

## Habitat suitability modeling of amphibian species in southern and central China: environmental correlates and potential richness mapping

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Received September 22, 2012; accepted March 27, 2013

Successful wildlife management must take into account suitable habitat areas. Information on the correlation between distribution ranges and environmental conditions would, therefore, improve the efficacy of *in-situ* conservation of wildlife. In this contribution, correlations between environmental factors and the distribution of 51 amphibians in southern and central China were investigated. Ecological niche factor analysis (ENFA) at a spatial resolution of 1° latitude×1° longitude identified a mixture of climatic and habitat factors as important predictors of the occurrence of individual species. The aims of the present work were (i) to evaluate potential distributions of amphibians based on the suitability of areas; (ii) to identify the major environmental descriptors upon which they depend; and (iii) to identify areas of potential high richness that have been overlooked in available inventories. Most of the predicted species ranges of species covered the majority of southern and central China. Six richness hotspots were predicted, of which four have been described previously, but two overlooked (SE Fujian and SE Qinghai). The prediction model was considered to be relatively accurate and it is recommended that these two new potential hotspots should be subjected to further evaluation and sampling efforts. Amphibians have high ecological preference for high humidity and precipitation, and low annual frost days. ENFA is a useful tool in wildlife conservation assessment because it is able to identify potential hotspots where studies on the correlations between environmental descriptors and the occurrence of particular species could be focused.

**ecological niche factor analysis, habitat suitability modeling, amphibians, China, distributional areas**

**Citation:** Chen Y H. Habitat suitability modeling of amphibian species in southern and central China: environmental correlates and potential richness mapping. *Sci China Life Sci*, 2013, 56: 476–484, doi: 10.1007/s11427-013-4475-3

Conserving biological diversity [1] is one main objective and benefit of sustainable development of humans in relation to the environment. Wildlife management cannot be fully achieved without considering the suitability of geographic home ranges and habitats for the maintenance of animal populations. Predicting suitable ranges has become an effective means of assisting wildlife conservation, as exhibited in many previous studies [2–4].

The term ‘hotspot’ [1] is widely used in conservation biology to refer to areas with high species richness and it is

employed in this way hereafter. Hotspots may occur from local to intercontinental scales [1,5–7].

Amphibians are considered to be indicators that can orient the direction of environmental management and protection [8,9]. There is increasing evidence that the extinction rate of amphibians around the world has accelerated in recent years as a result of global climate change and human disturbance [8–12]. Studies of the habitats and distributions of amphibians to enlighten the conservation of this wildlife group are urgently required [5,6,11].

For conservation purposes, the study of the distribution patterns of species richness in various habitats or regions,

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and their ecological determinants, are vital steps for understanding the processes that affect the spatial distribution of biological diversity. The underlying widely accepted assumption that environmental heterogeneity and the occurrence of species are interconnected within a geographic range has allowed environmental variation to be used to predict suitable ranges for species [13]. Recent advances in techniques that combined advanced mathematical procedures with geographical information systems have improved the validity of species-distribution modeling [14–17].

Geographical information systems and ecological niche modeling techniques are increasingly being used to model potential distributions of species and to identify suitable habitats with the aim of improving decision-making in wildlife management [4]. The majority of these methods are based on presence and/or absence data sets for species, and they make the intuitive assumption that the presence of a species is an indicator of suitable habitat and that its absence indicates an unsuitable habitat [7,18]. In this study, reliable absence data were not available for most species. Therefore selecting a relevant alternative tool for the modeling procedure was paramount.

Ecological Niche-Factor Analysis (ENFA), a tailored modeling technique that employs only presence data [19,20], could eliminate the problems caused by the influence of trivial absence data. The approach could be used to identify the correlations between eco-geographical variables (EGVs) and amphibian richness and to model the suitability of habitat areas [7]. Using this approach, this paper aims (i) to model the potential distribution of individual amphibian species; (ii) to evaluate the effects of environmental variables on the distribution of amphibian richness in southern and central China, an area highly suitable for this kind of study because of its extremely high species diversity; and (iii) to reveal some potential hotspots that may have been overlooked previously.

## 1 Materials and methods

### 1.1 Data collection

Amphibian distributional information was collected from a range of literature [5] and online resources (CSIS: China Species Information System, <http://www.baohu.org/>). A potential problem with these sources is that the historical distribution records might not reflect the current distribution of amphibians in some areas and, indeed, some species might have become locally extinct, since the last time they were recorded. However, in the present study, we assumed that such local extinctions did not significantly affect estimations of the contemporary distributional status of amphibians. All retrieved distributional records were used in subsequent analyses. The names of these 51 amphibians are presented in Table 1.

The original geographic locations of 51 amphibians

(Figure 1; more detailed distributional records for each species are provided in Table S1) were then entered into a georeferenced database, using 1° latitude×1° longitude squares as a reference grid. A total of 147 squares were studied. The criterion for the selection of the 51 species of amphibians was that they should occur in most of the southern and central regions of China and are generally absent from (or marginally distributed in) northern, northeastern and western areas. The selected amphibians have relatively diversified habitats, including rivers, forests, and marshes. Southern and central China is characterized by mountainous landscapes which exhibit most of these habitat features, with ample rainfall and mild temperatures [21,22]. Most of species are endemic to China. A few of the species occur in other Southeast Asian countries but their major ranges are in southern and central China. For example, the margins of the distributional range of *Bufo andrewsi* extend into the northern part of Myanmar and Vietnam.

Data on 11 EGVs describing each grid cell of the study were gathered for the analysis. These were aspect, elevation, surface water flow, annual frost days, slope, precipitation, annual minimal temperature, annual average temperature, annual maximal temperature, evaporation, and humidity. These environmental variables were downloaded from the website ([http://scilla.man.poznan.pl/euforia/grid\\_test/Kepler-1.0.0-install/lib/testdata/garp/NA\\_ASC/](http://scilla.man.poznan.pl/euforia/grid_test/Kepler-1.0.0-install/lib/testdata/garp/NA_ASC/)). The rationale of choosing these variables was primarily that they have been widely introduced to predict species distributions [5,23,24]. Furthermore, these variables reflect different aspects of the ecological conditions of amphibian habitats, including physical (e.g., elevation) and climatic (e.g., annual average temperature) features.

### 1.2 Ecological niche factor analysis

The principle of ENFA is to compare the distributions of the EGVs associated with the presence data set with the EGVs in the whole area under study. Outputs of ENFA contain multiple parameters, two of which are ‘factor scores’ and eigenvalues.

The ‘marginality factor’ is defined as the standardized difference between the species mean and the global mean of all descriptors, i.e., it describes the direction in which the species niche differs most from the available conditions in the study area [16]. The coefficients of the scores matrix related to the marginality factor indicate the correlation between each EGV and the factor. Marginality coefficients range from –1.0 to +1.0; positive values indicate that the species prefers high values of this EGV, while negative values indicate it prefers low values [7,16].

Other factors are ‘specialization factors’, which demonstrate how specialized the species is with respect to each EGV. Higher coefficients are associated with a more restricted value of each EGV [3,16].

‘Global marginality’ and ‘global tolerance’ values sum-

**Table 1** Taxonomic classification of 51 amphibians studied

ID	Order	Family	Genus	Species
1	Anura	Bombinatoridae	<i>Bombina</i>	<i>Bombina fortinuptialis</i>
2	Anura	Bombinatoridae	<i>Bombina</i>	<i>Bombina maxima</i>
3	Anura	Bufo	<i>Bufo</i>	<i>Bufo andrewsi</i>
4	Anura	Bufo	<i>Bufo</i>	<i>Bufo minshanicus</i>
5	Anura	Bufo	<i>Bufo</i>	<i>Bufo tibetanus</i>
6	Anura	Hyla	<i>Hyla</i>	<i>Hyla chinensis</i>
7	Anura	Hyla	<i>Hyla</i>	<i>Hyla sanchiangensis</i>
8	Anura	Megophryidae	<i>Brachytarsophrys</i>	<i>Brachytarsophrys platyparietus</i>
9	Anura	Megophryidae	<i>Oreolalax</i>	<i>Oreolalax omeimontis</i>
10	Anura	Megophryidae	<i>Oreolalax</i>	<i>Oreolalax rugosus</i>
11	Anura	Megophryidae	<i>Oreolalax</i>	<i>Oreolalax xiangchengensis</i>
12	Anura	Megophryidae	<i>Scutiger</i>	<i>Scutiger brevipes</i>
13	Anura	Megophryidae	<i>Scutiger</i>	<i>Scutiger maculatus</i>
14	Anura	Megophryidae	<i>Scutiger</i>	<i>Scutiger mammatus</i>
15	Anura	Megophryidae	<i>Scutiger</i>	<i>Scutiger ruginosus</i>
16	Anura	Megophryidae	<i>Scutiger</i>	<i>Scutiger tuberculatus</i>
17	Anura	Megophryidae	<i>Vibrissaphora</i>	<i>Vibrissaphora boringii</i>
18	Anura	Microhylidae	<i>Kaloula</i>	<i>Kaloula verrucosa</i>
19	Anura	Ranidae	<i>Amolops</i>	<i>Amolops granulatus</i>
20	Anura	Ranidae	<i>Amolops</i>	<i>Amolops mantzorum</i>
21	Anura	Ranidae	<i>Amolops</i>	<i>Amolops wuyiensis</i>
22	Anura	Ranidae	<i>Chaparana</i>	<i>Chaparana quadranus</i>
23	Anura	Ranidae	<i>Ingerana</i>	<i>Ingerana xizangensis</i>
24	Anura	Ranidae	<i>Nanorana</i>	<i>Nanorana pleskei</i>
25	Anura	Ranidae	<i>Paa</i>	<i>Paa boulengeri</i>
26	Anura	Ranidae	<i>Paa</i>	<i>Paa exilispinosa</i>
27	Anura	Ranidae	<i>Paa</i>	<i>Paa liui</i>
28	Caudata	Salamandridae	<i>Tylotriton</i>	<i>Tylotriton shanjing</i>
29	Caudata	Salamandridae	<i>Pachytriton</i>	<i>Pachytriton labiatus</i>
30	Caudata	Salamandridae	<i>Cynops</i>	<i>Cynops orientalis</i>
31	Caudata	Hynobiidae	<i>Hynobius</i>	<i>Hynobius chinensis</i>
32	Caudata	Hynobiidae	<i>Batrachuperus</i>	<i>Batrachuperus pinchonii</i>
33	Caudata	Cryptobranchidae	<i>Andrias</i>	<i>Andrias davidianus</i>
34	Anura	Rhacophoridae	<i>Rhacophorus</i>	<i>Rhacophorus taipeianus</i>
35	Anura	Rhacophoridae	<i>Polypedates</i>	<i>Polypedates yaoshanensis</i>
36	Anura	Rhacophoridae	<i>Polypedates</i>	<i>Polypedates omeimontis</i>
37	Anura	Rhacophoridae	<i>Polypedates</i>	<i>Polypedates hungfuensis</i>
38	Anura	Rhacophoridae	<i>Polypedates</i>	<i>Polypedates chenfui</i>
39	Anura	Ranidae	<i>Odorrana</i>	<i>Rana versabilis</i>
40	Anura	Ranidae	<i>Rana</i>	<i>Rana shuchinae</i>
41	Anura	Ranidae	<i>Odorrana</i>	<i>Rana schmackeri</i>
42	Anura	Ranidae	<i>Babina</i>	<i>Rana pleuraden</i>
43	Anura	Ranidae	<i>Pelophylax</i>	<i>Rana plancyi</i>
44	Anura	Ranidae	<i>Pelophylax</i>	<i>Rana nigrolineata</i>
45	Anura	Ranidae	<i>Odorrana</i>	<i>Rana margaretae</i>
46	Anura	Ranidae	<i>Odorrana</i>	<i>Rana lungshengensis</i>
47	Anura	Ranidae	<i>Hylarana</i>	<i>Rana latouchii</i>
48	Anura	Ranidae	<i>Odorrana</i>	<i>Rana jingdongensis</i>
49	Anura	Ranidae	<i>Babina</i>	<i>Rana daunchina</i>
50	Anura	Ranidae	<i>Rana</i>	<i>Rana chaochiaoensis</i>
51	Anura	Ranidae	<i>Babina</i>	<i>Rana adenopleura</i>



**Figure 1** Overall distributional records of 51 amphibians in southern and central parts of China for the present study. Detailed distributional information of each species is provided in Table S1.

marize the relationship between the species and its environment. Global marginality is a measure of the distance between species niche and the mean environmental conditions in the studied area. Global tolerance is a measure of the capacity of a species to tolerate environmental variations in the study area. A high marginality value indicates that the ecological requirements of the species differ considerably from the average habitat conditions. A low tolerance value in the range from 0-1 indicates a high degree of specialization (specialist species), and high tolerance value indicates a generalist species [3,7,16].

ENFA was implemented using the software Biomapper 3.0 [19], following the procedures outlined by Hirzel et al. [16]. EGVs were tested to exclude colinearity using Pearson's correlation coefficient with Statistica v6.0 (Statsoft; <http://www.statsoft.com/>).

### 1.3 Predicted species richness

Habitat suitability maps for each species were derived using ENFA with the distance geometric mean algorithm [7,25]. The habitat suitability maps were presented in the form of a grid in which each square has a value ranging from 0 to 100, corresponding to no suitability and high habitat suitability, respectively. If a species was predicted to occur in an area with a probability more than 50%, it was regarded empirically to be present in the area (assigned the value '1'); otherwise it was deemed to be absent from the area (assigned the value '0') [7]. By combining the predicted presence/absence information for all species in the overall areas studied, a final predicted richness map was produced.

To assess the validity of predicted range relative to the

observed range, the area under the curve (AUC) of the receiver operating characteristic (ROC) was calculated. High values of AUC indicate that the prediction is reliable. When  $AUC > 0.7$ , we concluded the prediction was statistically reliable.

A current richness map was also generated and compared with the predicted richness map. In addition, the current amphibian richness mapping observed by Chen and Bi [5] based on all amphibian species in China was used to examine the relative robustness of the richness prediction model in this study. To delimit the approximate boundaries of hotspots, the origin of each hotspot was determined (grid cells with maximum richness). This origin, plus the nearest 24 adjacent grid cells, was identified as the approximate boundary of each hotspot. If more than five grid cells of the boundaries of two hotspots were overlapped, they were merged as a single hotspot.

To reveal the discrepancy between predicted richness and observed richness, a cross-tabulation analysis was performed with a confusion matrix [7]. Each column of the matrix represented the predicted species richness and each row represented the observed species richness. The number of squares within each class of observed species was compared against the number of squares of each class of predicted species richness. In this study, five classes of predicted and observed species richness were assigned.

## 2 Results

### 2.1 Environmental correlates

According to the values of the first marginality factor, we

**Table 2** Ecogeographical variables (EGVs) and scores of the marginality factor obtained by ecological niche factor analysis for individual amphibian species<sup>a)</sup>

Species	ASP	ELE	SWF	AFD	PRE	SLO	MinT	AvT	MaxT	EVA	HUM	Global Marginality	Global Tolerance
1	0.028	-0.279	0.04	-0.43*	0.408*	-0.086	0.374	0.36	-0.051	0.387*	0.373	0.510194	0.582221
2	0.132	0.145	0.125	-0.394*	0.395*	0.319	0.324	0.319	-0.12	0.228	0.509*	0.510025	0.57569
3	0.121	0.132	-0.029	-0.303	0.404*	0.34*	0.288	0.272	-0.27	0.199	0.572*	0.510241	0.601716
4	0.233	0.406*	0.135	0.242	0.13	0.486*	-0.077	-0.08	-0.262	-0.228	0.564*	0.510222	0.623817
5	0.113	0.527*	0.011	0.278	0.164	0.413*	-0.179	-0.186	-0.257	-0.356	0.419*	0.510294	0.626866
6	-0.047	-0.287	0.025	-0.415*	0.417*	0.075	0.381	0.358	-0.066	0.388*	0.366	0.50998	0.615657
7	0.011	-0.24	0.033	-0.423*	0.43*	0.066	0.375	0.353	-0.043	0.388	0.394*	0.510168	0.621437
8	0.039	0.002	-0.035	-0.42*	0.423*	0.203	0.356	0.354	-0.152	0.298	0.488*	0.510559	0.588208
9	0.066	0.083	-0.235	-0.187	0.314	0.36*	0.206	0.173	-0.613*	0.121	0.455*	0.51006	0.607764
10	0.178	0.26	-0.026	-0.269	0.369*	0.446*	0.239	0.233	-0.326	0.127	0.509*	0.510279	0.596939
11	0.073	0.435*	0.267	-0.082	0.375	0.514*	0.137	0.135	-0.159	-0.076	0.505*	0.510322	0.604366
12	0.221	0.481*	0.1	0.22	0.231	0.393*	-0.096	-0.088	-0.208	-0.284	0.559*	0.510146	0.624151
13	0.299	0.421*	-0.021	0.175	0.221	0.456*	-0.061	-0.047	-0.308	-0.235	0.537*	0.509917	0.624459
14	0.058	0.521*	0.014	0.293	0.146	0.395*	-0.186	-0.186	-0.278	-0.354	0.436*	0.510224	0.627667
15	-0.031	0.555*	-0.19	0.01	0.354*	0.282	0.064	0.102	-0.282	-0.147	0.578*	0.510139	0.61263
16	0.354*	0.275	0.336	-0.182	0.332	0.496*	0.168	0.161	-0.111	0.01	0.479*	0.510002	0.595733
17	-0.167	-0.171	0.094	-0.434*	0.381*	0.042	0.368	0.332	-0.052	0.361	0.469*	0.510174	0.590525
18	0.087	0.151	0.064	-0.403*	0.396*	0.35	0.333	0.339	-0.148	0.255	0.46*	0.510339	0.583083
19	0.076	-0.09	-0.044	-0.354*	0.375*	0.274	0.342	0.302	-0.336	0.279	0.495*	0.510398	0.581387
20	0.138	0.248	-0.105	-0.235	0.374*	0.33	0.24	0.239	-0.383*	0.112	0.574*	0.50995	0.612992
21	0.062	-0.208	-0.087	-0.375*	0.436*	0.253	0.345	0.324	-0.234	0.36	0.378*	0.510369	0.621879
22	0.182	-0.168	0.076	-0.378*	0.366	0.263	0.399*	0.354	-0.201	0.33	0.39*	0.509962	0.595132
23	0.18	0.429*	-0.196	0.105	0.193	0.561*	-0.016	-0.015	-0.599*	-0.071	0.131	0.510035	0.591984
24	0.15	0.5*	-0.051	0.3	0.156	0.285	-0.173	-0.154	-0.276	-0.309*	0.552*	0.510374	0.625983
25	0.045	-0.124	-0.012	-0.433*	0.385*	0.123	0.385*	0.355	-0.107	0.347	0.476*	0.510477	0.5808
26	0.156	-0.273	0.123	-0.424*	0.413*	0.066	0.363	0.351	0.007	0.376*	0.367	0.510148	0.602886
27	-0.156	0.267	-0.003	-0.36*	0.4*	0.218	0.298	0.324	-0.246	0.173	0.532*	0.510206	0.563111
28	0.051	0.091	-0.203	-0.408*	0.364*	0.214	0.323	0.345	-0.286	0.29	0.462*	0.510087	0.603882
29	0.035	-0.2	-0.037	-0.419*	0.417*	0.134	0.372	0.35	-0.139	0.386	0.401*	0.510205	0.621923
30	0.014	-0.342	-0.101	-0.403*	0.42*	0.04	0.375	0.354	-0.087	0.391*	0.326	0.510316	0.62125
31	-0.079	-0.305	0.292	-0.396*	0.361*	-0.07	0.371*	0.352	0.152	0.357	0.334	0.51026	0.598815
32	0.228	0.28	0.025	-0.127	0.36*	0.428*	0.183	0.173	-0.34	0.026	0.6*	0.510106	0.622776
33	0.029	-0.172	0.002	-0.425*	0.395*	0.137	0.388	0.356	-0.104	0.369	0.435*	0.510033	0.594783
34	-0.051	-0.2	0.095	-0.427*	0.437*	0.09	0.388*	0.367	-0.037	0.387	0.361	0.510132	0.585525
35	0.083	-0.26	0.175	-0.418*	0.412*	-0.044	0.362	0.345	-0.001	0.375	0.397*	0.510159	0.567722
36	0.052	-0.084	0.112	-0.422*	0.392*	0.156	0.376	0.349	-0.091	0.339	0.485*	0.510202	0.559883
37	0.2	-0.086	0.113	-0.242	0.432*	0.305*	0.262	0.248	-0.258	0.187	0.608*	0.510133	0.544859
38	-0.023	-0.108	0.038	-0.424*	0.378*	0.186	0.37	0.332	-0.147	0.339	0.495*	0.510095	0.566371
39	0.077	-0.212	0	-0.412*	0.435*	0.076	0.365	0.343	-0.083	0.378	0.429*	0.510282	0.619725
40	-0.083	0.49*	0.145	-0.078	0.391	0.437*	0.143	0.113	-0.21	-0.039	0.55*	0.510022	0.58649
41	-0.022	-0.189	-0.022	-0.425*	0.405*	0.088	0.374	0.347	-0.104	0.367	0.454*	0.510456	0.619142
42	0.12	0.137	-0.026	-0.395*	0.385*	0.324	0.316	0.315	-0.187	0.245	0.512*	0.510023	0.577003
43	-0.001	-0.385	0.025	-0.411*	0.385	-0.035	0.398*	0.38	0.018	0.396*	0.27	0.510221	0.59615
44	-0.153	-0.034	0.169	-0.455*	0.337	0.146	0.361	0.386*	0.052	0.356	0.443*	0.510215	0.578266
45	-0.006	-0.072	-0.072	-0.406*	0.383*	0.191	0.359	0.327	-0.23	0.323	0.499*	0.510319	0.571161
46	-0.067	-0.164	0.022	-0.433*	0.398*	0.028	0.367	0.338	-0.051	0.373	0.481*	0.510349	0.605162
47	0.007	-0.268	-0.006	-0.417*	0.428*	0.08	0.381	0.36	-0.076	0.392*	0.36	0.509996	0.612248
48	-0.144	0.044	0.033	-0.454*	0.35	0.205	0.35	0.375*	-0.137	0.328	0.464*	0.509994	0.598808
49	-0.027	-0.095	0.084	-0.465*	0.347	0.097	0.376*	0.339	0.006	0.366	0.498*	0.510496	0.575355
50	-0.003	0.208	0.015	-0.364*	0.396*	0.302	0.31	0.305	-0.198	0.217	0.548*	0.510137	0.581955
51	-0.042	-0.187	0.026	-0.428*	0.422*	0.106	0.378	0.357	-0.067	0.382	0.411*	0.510097	0.617251
%	2%	19.60%	0	66.70%	68.20%	27.50%	11.80%	3.90%	5.90%	13.70%	82.40%		

a) \* denotes the three most important explaining EGVs for individual species. % denotes percentage of occurrence of each EGV as an important explaining factor for each species. The numbering of species follows that in Table 1. ASP, aspects; ELE, elevation; SWF, surface water flow; AFD, annual frost days; SLO, slope; PRE, precipitation; MinT, annual minimal temperature; AvT, annual average temperature; MaxT, annual maximal temperature; EVA, evaporation; HUM, humidity.

identified that factors precipitation (frequency of selection as an important factor: 82.4%) and humidity (68.2%) were consistently positively correlated with species occurrence, whereas annual frost days (66.7%) was negatively related (Table 2). Some variables were only occasionally identified as diagnostic factors for particular species, for example, surface water flow.

Global marginality and tolerance indices (Table 2) showed that the 51 studied amphibians tended to inhabit general habitats. No preferences for specific or extreme habitats were observed among the different species.

## 2.2 Current richness

The current observed species richness map based on the distribution of 51 species (Figures 1 and 2) indicated that SW China was the principal hotspot for amphibians, while other areas such as NW China and NE China were generally deficient in amphibian species. Two large hotspots identified were the areas extending from the Yunnan-Guizhou Plateau to Sichuan Basin and from the range of N Guangxi to S Hunan.

## 2.3 Predicted richness

Except for *Ingerana xizangensis* and *Polypedates hungfuenensis*, which had AUCs less than 0.7, all species were well predicted (AUCs>0.7). After discarding the two inaccurately predicted maps, the other predicted maps were merged to generate a final predicted richness map.

The distribution map of predicted species richness (Figure 2) identified six hotspots: E Xizang; SE Qinghai; the

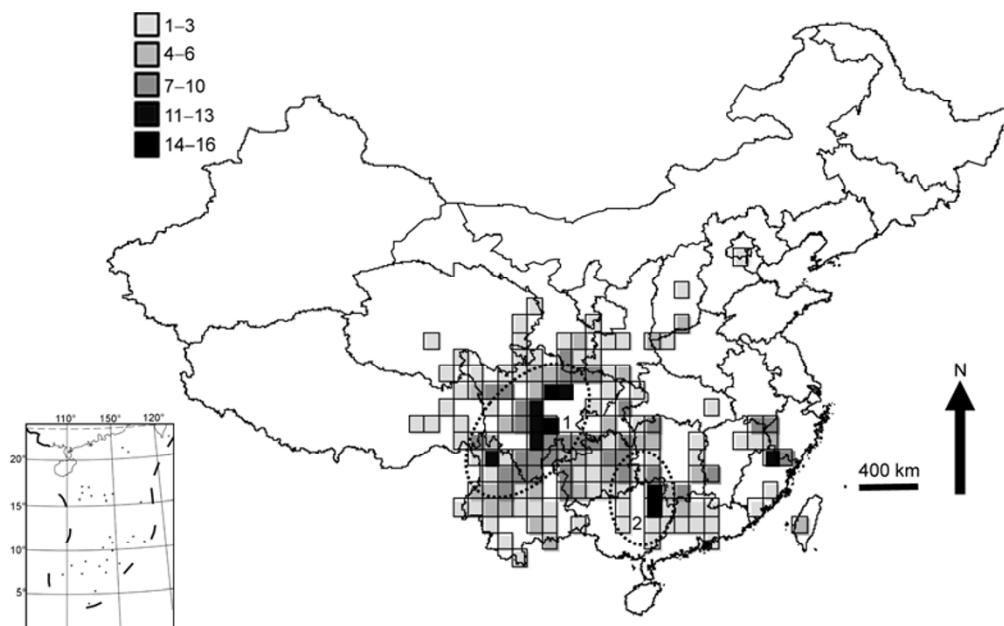
area from Yunnan-Guizhou Plateau to Sichuan Basin; the area from N Guangxi to S Hunan; the transition zone adjacent to Jiangxi, Anhui and Zhejiang; and SE Fujian. The area from Yunnan-Guizhou Plateau to Sichuan Basin has the highest richness (the top grid cell had 21 species). Two of these predicted hotspots corresponded to the observed hotspots (Figure 3). Four of them were described (or partially) by Chen and Bi [5], i.e., the area from Guangxi to S Hunan; the transition zone adjacent to Jiangxi, Anhui and Zhejiang; East Xizang; and the area from Yunnan-Guizhou Plateau to Sichuan Basin. This implied that the richness prediction model was valid. Moreover, ENFA suggested two more potential hotspots (SE Qinghai and SE Fujian), which had not observed in fieldwork but were predicted to have high species richness.

Cross-tabulation of predicted against observed species richness for each grid cell showed 33.1% with the same classification, indicating a relatively low consistency between observed and predicted richness of the squares. As such, the observed species richness was thought to be largely underestimated.

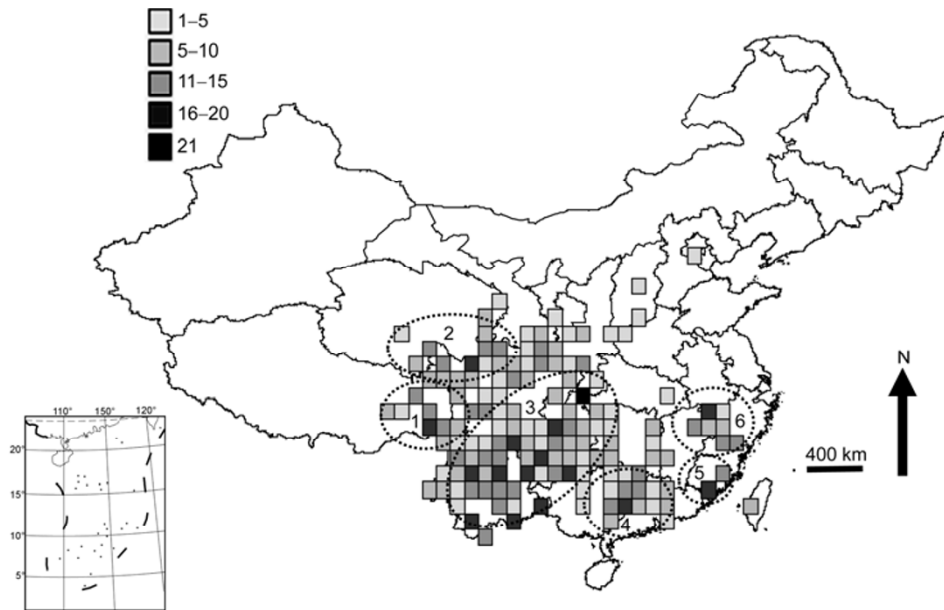
## 3 Discussion

### 3.1 Ecological niche factor analysis: environmental correlates

The advantage of ENFA is that it provides correlated environmental information for individual species (Table 2). For this reason it was selected for the distribution modeling of multiple species in this study. In addition, this approach provides parameters related to the habitat characteristics of



**Figure 2** Current richness map of 51 amphibians in southern and central parts of China (grey shading from light to heavy represents species richness from low to high). The dotted ellipses denote the approximate boundaries of two hotspots, referred to as: 1, Sichuan Basin; 2, the area extending from N Guangxi to S Hunan.



**Figure 3** Predicted richness map of 51 amphibians in southern and central parts of China (grey shading from light to heavy represents species richness from low to high). The dotted ellipses denote the approximate boundaries of six hotspots, referred to as: 1, E Xizang; 2, SE Qinghai; 3, the area extending from Yunnan-Guizhou Plateau to Sichuan Basin; 4, the area from N Guangxi to S Hunan; 5, SE Fujian; 6, the transition zone adjacent to Anhui, Zhejiang and Jiangxi.

species, e.g., tolerance, and marginality, which are not available in other modeling techniques, such as BioClim [26], GARP [27], and Maxent [28].

The present study showed that combinations of environmental factors are the best predictors of amphibian species occurrence at a regional scale. These factors generally are water-associated climatic variables and have been well-established previously. They include precipitation, humidity and annual frost days [7,29]. Humidity was a principal factor affecting the spatial distribution of amphibians. Among the species examined, 82% showed a preference for high humidity, and for 29 species, it was the most important factor (e.g., species *Batrachuperus pinchonii*, *Polypedates hungfuensis* and *Bufo andrewsi*). Such an observation is intuitively reasonable because amphibians are a water-dependent taxonomic group. Other environmental factors related to water were of course also strongly correlated with amphibian richness, including their preference for high precipitation and low numbers of annual frost days.

Interestingly, other factors were poorly correlated with amphibian richness. For example, the topographical variables-altitude and slope appeared to be peripheral factors, as indicated by the percentage of species that select them as important (Table 2). This result is inconsistent with some earlier studies that have argued that topographical variables are important [7]. A possible explanation is that extreme topographical conditions are located in mountainous and rugged areas where no amphibians occur. It is well known that, amphibians are sensitive to circumambient environmental situations. Most species preferentially inhabit more average topographical ranges in which the heterogeneity of these factors is low, causing them to be unimportant. Temperature

also seems not to be an important factor influencing amphibian richness in China, possibly for analogous reasons.

Although there were some discrepancies in the identification of important environmental variables compared with previous studies, all identified that variables related to water availability to be of great importance in interpreting amphibian richness, irrespective of the spatial scales of the geographic areas studied [5,7,29]. This observation helps to clarify the relative importance of water (i.e., precipitation and humidity) and energy (i.e., temperature) in the physiological requirements for amphibian richness. Our comparative data suggested that Water plays a more influential role than energy.

With respect to prediction modeling of individual species, all of those studied are specialist species requiring idiosyncratic ecological conditions. For example, *Kaloula verrucosa*, the global marginality was 1.429 and the global tolerance was 0.109; for *Amolops mantzorum*, the global marginality was 1.112 and the tolerance was 0.196. It is not surprising to obtain so many specialists at the  $1^{\circ} \times 1^{\circ}$  spatial resolution employed here, because marginality and specialization increase with spatial scale [18]. Variables that are complex at a fine resolution tend to be simplified at a coarser spatial scale.

### 3.2 Ecological niche factor analysis in conservation planning

As demonstrated in this and other studies [7], ENFA could be used to identify potentially important areas in relation to conservation strategies that have not yet been exhaustively surveyed. These areas would be identified as having high

richness in prediction model but have shown relatively low species richness in currently available cumulative inventories.

The SE Fujian hotspot is such an area that has been overlooked in previous studies and currently is not reported to have high species richness [5]. As predicted, this area involves diversified ecological niches for the survival requirements of around 19 species, comprising 37% of total species studied. SE Qinghai is another example. In the observed data, there were around nine species inhabiting this area. However, it was predicted with high probability that 24 species would occur in this area.

Another hotspot, in which the observed species number was relatively lower than that identified through ENFA, was the area extending from N Guangxi to S Hunan. Here, the richest grid cell contained 16 species in current observations but prediction modeling suggested it would probably have more species (18 species). This implies that the diversity patterns of some poorly sampled areas are still largely unknown, even for some recognized hotspots. Further field-work is required to build a comprehensive picture of the diversity status of these areas.

Although diversity estimators are widely applied to predict richness [30,31], an advantage of ENFA is its integration of the environmental envelope and the generation of predicted richness on a more 'biological' basis than solely statistical estimations. Environmental attributes and species richness are closely linked.

The issue of transferability of species distribution modeling has been well recognized [32,33]. As indicated in our study, four of the six predicted hotspots had been revealed in previous empirical surveys [5]. Therefore predicted richness mapping supports current richness mapping and is remarkably reliable. Because of the limited sampling effort, current richness mapping does not fully reflect the true biodiversity status of studied areas. Nevertheless, predicted richness mapping might provide an alternative and easier pathway to monitor biodiversity. Although prediction modeling is simply a consequence of mathematical fitness, it could provide an effective guideline to further surveying efforts. For example, SE Fujian and SE Qinghai might be hotspots and that are not yet documented in current inventories because they have been poorly surveyed. Further sampling efforts or conservation planning should pay particular attention to these areas.

The purpose of selecting the nearest 24 adjacent grid cells as the boundaries of the hotspots was to reduce the number of the hotspots and for the convenience of subsequent analysis. By selecting fewer adjacent grid cells as boundaries, more hotspots would be identified. However, boundary delimitation criteria of the hotspots do not greatly influence the comparative results or their interpretation. For example, the area from Yunnan-Guizhou Plateau to Sichuan Basin is a large hotspot; if it is divided into smaller hotspots, all of these smaller hotspots still correspond to those in the current richness map [5] and would not provide additional insights.

### 3.3 Limitations of the present study and implications for further studies

ENFA was employed to assist the management of wildlife distribution. We have gained some insights into the environmental requirements of amphibian richness in East Asia and have revealed some hotspots suitable for conservation. Some technical aspects of the present study should be mentioned. Firstly, a crucial issue is to select appropriate prediction techniques. If the modeling techniques are not robust, the results will be unreliable. The merits of ENFA have been demonstrated in many studies [2–4,7,13,34]. Secondly, the environmental factors should be updated. If more variables were included, more environmental information would be generated for the studied species. However, because some variables in the environmental envelope are rather colinear, care should be taken to avoid redundant variables. Also, it should be noted is that our prediction models were developed using  $1^{\circ}\times 1^{\circ}$  grid cells. As a consequence, the prediction maps are only an approximation of the accurate distribution. However, a large spatial resolution reduces the complexity and uncertainty associated with environmental variability.

There were other limitations in the present study. For example, the species distribution records were collected from a number of different sources, sampling biases could not be avoided, e.g., associated with the expertise of different recorders, sampling location selection [35], the seasonality of amphibian migration [36,37], and local extinction of some species in previously recorded field sites. Moreover, the limited prediction power of ENFA method might lead to misleading identification of hotspot regions. For example, there were discrepancies between the hotspots identified in the present study and those identified by a previous study [5]. All of these factors could shed doubt on the robustness of richness mapping using ENFA. Therefore, it is important to carry out further extensive field-work to survey the same amphibians across the hotspot regions to evaluate the validity and reliability of the present ENFA models.

Current knowledge of the ecology and distribution of amphibian species in China, especially of endemic and rare species, is still limited by sampling intensity. The work presented herein is one of the first contributions to be based around an ecological perspective [5,29]. To improve amphibian conservation and management, further work is needed on their basic ecological attributes such as population dynamic and diet [3].

*This work was partially supported by a University of British Columbia scholarship.*

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## Supporting Information

**Table S1** Detailed distributional records of 51 amphibian species in southern and central parts of China in the present study

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