	0.011	5.99	<0.001	5.46	1.26
MAT	−0.104	0.035	−0.93	0.354	0.29	1.19
MAP	0.595	0.000	8.73	<0.001	55.39	4.81
RS	0.252	0.000	7.42	<0.001	27.98	2.91

Abbreviations: Anomaly, temperature anomaly since the Last Glacial Maximum; EleR, elevation range within grid cells; GBM, variable importance calculated by generalized boosted regression models; HPD, human population density; MAP, mean annual precipitation; MAT, mean annual temperature; RF, variable importance calculated by random forest; RS, species observed range size; *Z*, regression coefficient divided by the SE.
[a]Estimate, standardized regression coefficients.

Species range filling

The importance ranking (hierarchy) of explanatory variables for species range filling differed among the 3 regression approaches (beta regression, GBM, and RF); however, MAP and observed RS had the greatest effect on amphibian distributions, regardless of any of the human activity factors separately and combined (i.e., HPD [Table 1], HFP, cropland, and combined [Appendices S12–S14]). Unexpectedly, human activities were the least, or almost least, important factor, especially with GBM and RF (Appendices S12–S14). The MAP and RS were positively associated with range filling based on the beta regression method. The impact of human activities on species that had both widespread and narrow ranges tended to be weaker than climate, range size, or other natural factors. However, human activities had a greater influence on species with narrow ranges compared with more widespread species (Appendices S59–S66). Analysis of the spatial patterns of species range filling showed that amphibian species in southeastern China tended to be associated with higher range filling (Figure 1a), especially in moist regions (higher MAP) (Figure 1b,d). In contrast, the association of range filling with human activity (HPD, HFP, and cropland) (Figure 1c,d; Appendix S3) and other variables was weak (Appendix S4).

Geographic range filling

The pattern of geographic range filling by amphibians was similar to that recorded at the species level. Higher range filling mainly occurred in southeastern China (Figure 2a) and was consistent with the spatial pattern of MAP. The results of multiple regression, GBM, and RF were consistent;

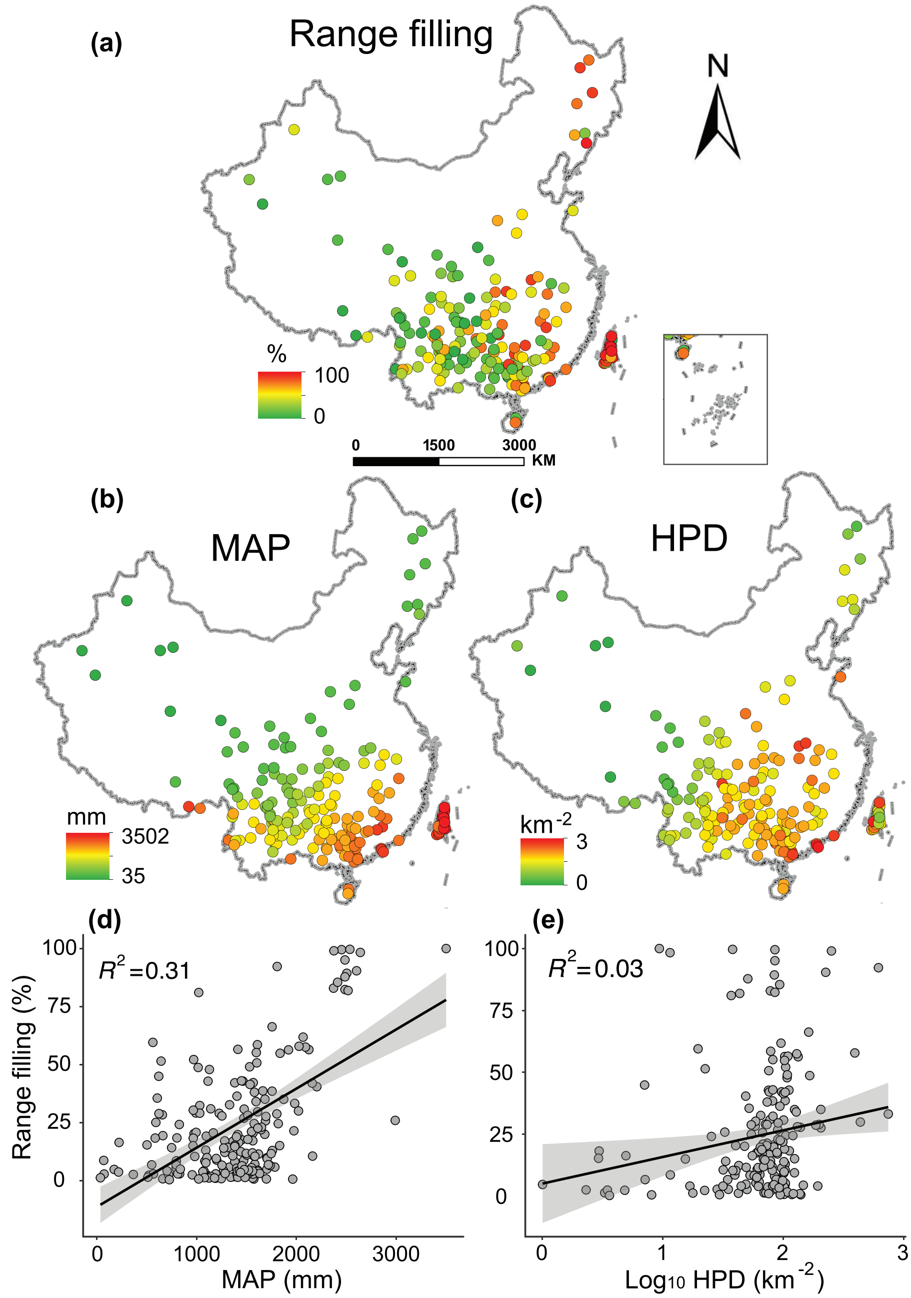

FIGURE 1 In China, (a) range filling of amphibians for study species center locations, (b) mean annual precipitation (MAP) of study species center locations, (c) human population density (HPD) of study species center locations, (d) relationship between range filling and MAP, and (e) relationship between range filling and $\log_{10}$ transformation of HPD

geographic range filling had the strongest associations with MAP (Table 2; Appendices S51 & S52), and this effect was stronger than human activities (HPD, HFP, cropland, spatial distribution) (Figure 2c; Appendix S5) and other factors (Appendix S6), including EleR, MAT, and anomaly.

DISCUSSION

Both species and spatial range filling analyses showed that recent MAP had more of an effect than human activities on whether amphibians occupied their potential distributions in China, followed by species range size at the species level. Our findings were consistent with the distribution patterns obtained for amphibian richness globally, with annual precipitation and MAT playing the most important roles (Buckley & Jetz, 2007).

The impact of precipitation on amphibian distributions might be related to their dependency on water. Most amphibians are aquatic breeders (Lion et al., 2019) and spend their early life-history stages in water (Wells, 2010). However, several amphibians occur in small wetlands in arid areas (e.g., *Bufotes pewzowi*, *Strauchbufo raddei*) (Fei et al., 2012) (Appendix S2). The reproduction of amphibians is generally

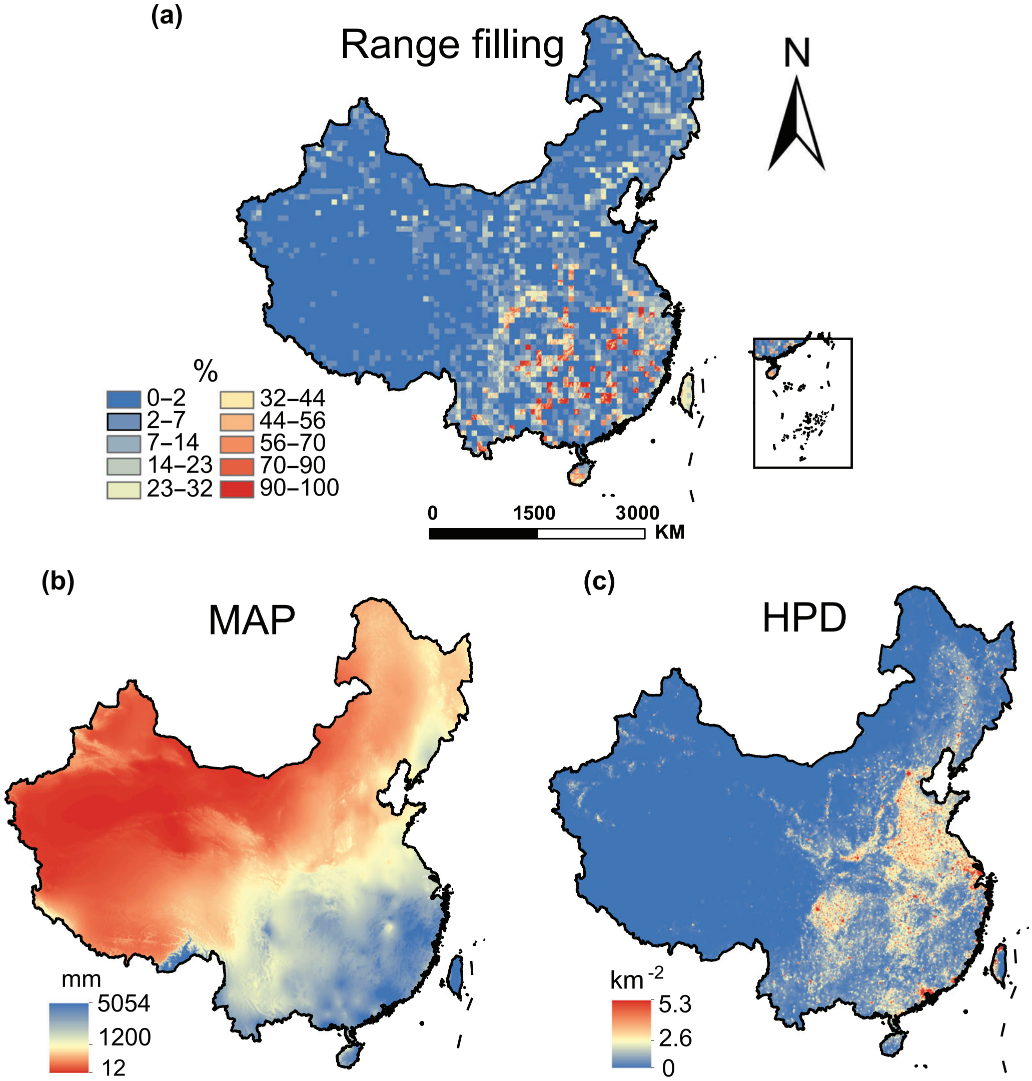

FIGURE 2 In China, geographic patterns of (a) grid-cell mean range filling of amphibians, (b) mean annual precipitation (MAP), and (c) $\log_{10}$ transformation of human population density (HPD)

linked to precipitation patterns (Bucciarelli et al., 2020). For instance, precipitation influences the reproductive success of the salamander *Ambystoma tigrinum*. The survival of this species in breeding ponds was generally high in years with average or high precipitation (Church et al., 2007). Precipitation strongly affects the survival of amphibians. Long periods of drought negatively affect adult survival and depress population growth rates in European amphibians (Cayuela et al., 2016). The extinction of the golden toad (*Bufo periglenes*) in Costa Rica was correlated with changes in the frequency of montane dry-season mist (Pounds et al., 1999). Similarly, amphibians in tropical montane cloud forests are particularly susceptible to changes in water availability, due to altered cloud formation patterns (Still et al., 1999). In general, precipitation and related water availability are extremely important to the reproduction and survival of amphibians at local sites. Because of this, precipitation also influences whether amphibians occupy habitats and geographical distribution patterns.

We also found that species range size affects the current distributions of amphibians. Specifically, widespread species exhibited higher range filling than species with narrow ranges (Table 1; Appendix S7). This phenomenon might be attributed to widespread species generally having higher dispersal capacity (Penner & Rödel, 2019); similar findings were obtained for other taxa, such as birds and plants (Laube et al., 2013; Estrada et al., 2015). Higher dispersal capacity could lead to species occupying their potential climate distributions. In contrast, the potential distribution areas of species with narrow ranges are often not fully occupied, due to dispersal limitations (Soberón, 2007; Wisz et al., 2013). Therefore, future conservation planning should place emphasis on amphibians occupying arid areas and those with narrow ranges.

It is widely accepted that recent human activities are contributing to the decline in amphibians (Chen et al., 2019; Rosser & Mainka, 2002). However, our results showed that human activities did not have as much of an effect as precipitation and

TABLE 2 Multiple linear regressions results and variable importance for generalized boosted regression models (GBM) and Random Forest of mean range filling in grid cells for all amphibian species relative to the explanatory variables

Variable	Estimate[a]	SE	*t*	*p*	GBM	RF
HPD	0.015	0.001	0.92	0.356	13.96	8.11
EleR	0.053	0.000	3.15	0.002	15.02	8.41
Anomaly	−0.004	0.002	−0.18	0.857	4.84	9.14
MAT	0.153	0.000	5.73	<0.001	6.16	10.08
MAP	0.375	0.000	17.74	<0.001	60.02	15.34

Abbreviations: Anomaly, temperature anomaly since the Last Glacial Maximum; EleR, elevation range within grid cells; GBM, variable importance calculated by generalized boosted regression models; HPD, human population density; MAP, mean annual precipitation; MAT, mean annual temperature; RF, variable importance calculated by random forest.
[a]Estimate, standardized regression coefficients.

range size on whether amphibians occupied their potential climatic range across China. This result could be attributed to our use of different metrics to previous studies. For instance, previous studies focused on changes in amphibians at the population level (Houlahan et al., 2000) and with respect to richness (Stuart et al., 2004). In contrast, we used a novel proxy of species distribution based on the proportion of potential distribution range filled by amphibians.

We implemented assessments at different scales. Species vulnerability is typically assessed at the community (e.g., richness) and population (e.g., abundance) levels based on data collected at the local (site) level. In contrast, we focused on the individual level (e.g., survival or maintenance) and species level (e.g., distribution) based on data collected at a regional level (Sievers et al., 2018). For example, the modification of aquatic habitat in urban areas generally reduces amphibian richness the most (Minton, 1968). However, at the scale we applied, if amphibians were to continue to exist in urban areas, they would occupy their potential range.

The effect of human disturbance also depends on spatial scale (Hamer & Hill, 2000). For example, a recent multiple spatial scale study showed that human disturbances affected the survival of caribou (*Rangifer tarandus*) in specific regions and areas (Plante et al., 2020). In contrast, we evaluated the entire distribution of species at a large scale.

Human disturbance can also have a positive impact on amphibians. Human settlements frequently encroach on amphibian habitats. However, constructed aquatic areas could provide amphibians with alternative habitats (Savard et al., 2000; Holzer, 2014). For instance, in Melbourne, Australia, frogs are widely distributed in ponds and abundance is greater in ponds surrounded by a high proportion of open green space (Harmer & Parris, 2011). Large quantities of human food are also often discarded in urban areas, providing a plentiful food source for amphibians, which might weaken the negative impact of human activity (McKinney, 2008).

Amphibians might also be more resistant to human activities than previously considered (i.e., urbanization). Ducatez and Shine (2017) found that, out of all terrestrial vertebrates, amphibians are the least affected by human activities. This might be attributed to the smaller body size of amphibians (O'Gorman & Hone, 2012); small organisms are more specialized and able to exploit the "mosaic nature of the environment" (Hutchinson & MacArthur, 1959). Urbanization creates greater spatial heterogeneity (mosaic environment) and could provide conditions that amphibians need to survive, such as relatively small areas of habitat (Savard et al., 2000). Our findings highlight the importance of using multiple measures, spatial scales, and viewpoints to assess the effects of human activities on the status of different species.

We found that the regions with the highest level of species range filling and geographic range filling were in southeastern China (Figures 1a & 2a). However, precipitation over most of this region is predicted to decline in the future (Mo et al., 2007; Wang & Yu, 2014) (Appendix S8). Consequently, range filling by amphibians in these areas will also likely decline. Southeastern China is considered an amphibian diversity hotspot (Jenkins et al., 2013). Thus, a reduction of precipitation in this region could lead to the loss of amphibian habitat. Climate change is primarily anthropic (IPCC, 2013). A warming climate is predicted to enhance evapotranspiration and result in a concomitant decline in precipitation levels. In contrast, the effect of a warming climate on montane areas in the middle and southwestern parts of China (i.e., Qinghai–Tibet Plateau) is predicted to lead to an increased precipitation (Mo et al., 2007; Wang & Yu, 2014) and water availability, due to higher snow melt (Hu & Liang, 2013). This scenario might result in a more habitat for amphibians in these regions, providing an opportunity for amphibians to migrate toward higher elevations in the near future to escape climate change and reduced precipitation (Duan et al., 2016), although the tolerances of amphibians to temperature and humidity are different among species (Sunday et al., 2012). However, migration toward higher elevations might be hindered by the low dispersal capacity of many amphibians (Smith & Smith, 1998) and by adverse effects of ultraviolet radiation (Blaustein et al., 1994; Blaustein et al., 2003; Macías et al., 2007). Furthermore, geographical barriers, such as mountains and arid areas, would also likely limit the migration of amphibians into these regions (e.g., Ghalambor et al., 2006). Besides, the tolerances of amphibians to temperature and humidity are different among species.

The indicators of human activities we used might not represent all possible predictors in explaining human activities. However, HFP, HPD, and cropland are universally used to determine the effects of human activities on species distributions (e.g., Xu et al., 2019). The average HFP of amphibian species in this study was 9.97 (range: 2.00−34.04) (Appendix S67), indicating that our data captured a good representation of human activity from low to high pressure (Venter et al., 2016). For example, the human footprint is a cumulative quantitative measurement of humanity's impact that provides an overview of regions where humans have the greatest and lowest presence (Sanderson et al., 2002; Venter et al., 2016). It is a strong predictor of modern range collapses (Yackulic et al., 2011) and of threat status of species (Safi & Pettorelli, 2010), species population size, and dispersal ability (Hand et al., 2014). It is also associated with invasion capacity of species (Beans et al., 2012).

We did not evaluate biotic interactions, evolutionary change, or other nonclimatic environmental or human-related factors, all of which could affect amphibian distributions. The extent and resolution of this study were beyond the scale domain at which these factors typically limit amphibian ranges (Pearson & Dawson, 2003; Plante et al., 2020). We also did not analyze some other factors that may have large effects on range filling of amphibians, such as dispersal capacity and habitat connectivity, because the data related to these factors are rarely available for amphibians in China. It would be of great interest to include these factors in the analysis once those data are available. The data on amphibians we compiled provide the best available resource on this group because it contains information on almost one-half of the amphibian species in China, most genera, all families, most habitats, and all provinces (Appendix S2). However, our data should be treated with caution because the occurrences we used might already be dated due to anthropogenic effects. In the future, when more data on the distributions of amphibians have been collected by researchers and via citizen science, information on the factors influencing the current distributions of amphibians could be explored in more detail. There may also be some mistakes in the distribution data on amphibians in nature reserve reports; we recommend researchers verify these data with IUCN range maps and Fei et al. (2012).

China is one of the few countries worldwide that supports extremely high biodiversity; over 400 amphibian species have been identified in China so far (Chen et al., 2019; Jiang et al., 2016; MEP & CAS, 2015). Our results indicated that precipitation (climate) and range size (dispersal capacity) affect the capacity of amphibians to occupy their habitats in China. The impact of climate change and range size dependence on amphibians has been widely confirmed (Alford et al., 2007; McMenamin et al., 2008; IUCN, 2017) and should be taken into account in future conservation planning (e.g., Chen et al., 2017; Peng et al., 2022). The role of natural factors controlling species distributions will likely be further distorted as human activities continue to increase (Xu et al., 2019). During the process of urbanization, aquatic habitats for amphibians should be created to facilitate long-term resilience and survival (Wells, 2010; Hamer & McDonnell, 2008).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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