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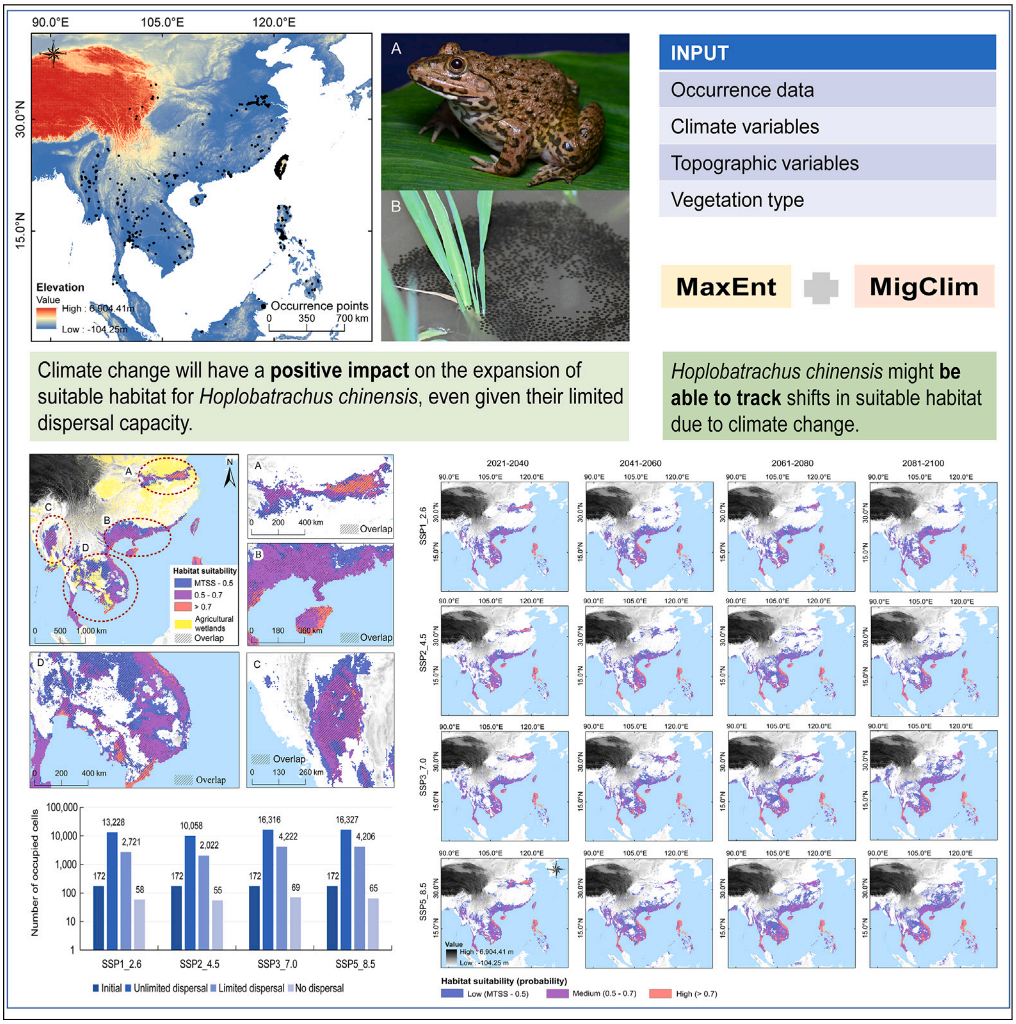

Xiaoli Zhang, Siti N. Othman, Dallin B. Kohler, Zhichao Wu, Zhenqi Wang, Amaël Borzée

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Highlights

Temperature is a key factor affecting the distribution of *Hoplobatrachus chinensis*

Climate change will expand the suitable habitat of *Hoplobatrachus chinensis*

The species has a 25% overlap between suitable habitats and agricultural wetlands

H. chinensis might be able to track shifts in suitable habitats under climate change

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Combined climate change and dispersal capacity positively affect *Hoplobatrachus chinensis* occupancy of agricultural wetlands

Xiaoli Zhang,[1] Siti N. Othman,[2] Dallin B. Kohler,[1] Zhichao Wu,[3] Zhenqi Wang,[2] and Amaël Borzée[2,4,5,6,*]

SUMMARY

Global warming significantly impacts amphibian populations globally, and modeling helps understand these effects. Here, we used MaxEnt and MigClim models to predict the impact of climate change on habitat suitability for *Hoplobatrachus chinensis*. Our results indicate that temperature is a key factor affecting *H. chinensis* distribution. Increasing temperatures positively correlated with habitat suitability, with suitable habitat expanding northward by 2060 while maintaining suitability in the southern parts of the range. We found a 25.18% overlap between the current potential suitable habitat of *H. chinensis* and agricultural wetlands. Our model indicated that *H. chinensis* might be able to track shifts in suitable habitats under climate change given a 15 km dispersal ability per generation. Climate change will likely expand suitable habitat for *H. chinensis*. Our predictions offer important guidance for the conservation of the species, especially for the integrated role of natural and agricultural wetlands such as rice paddies.

INTRODUCTION

Global climate change is a major threat to biodiversity across ecosystems,[1] and it is one of the main drivers altering the distribution of suitable habitat, breeding phenology, and dispersal patterns of species.[2–4] The global climate is undergoing dramatic changes due to anthropogenic emissions of greenhouse gases, resulting in an increase in the world's average temperature of 0.6°C over the last century,[5] with temperatures increases expected to reach or exceed 1.5°C over the next 20 years.[6]

Suitable climatic niches will shift as the climate changes, but not all species will be able to keep pace with these shifts.[7] Critically, most terrestrial species are unlikely to be able to follow their optimal climatic niches as they might have limited dispersal capacities and may be blocked by natural and anthropic barriers,[8] driving them to either adapt[9] or become extinct.[10] As a result, species with low dispersal capacity are at a higher risk of population extinctions and declines than highly vagile species.[11] In contrast, species that exploit human-modified habitats, such as rice paddies, may be able to disperse more easily across landscapes through human infrastructures.[12] Therefore, predicting and assessing the impacts of future climate change on the potentially suitable distribution and dispersal of species is critical for conservation.

Among all vertebrates, amphibians are the group with the highest number of species with ranges that are not protected or included in protected areas (24%),[13,14] and they are highly vulnerable to climate change due to their biology and low dispersal capacity.[15] There are 8450 species of amphibians worldwide (www.amphibiansoftheworld.amnh.org), 40.7% of which are threatened.[1] Numerous studies have shown that climate change alters patterns of amphibian distribution, either reducing or shifting suitable ranges.[16,17] Amphibians are expected to show significant responses to fast-changing climates due to their high habitat specialization, short dispersal and migration distances, and physiological constraints associated with thermoregulation.[18] For example, it is forecasted that the range of *Bufo gargarizans* will shift to higher latitudes and elevations as temperatures increase, reducing the amount of suitable habitat.[17]

Amphibians have evolved life-history strategies to mitigate the negative impacts of changing precipitation patterns.[19] However, when the effect of climate change is intensified by anthropogenic activities,[20] their ability to adapt to today's extreme climatic events such as droughts and rapid temperature rises, as well as more generalized environmental changes, may not be sufficient to sustain populations.[18] In the face of climate change and human threats, some amphibians in agricultural landscapes are either seeing a decline in their habitat range or undergoing population displacement.[17,21] For instance, agricultural activities in rice paddies have had negative effects on abundances and distribution of the endemic Japanese frog *Glandirana susurra*.[22]

Recent advances in ecological niche modeling (ENM) and species dispersal modeling techniques provide an opportunity to predict the geographic distribution patterns of species based on their dispersal capabilities.[23,24] ENMs can determine suitable habitats for target species

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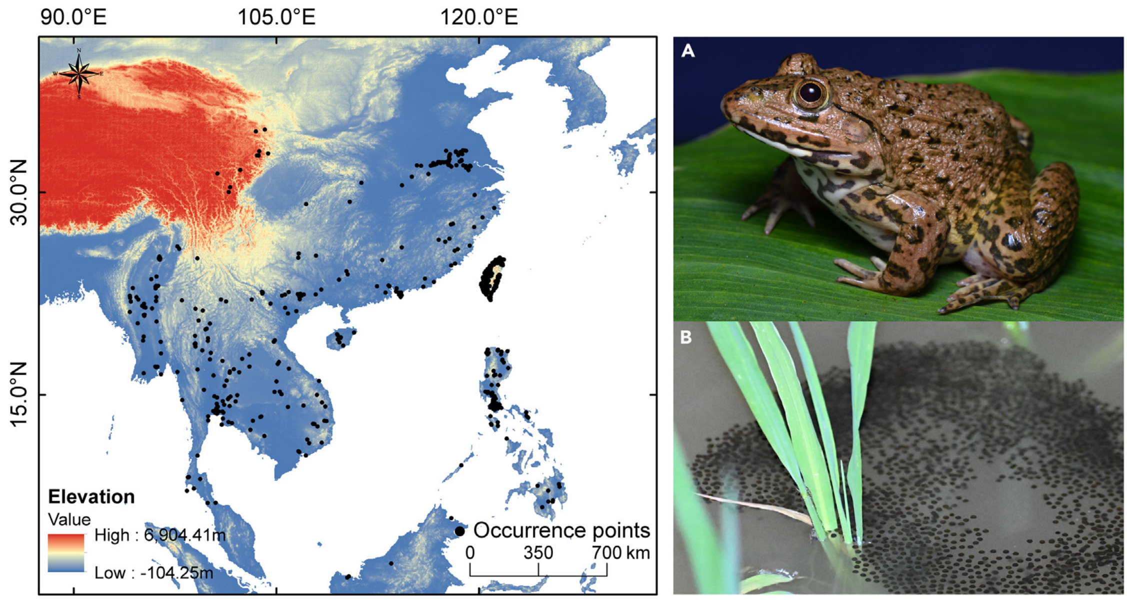

Figure 1. Geographic locations of *Hoplobatrachus chinensis*

(A) *Hoplobatrachus chinensis* adult, photograph by Vishal Kumar Prasad; (B) *Hoplobatrachus chinensis* eggs, photograph by Amaël Borzée. All pictures were taken from the lowlands of Jiangsu in 2023.

based on occurrence data and relevant environmental factors,[25] and they can be used for the assessment of extinction risk and the planning and construction of protected areas.[26] However, predictive distribution maps for species generated solely through ecotope modeling methods may be unrealistic if the ability of a species to colonize existing habitats in the future is not considered.[27] It is therefore important to take dispersal abilities into account, especially for species with low dispersal abilities. Compared to other vertebrates, the migratory behavior of amphibians is strongly constrained by the demands of water balance and thermoregulation.[28] Anuran amphibians have a weak dispersal capacity, with a migratory range of up to 15 km at most.[28–30]

Recent studies have resulted in realistic ENMs using various modeling approaches.[31] For example, Sen et al.[27] used MaxEnt[32] and Migclim[33] to project distribution patterns and ecological niche overlap between a terrestrial snail (*Indrella ampulla*) and cardamom (*Ellettaria cardamomum*) under current and future climate scenarios. The results showed that the ecological niche overlap of the two species was high.[27] These predictions improve the accuracy of the modeling results compared to unrealistic assumptions of unlimited or no dispersal.[27,31] Combining the predictions of ENMs and migration models can provide better guidance for amphibian conservation.

The target species of this study is *Hoplobatrachus chinensis* (Figure 1). Previous research on the species has focused on behavior,[34] individual development, temperature regulation,[35] and artificial breeding.[36] However, the effects of global warming on the habitat suitability of *H. chinensis* have not been comprehensively studied. This study aims to (1) elucidate the response of Asian *H. chinensis* to climate change from the perspective of distribution patterns and dispersal capacity; (2) calculate the overlap of potentially suitable habitat for *H. chinensis* with agricultural wetlands under the impacts of climate change; and (3) provide supporting data for changes in amphibian diversity patterns under various climate change scenarios.

RESULTS

We divided the predictor variables into two datasets to conduct two analyses separately. Dataset 1 included 19 bioclimatic variables and dataset 2 included 19 bioclimatic variables, vegetation type, slope, and aspect. In order to better present the past modeling results, we present the results of dataset 1 for the past results, while for future predictions, dispersion, and overlap analysis, we present the results of dataset 2. The other results are included in the Appendix (Document S1 Figures S4–S7) and referred to for comparison when required.

Model accuracy and key environmental variables

We used the corrected Akaike information criterion (AICc), the area under the receiver operating characteristic curve (AUC) and the true skill statistic (TSS) to assess the performance of the model predictions. All the algorithms applied reached an acceptable performance, with both TSS (0.73) and AUC (0.927) metrics reaching acceptable values (TSS >0.7, AUC >0.9), indicating that the ENMs had an excellent overall prediction ability (Document S1 Figure S1). Among all variables, the top five factors were vegetation type (Vegetation), annual mean temperature (Bio1), mean temperature of wettest quarter (Bio8), monthly mean diurnal temperature (Bio2), and range of annual temperature (Bio7). Together, all five variables explained 79.20% of variation in the model (Table 1, Document S1 Table S1). The jackknife test for variables showed high training and testing gain values and high-test AUC values for the same five variables (Document S1 Figures S2 and S5).

Table 1. Key variables affecting the distribution of H. chinensis and percentage contribution

Variables	Description	Percent contribution
Vegetation	Vegetation type	30.30
Bio1	Annual mean temperature	21.00
Bio8	Mean temperature of wettest quarter	14.70
Bio2	Monthly mean diurnal temperature	9.10
Bio7	Rang of annual temperature	4.10

Distribution of potential suitable habitats

We obtained potential suitable distribution areas for *H. chinensis* under the Last Interglacial, Last Glacial Maximum, Mid-Holocene and current climate scenarios (Figure 2). Under the Last Interglacial and Last Glacial Maximum climate scenario, we found suitable habitat for *H. chinensis* across the eastern Indomalayan region. We found that the high suitable habitat for *H. chinensis* under the Last Interglacial climate scenario was very narrow, mainly in Southeast Asia (Vietnam and the Philippines, Figure 2 LIG). By the Last Glacial Maximum, the suitable habitat of *H. chinensis* contracted rapidly, and only sections of South and Southeast Asia remained suitable habitat for the species (Figure 2 LIG to LGM), including present-day Mainland China (Guangxi) and Hainan Island, Thailand, Myanmar, Vietnam, Cambodia, and the Philippines (Figure 2 LGM). Under the Mid-Holocene climate scenario, the suitable habitats for the species expanded northward, including current Mainland China (Guangxi, Guangdong, Fujian), Hainan and Taiwan Islands, and a portion of current southern Indomalaya: Thailand, Myanmar, Vietnam, Cambodia, Lao PDR, Malaysia, and the Philippines (Figure 2 MH, LGM to MH). Highly suitable habitats during the Mid-Holocene climate were present in southern Mainland China (Fujian, Guangdong) and Hainan and Taiwan Islands, Thailand and the Philippines (Figure 2 MH). Compared to results from past climate scenarios, potential suitable habitat for *H. chinensis* expanded under the current climate scenario (Figure 2 Current, MH to Current), reaching southern Mainland China (Jiangsu, Anhui, Henan, Hubei, Fujian, Guangdong, and Guangxi), Hainan and Taiwan Islands, as well as southeast Asia (Vietnam, southern Myanmar, Thailand, southern Laos, Cambodia, and Philippines). Under the current climate scenario, highly suitable habitats were found mainly in Mainland China (Jiangsu, Anhui, Henan, and Hubei), Hainan and Taiwan Islands, as well as in some Southeast Asian countries (Philippines, Myanmar, Thailand, Vietnam, and Cambodia).

Generally, our projections for the future indicated that the potential suitable habitats for the species differed between the SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5 scenarios (Figure 3). We predicted a significant increase in highly suitable habitat for *H. chinensis* from the current period to 2100. This expansion was projected primarily in present-day southern Mainland China (Zhejiang, Jiangxi, Hunan, Guizhou), Thailand, Vietnam, Cambodia, and the Philippines (Figure 3). The climate under the SSP1-2.6 scenario provided similar results to those of the current climate, and the suitable habitat for *H. chinensis* remained essentially unchanged. Under medium climate change scenarios (SSP2-4.5, SSP3-7.0), *H. chinensis* did not experience widespread loss of potentially suitable habitat and remained in relative equilibrium from 2021 to 2080. Under the SSP3-7.0 climate change scenario, the suitable range of the species expanded widely into Zhejiang, Jiangxi, Hunan, Chongqing, Guizhou, and Yunnan in Mainland China from 2080 to 2100 (Figure 3). When climate change temperatures were at their highest (SSP5-8.5), the potential suitable habitat for *H. chinensis* initially expanded progressively with increasing temperatures, mainly in present-day eastern, central, and southern China, as well as in some portion of southern Indomalaya, i.e., Thailand and Cambodia (Figure 3).

Dispersal scenario analysis

We simulated projections of suitable habitat for *H. chinensis* under unlimited dispersal conditions and different climate change scenarios (Figure 4; Table 2). The unlimited dispersal scenario resulted in the maximum amount of forecasted suitable habitat for *H. chinensis*. The potentially realized range for this species expanded to 76.91 times its initial area under the SSP1-2.6 scenario. Under the SSP2-4.5 scenario, suitable habitat was forecasted to contract slightly during the second time period of the analyses before expanding from 2060. Under the SSP5-8.5 scenario, the expansion of potentially realized range for the species reached a maximum area 94.92 times its initial distribution (Table 2).

When considering barriers to dispersal, the expansion of potentially realized range for the frogs was relatively slow, and generally characterized by expansion-contraction (Table 2). Due to the dispersal barriers, with a range expansion of 11.76 times the initial range, the potentially realized range for the species was minimized in the SSP2-4.5 scenario. Under SSP3-7.0 scenario, as temperatures continue to rise, the occupied suitable habitat for the species continued to expand, with a range of 24.55 times the initial range. Compared with the other two dispersal patterns, under the no dispersal scenario, the potentially realized range for *H. chinensis* would decrease dramatically (Table 2), with 66.28% and 62.21% habitat loss under the SSP1-2.6 and SSP5-8.5 scenarios from 2000 to 2100, respectively.

Prediction of overlap between suitable habitats and agricultural wetlands

The overlap between suitable habitats for *H. chinensis* and agricultural wetlands was low (Figure 5). The overlap between the current suitable habitat and agricultural wetlands was 25.18%, with areas of overlap in East Asia mainly distributed in Jiangsu, Anhui, Hubei, Fujian, Guangxi, Guangdong, Hainan, and Taiwan Islands (Figures 5A and 4B). The suitable habitat also extended to Southeast Asia, encompassing southern Myanmar, central and southern Thailand, Cambodia, Lao PDR, and Vietnam (Figures 5C and 4D). However, not all areas of agricultural wetlands that overlapped with the suitable habitats of *H. chinensis* were uniformly suitable. There were distinct patches in the overlapping areas that were predicted to be highly suitable (pink) as opposed to certain patches that are poor or not suitable (blue to white regions; Figure 5).

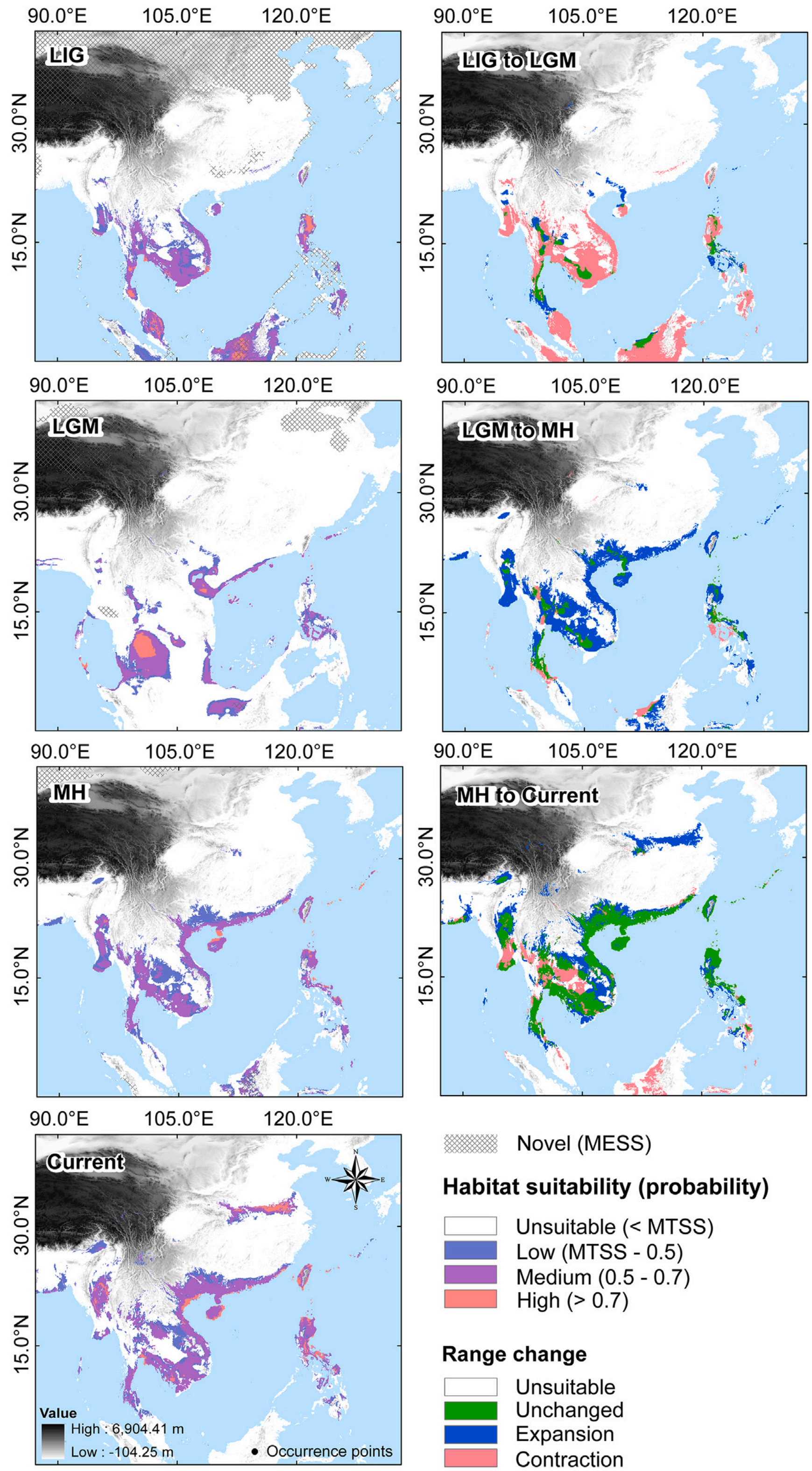
LIG
LIG to LGM
LGM
LGM to MH
MH
MH to Current
Current
90.0°E
105.0°E
120.0°E
30.0°N
15.0°N
Value
High : 6,904.41 m
Low : -104.25 m
Occurrence points
Novel (MESS)
Habitat suitability (probability)
Unsuitable (< MTSS)
Low (MTSS - 0.5)
Medium (0.5 - 0.7)
High (> 0.7)
Range change
Unsuitable
Unchanged
Expansion
Contraction

Figure 2. Potential suitable habitats for *H. chinensis* in southeastern Asia under past climate scenarios, as well as the changes between historical and current distributions

Past predictions are overlaid with multivariate environmental similarity surface (MESS) analysis results representing novel climates with no present-day analogues. Habitat stability shows areas with consistently stable suitable climate for the species over a 130,000 year period.

See also Figure S6.

DISCUSSION

Important predictors of habitat suitability

Our result indicated that among the 19 environmental variables used, the top five contributing factors were vegetation type, annual mean temperature (Bio1), monthly mean diurnal temperature (Bio2), rang of annual temperature (Bio7), and mean temperature of wettest quarter (Bio8), with vegetation type (30.30%) having the greatest influence on suitable habitat for *H. chinensis* (Table 1, Document S1 Figure S3). In

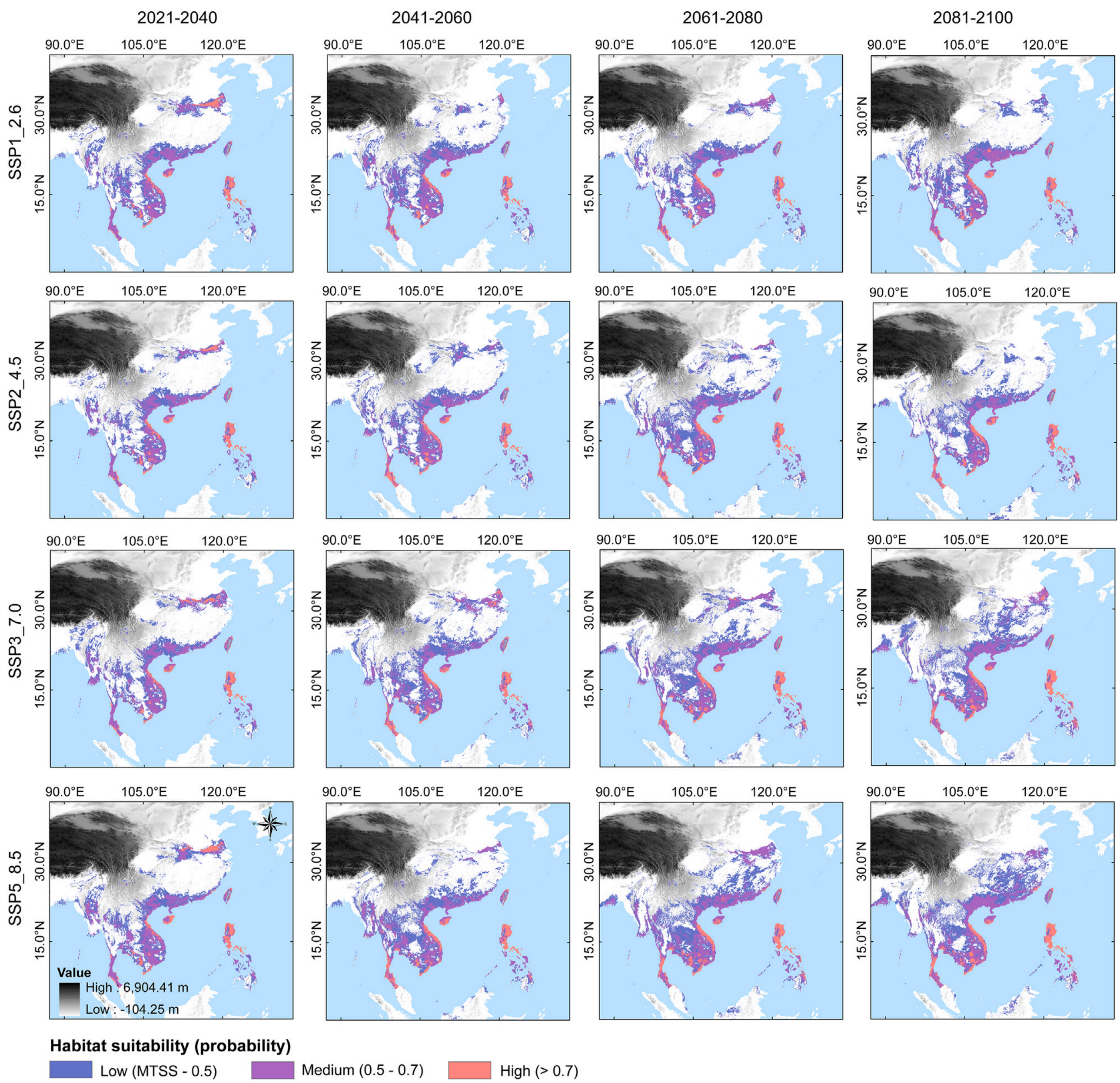

Figure 3. Projected future potential suitable habitats for *H. chinensis* from 2021 to 2100 under four emissions scenarios

Classification of future potential suitable habitats was refined using ArcGIS 10.6 by maximum training sensitivity plus specificity thresholds (MTSS).

See also Figure S7.

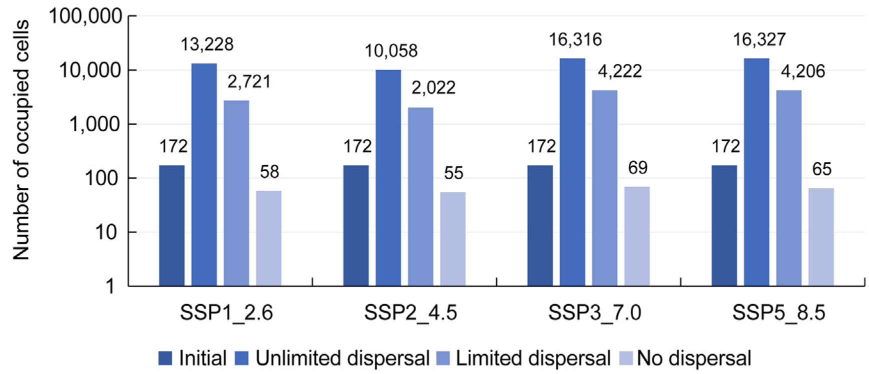

Figure 4. Occupied cells of *H. chinensis* under three dispersal scenarios in future climatic projections

combination, changes in temperature (48.90%) had a greater impact on the distribution models of *H. chinensis* than changes in vegetation type (30%). Factors affecting the selection of animal habitats are complex, including the physiological characteristics of the species itself, food abundance, and shelter availability.[37] For amphibians, which are ectotherms, their distribution is to a large extent constrained by temperature and water availability.[38] Our results contrast with previous studies, which showed that precipitation had a greater impact on the potential range of anurans.[17] This discrepancy is likely related to the non-stationary effect of variables across space and taxa.[39] For example, Xia et al.[40] utilized SDMs to predict potential suitable distribution areas for *Rana hanluica*, and the results indicated that the precipitation of driest month was the key environmental factor influencing the geographic distribution of the species. Conversely, our study indicates that temperature is the key factor influencing the past, current, and future distribution of *H. chinensis.* Our results can be explained by the geographic location of the study, and the habitat selection mechanism of *H. chinensis.* Here, during the Last Interglacial, Last Glacial Maximum, and Mid-Holocene, there was a large range of potential habitat in southern China and Southeast Asia. These areas are located in subtropical and tropical regions, with a distinct monsoon climate characterized by simultaneous rain and heat.[41] In addition, *H. chinensis* is sensitive to temperature changes and has poor cold tolerance.[42] Within a certain temperature range, the mortality rate of *H. chinensis* is significantly correlated with ambient temperature.[42] When the ambient temperature drops below 20°C, its activity is limited to warmer waters.[43] The species also stops feeding and starts hibernating when the temperature is lower than 12°C and dies easily at temperatures below 4°C in Jinhua, Zhejiang, China.[42] Thus, it is reasonable that temperature is an important indicator of suitable habitat for *H. chinensis.* Dramatic changes in local weather conditions caused by global climate change may increase their survival and mortality risk, which may ultimately affect the development and stability of wild populations of *H. chinensis.*

However, while our models showed temperature to be crucial for explaining the present distribution of *H. chinensis*, it is important to note that climatic conditions have varied significantly from past to present, and precipitation has likely influenced the distribution of these amphibians to an extent. The species is an amphibian with high humidity requirements,[42] and it is often present in rice paddies with water and their surrounding wetlands. Amphibian reproduction is generally linked to precipitation patterns,[30] and adults must use environmental cues to time their movements with seasonal precipitation that fill wetlands to give larvae enough time to develop before water levels recede,[44] or align with the artificial flooding of rice paddies to exploit the artificial hydroperiod.[45] Climate change is forecasted to follow a complex pattern, with non-uniform changes in precipitation regimes,[6] and extended droughts are expected to negatively impacts population fecundity and adult survivorship in amphibians.[30] Therefore, *H. chinensis* is more likely to persist in areas with better precipitation conditions or sustained agricultural flooding such as rice paddies, provided that temperature conditions are met.

Table 2. Percentage of cells occupied by suitable H. chinensis habitat under three dispersal scenarios in various future climatic projections

Scenarios	Unlimited dispersal/ Increase/times/Loss/%	Limited dispersal/Increase/ times/Loss/%	No dispersal/Increase/ times/Loss/%
Initial	172	172	172
SSP1-2.6 (2000–2100)	Increase 76.91 times	Increase 15.82 times	Loss of 66.28%
SSP2-4.5 (2000–2100)	Increase 58.48 times	Increase 11.76 times	Loss of 68.02%
SSP3-7.0 (2000–2100)	Increase 94.86 times	Increase 24.55 times	Loss of 59.88%
SSP5-8.5 (2000–2100)	Increase 94.92 times	Increase 24.45 times	Loss of 62.21%

All changes in area calculated using the MigClim v. 1.5 package in R v. 4.3.1.

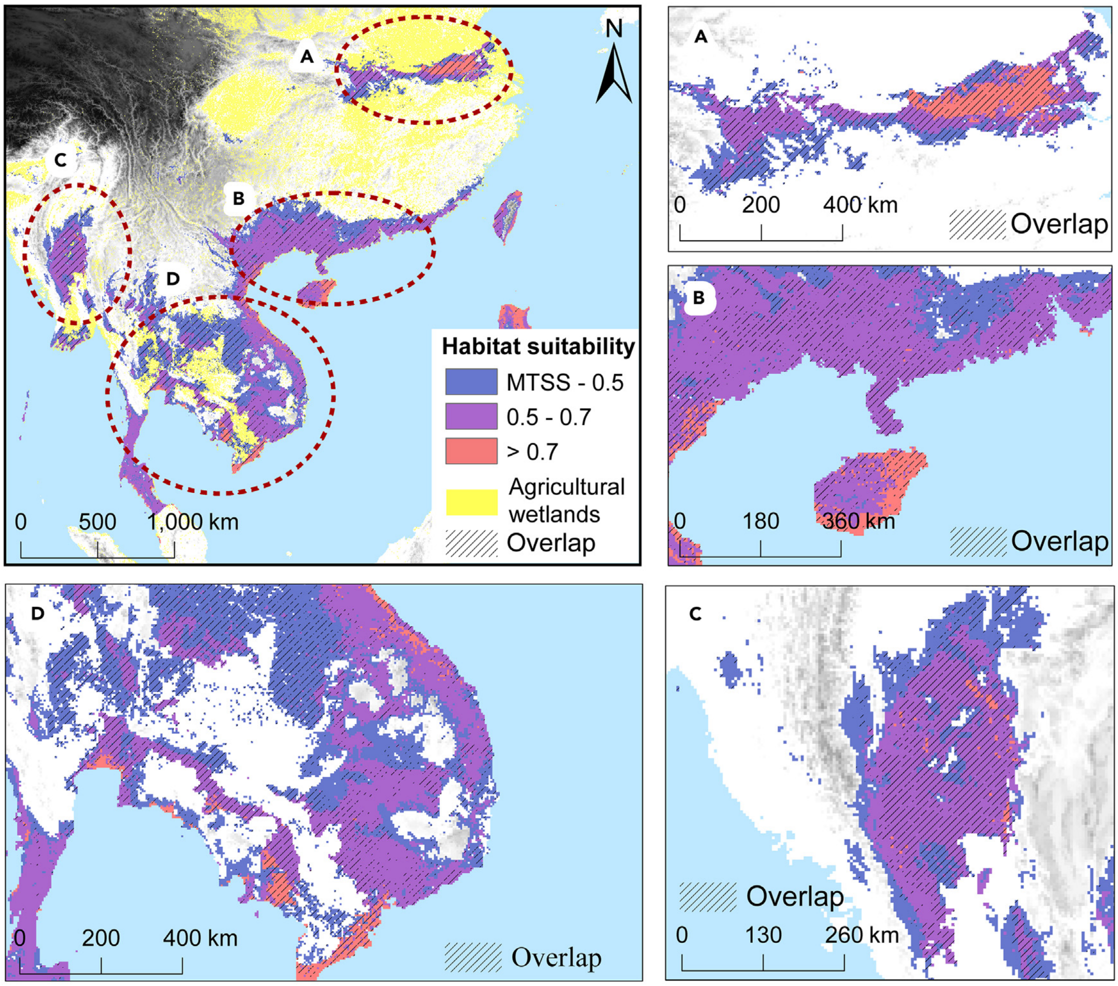

Figure 5. Projected overlap between the suitable habitat and agricultural wetlands under the current climate scenario for *Hoplobatrachus chinensis* in East Asia

The overlap area was calculated using ArcGIS 10.6.

(A) Focus on Jiangsu, Anhui and Hubei in China; (B) Guangxi, Guangdong and Hainan Island in China; (C) Myanmar; (D) Thailand, Cambodia, Lao PDR and Vietnam.

Once hydrothermal conditions are met, sheltering and food resources become two other important factors for habitat selection.[46] Adequate microhabitat must facilitate hiding without impeding the movement of the animals,[42] and vegetation type, vegetation height and cover were the main factors affecting habitat selection in *H. chinensis*.[42,47] Correlatively, temperature and precipitation are closely related to vegetation type, vegetation height, and cover,[48] and *H. chinensis* preferentially selects areas with moderate vegetation height and cover, providing cover from predation and disturbances without affecting their activities and predation.[47] This type of vegetation matches with rice fields, further supporting our results, and even though vegetation type contributed only to 30.30% of our results, together with temperature and precipitation it influences habitat selection by *H. chinensis*.

Predicted habitats suitability and dispersal patterns

The comparison of modeled distributions under historical periods and current climate scenarios suggested that there has been a gradual expansion of suitable habitat for *H. chinensis* since the Last Interglacial (Figure 2), particularly in southern China and much of southeast Asia. Suitable habitats expanded toward eastern China, and the extreme southern portions of the Eastern Palearctic realm, covering Jiangsu and Anhui in central China. During the Last Glacial Maximum, there was a major contraction of the suitable habitat for *H. chinensis*, especially in Southeast Asia, likely related to the climate and sea-land changes of the period.[49,50] The Last Glacial Maximum is the most recent glacial interval in which the sea-land range and climatic conditions were completely different from those of the present day.[51,52] During this period, cold, dry climate and land losses drastically reduced the suitable habitat for *H. chinensis*. In terms of the historical range of *H. chinensis*, Last Interglacial, Last Glacial Maximum, and Mid-Holocene model results showed southern Myanmar, Thailand, Vietnam, the Philippines, and Guangxi in Mainland China and Hainan Island to host stable habitat over time. Those areas that remain unchanged may serve as refuge for *H. chinensis* in harsh climates, because these refuges have physical characteristics that buffer the rate of contemporary climate change.[53] Under future climate scenarios, suitable habitat for *H. chinensis* is likely to expand northward into most of eastern and southern China (Figure 3). Warm and humid climatic environment creates beneficial conditions for *H. chinensis* habitats.

Most amphibians have complex life cycles and dispersal usually occurs after metamorphosis, but conditions prior to metamorphosis can also affect the costs and benefits of staying versus those of dispersing.[30] Amphibians have a low but non-zero dispersal capacity,[15,30] making the limited dispersal scenario more indicative of natural patterns than the unlimited and no-dispersal scenarios. Under the limited dispersal scenario, even considering dispersal barriers, our results suggested that the range of potentially suitable habitat for *H.* chinensis will maintain its expansionary trend in the future. Potentially suitable habitats for *H. chinensis* expanded in eastern China, at the southern edge of the Palearctic realm, driven by increasing temperatures. However, dramatic changes in temperature may severely disrupt amphibian survival and population stability as extreme weather events become more frequent, unseasonal, and short-term,[6] overall the results clearly indicated that the future climate will positively impact the northward expansion of *H. chinensis*. The species is ''lucky'' compared to others, since warmer temperatures will allow for range expansions rather than force contractions. For instance, out of the 141 Australian frog species, 23 and 47 species are predicted to lose at least 30% of their current area of climatic suitability by 2100, under low and high emissions scenarios, respectively.[54] Similarly, amphibians in China may lose 20% of their ranges on average because of climate change.[11]

The expansion predicted under the unlimited dispersal scenario is entirely plausible given that the species is moved frequently by humans as a food source, allowing it to colonize new habitat via long-distance dispersal. For instance, *H. chinensis* introduced to the Philippines by humans and have established a stable population, with individuals dispersing, surviving, and reproducing at multiple sites.[55] Individuals dispersed from areas where the species was first reported, and reached throughout the Philippines by leading-edge dispersal and by long-distance dispersal.[55] Both our results and recent studies[55] suggested that *H. chinensis* has not reached spatial saturation and the species will continue to spread.

A similar situation might be occurring in Jiangxi, Zhejiang and Fujian in China where there are many *H. chinensis* farms. During our surveys, we have found several individuals at numerous locations with scars on their snout resulting from captivity, likely escaped from captive breeding or from mercy releases.[56] As the origin of farmed individuals is unclear, and could be from south Asian unrelated clades,[57] there is a risk of invasion, and population expansion by unrelated clades, even within the native range of the species.

In addition, no dispersal scenario indicated that the potential suitable habitat for *H. chinensis* would be greatly reduced. This may be related to wetland connectivity as it also affects species dispersal.[58] Our focal species, *H. chinensis*, is a species typically present in rice paddies, and with the continued advancement of modern farming practices, agricultural intensification may have impeded the spread of this species as they reduce the connectivity of agricultural wetlands.[59] The impact of connectivity has been demonstrated in another species with similar ecological requirements, *Lithobates catesbeianus*, where individuals were able to reach wetlands far from introduction sites only when wetland connectivity was high, highlighting that habitat permeability mediates diffusion spread for this species.[60]

Predicted habitat overlap

There was a low degree of overlap (25.18%) between suitable habitat for *H. chinensis* and agricultural wetlands under present climatic scenarios. Areas of overlap between agricultural wetlands and highly suitable habitats were mainly in southern Asia, and moderately suitable habitat was concentrated further north in Southeast Asia and East Asia, reaching as far north as Anhui in China. Overall, the majority of overlapping suitable habitat was located in areas that had remained unchanged from Myanmar, Thailand, Cambodia, Vietnam and showed expansion in China. While rice paddies are suitable habitat for the species, the overlap percentage is rather low. This may be related to rice paddy management and modern farming practices, as they can have a different impact on amphibian population across regions.[45] For example, flooding of rice paddies during the fallow phase did not change amphibian abundance in Brazil[61] but did in California,[62] and modern farming practices in paddy fields have negatively affected the habitat and species richness of rice paddy-dwelling species.[22] The reproduction of *H. chinensis* and their juvenile growth and development overlaps with the growing period of crops in agricultural wetlands, and they are often exposed to various pesticide stresses,[63] potentially resulting in difficulties in exploiting rice paddies. In addition, the construction of extensive concrete ridges and ditches also negatively impacts amphibians by reducing the amount of available microhabitat,[43] and rice paddy-dwelling species change their habitats due to urban encroachment on agricultural wetlands.[64] Thus, it is likely that rice paddy management and modern farming practices, as well as urban encroachment, have caused a decline in *H. chinensis* populations in previously suitable agricultural landscapes, forcing the frogs to use alternative habitats. However, the importance of rice paddies for habitat connectivity in the species remains unclear.

Limitations of the study

Our research is based on datapoint available from the literature, and the species is likely present in areas for which no data are available. While this is likely to impact variables such as the area of suitable habitat, it will not impact the validity of our results. The predicted suitable habitats we have obtained in this study have limitations due to layers available, and conservation planning must also take into account local hydrogeological conditions, pollution, and food resources to be practically applicable. Yet this study still provides important macro-level habitat preference information to guide the conservation of *H. chinensis* wild populations.

Conclusions

Our results suggest that climate change will have a positive impact on the expansion of suitable habitat for *H. chinensis*, even given their limited dispersal capacity. Southeast Asia and southern China were important distribution areas for *H. chinensis* under historical and current climate scenarios. In addition, MigClim modeling results indicate that the dispersal capacity of the species is adequate to track future climate change in the absence of additional barriers to dispersion. Future climate change may increase the area of suitable habitat for *H. chinensis* in China and Southeast Asia, likely resulting in the range of the species expanding northward. We also found limited overlap between the currently suitable habitat and agricultural wetlands, indicating that while these habitats provide adequate aquatic habitat, other variables such as pesticide use and human disturbance make the habitat less suitable. This information is valuable to identify suitable habitat fir *H. chinensis* and predicting the effects of increased temperatures on the species under current and future climate scenarios. Moreover, the predictions and results are important guidance for the conservation of the *H. chinensis* in natural and semi-modified habitats.

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Amaël Borzée (amaelborzee@gmail.com).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- Data: Except for some of the occurrence data, which were obtained from field surveys, all other datasets used in this study are publicly available: some occurrence data used in this study were obtained from Global Biodiversity Information Facility database (GBIF: https://www.gbif.org/), Predictor variables used in this study were obtained from WorldClim database (https://worldclim.org/) and Paleoclim database (http://www.paleoclim.org/), Vegetation type used in this study were obtained from National Earth System Science Data Center (http://www.geodata.cn/), DEM used in this study were obtained from Geospatial Data Cloud (https://www.gscloud.cn/), Land use and land cover used in this study were obtained from Casearth (https://www.data.casearth.cn/).
- Code: This paper has reported original code in the Mendeley Data: https://doi.org/10.17632/72z78njbzb.1.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

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AUTHOR CONTRIBUTIONS

All authors contributed to the study conception and design. Data collection was done by X.Z., Z.Wang, and A.B., and analyses were performed by X.Z. and supervised by A.B. The first draft of the manuscript was written by X.Z. and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

DECLARATION OF INTERESTS

The authors declare no conflict of interest.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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  - Species introduction
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SUPPLEMENTAL INFORMATION

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Occurrence data	field surveys	Document S1 Table S2
Occurrence data	Global Biodiversity Information Facility database	https://www.gbif.org/; RRID: SCR_005904
Predictor variables	WorldClim database; Paleoclim database	https://worldclim.org/; RRID: SCR_010244 http://www.paleoclim.org/; RRID: SCR_025657
Vegetation type	National Earth System Science Data Center	http://www.geodata.cn/; RRID: SCR_025658
DEM	Geospatial Data Cloud	https://www.gscloud.cn/; RRID: SCR_025659
Land use and land cover	Casearth	https://www.data.casearth.cn/; RRID: SCR_025660
Software and algorithms		
ArcGIS	ESRI	https://www.arcgis.com/index.html; RRID: SCR_011081
Origin 2019b	OriginLab	https://www.originlab.com/; RRID : SCR_014212
R	R Core Team	https://www.r-project.org/; RRID: SCR_001905
MaxEnt.jar	American Museum of Natural History	https://biodiversityinformatics.amnh.org/open_source/maxent/; RRID: SCR_021830

METHODS DETAILS

Species introduction

Our focal species, *Hoplobatrachus chinensis*, belongs to the anuran family Dicroglossidae. *Hoplobatrachus rugulosus, Rana rugulosa or Rana tigerina* are all synonyms of *Hoplobatrachus chinensis*[65,66]. Though the name *H. rugulosus* has been used by some,[66,67] here we follow the most recently accepted nomenclature.[66] The species *H. chinensis* lives mainly in plains and hilly landscapes at altitudes between 20 and 1120 m (www.amphibiachina.org) and it is commonly found in moist habitats such as agricultural wetlands, ditches, pits, and ponds[35] in East and Southeast Asia (Figure 1).[68] The species is generally present in rice paddies and their surrounding areas, as rice paddies have the necessary conditions for development, growth, and breeding, such as shallow, slow-moving lentic water, moist surface soils, abundant food sources, and adequate sheltering microhabitat.[43] In recent decades, due to human disturbance, over-harvesting, and ecological degradation, *H. chinensis* has declined sharply in populations density and distribution area,[69] leading it to be classified as a national Class II protected species in China,[63,70] as well as an Appendix II aquatic wild species under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES, https://cites.org/eng). For instance, surveys of wild populations of *H. chinensis* in Jinhua, Zhejiang, found that areas with larger populations have suffered from habitat destruction in recent years, leading to a decrease in the number of populations.[43] Now, it is difficult to see wild *H. chinensis* in places such as Jinhua, Zhejiang and Weizhou Island in Beihai, and wild populations are at risk of extinction if this trend continues.[43,71]

Occurrence data and predictor variables

Occurrence data

We collected *H. chinensis* occurrence data from both field surveys and secondary sources, including the Global Biodiversity Information Facility database (GBIF: www.gbif.org; http://www.doi.org/10.15468/dL.t5ckf6). We conducted field surveys systematically following a grid pattern with a 10 km mesh size overlayed on the agricultural wetlands of Jiangsu and Anhui. Considering the home range size and movement abilities of the species, as well as previous modeling studies on an East Asian anuran,[72] a 10 km mesh size was considered a suitable size for the exclusion of habitat patches. In addition, *H. chinensis* is locally widespread and the mesh size we selected is adequate to limit redundancy and bias in our monitoring and the final occurrences data. Occurrence was determined through aural surveys, with 10 min spent listening for vocalizations of the species at each site. The aural surveys involved auditory monitoring for the presence of *H. chinensis* at predetermined sites based on habitat preference of the species to increase the probability of detection, a common method employed in anuran field surveys to assess population presence.[64] All surveys were conducted during the peak breeding season of the species in 2021, 2022, and 2023 (Document S1 Table S2), following the protocol from Borée et al..[64,73,74] In GBIF, we searched for species occurrence records for *H. chinensis* and the synonymous *H. rugulosus, Rana rugulosa*, and *Rana tigerina.* In total, we obtained 6793 presence records (1884–2023, Document S1 Table S3). We removed erroneous records and used the ''Spatially Rarefy Occurrence Data for SDMs (reduce spatial autocorrelation)'' tool in the SDMToolbox of ArcGIS 10.6 (ESRI, 2012) to remove duplicates and thin the data at a resolution of 10 km. The final cleaned occurrence dataset resulted in a total of 531 records to be used for modeling (Document S1 Table S4).

Predictor variables

We downloaded 20 environmental layers (elevation and 19 bioclimatic variables) for the present climate and future climatic scenarios (2023–2100) at a resolution of 2.5 min from the WorldClim database (http://www.worldclim.org) to model the distribution of *H. chinensis*. We also downloaded the same environmental data for different paleoclimates (Mid-Holocene, MH; Last Glacial Maximum, LGM; Last Interglacial, LIG) from the Paleoclim database (http://www.paleoclim.org/). For the future climatic scenarios, we used the Shared Socio-economic Pathways (SSPs) of the Coupled Model Intercomparison Project Phase 6 (CMIP6), which includes four scenarios (SSP1-2.6, SSP2-4.5, SSP3-7, SSP5-8.5; Eyring et al., 2016). The first value following the SSP represents the hypothetical shared socio-economic pathway and the second value represents the approximate global effective radiative forcing by 2100.[75] SSP1-2.6 is a sustainability scenario in which the radiative forcing stabilizes at about 2.6 W/m^2 in 2100, which would be significantly lower than the preindustrial revolution multi-model ensemble-averaged global average temperature result by 2°C.[75] SSP2-4.5 is a medium radiative forcing scenario, with the radiative forcing stabilizing at about 4.5 W/m^2 in 2100.[75] SSP3-7.0 is a medium-high radiative forcing scenario, with radiative forcing stabilizing at about 7.0 W/m^2 in 2100, which combines relatively high social vulnerability (SSP3) and relatively high radiative forcing.[75] SSP5-8.5 is a high forcing scenario, with the radiative forcing increasing to 8.5 W/m^2 in 2100.[75]

In addition, we added three non-climate data layers (vegetation type, slope, aspect). We downloaded the vegetation type layer from the National Earth System Science Data Center (http://www.geodata.cn) and we extracted slope and aspect from the DEM using ArcGIS's surface analysis tool, which was downloaded from the Geospatial Data Cloud (https://www.gscloud.cn/). We clipped all layers to encompass the range of the species in the Eastern Indomalaya and projected them to the geographic coordinate system WGS1984. We divided the above predictor variables into two datasets to model separately. Dataset 1 included 19 bioclimatic variables and dataset 2 included 19 bioclimatic variables, vegetation type, slope, and aspect.

Since multicollinearity between explanatory variables can lead to inaccurate prediction by excluding significant predictive variables,[76] we first tested the model using all variables. Then we calculated pairwise Pearson correlation coefficients for all combinations of variables. Based on the ecological requirements of *H. chinensis*,[43] we selected the most important variables affecting the distribution of the species and removed one of each pair of variables with a Pearson correlation coefficient greater than 0.7.[77] For example, precipitation of the driest month (Bio14) was highly correlated with precipitation of the driest quarter (Bio19, $\rho = 0.99$); and we removed Bio19 from this pair due to the aquatic-hydrostatic ecotype of *H. chinensis*.[78] This ecotype is characterized by the fact that the species survives and reproduces in bodies of water, and that adults live permanently near or in hydrostatic waters. After selection, dataset 1 contained 16 predictor variables and dataset 2 included 19 predictor variables.

Modeling habitat suitability

Using the final occurrence dataset with meaningful bioclimatic variables, we ran the habitat suitability models across different climates with MaxEnt modeling algorithm version 3.4.1.[32] To prepare maps of habitat suitability for *H. chinensis*, we pre-determined the ideal value of the regularization multiplier (RM) and feature combination of the MaxEnt model using the package ENMeval, running in R version 4.3.1 (R Core Teamt, 2023). We evaluated five feature types in MaxEnt: linear (L), quadratic (Q), hinge (H), product (P), and threshold (T). We analyzed the complexity of each feature under various parameter conditions and we selected the model with the lowest AICc. The best feature combination of parameters for the MaxEnt model for both datasets was LQPHT, with an RM value of 1.5.

Correcting for geographic sampling bias improves MaxEnt predictive performance.[79] In addition, environmental filtering can be used to assess environmental biases, which improve MaxEnt discriminatory ability.[80] We produced a bias file to adopt the target group background approach recommended by Phillips et al.,[81] an option available directly in MaxEnt. The bias file used consisted of a binary raster grid of the same resolution based on all amphibian records in Asia downloaded from GBIF, which reflects local survey effort.

All models for the species were developed with the occurrence data and 10,000 background points, representing the distribution of environmental conditions in the study region. We randomly selected 75% of the data to fit the models and held the remaining 25% for testing purposes. We ran 20 replicates per model. We used the maximum training sensitivity plus specificity thresholds (MTSS) to classify the output data[82] based on a suitability index: unsuitable (<MTSS), low suitability (MTSS-0.5), medium suitability (0.5–0.7), and high suitability (>0.7). We refined the classification of the potential suitable habitats using MTSS in ArcGIS 10.6 (ESRI, 2012). We made all changes in the refined area using the 'raster'[83] and 'sp'[84] packages in R v. 4.3.1 (R Core Team, 2023).

We ran a multivariate environmental similarity surface analysis (MESS) to evaluate the degree of climatic anomaly between current and future.[85,86] MESS measures the similarity (S) between the climatic conditions at a point in time and the reference layer. For $S > 0$, the smaller the S value, the greater the difference between the climatic variables of the point and the reference layer.[85,86] When $S = 100$, there is no difference between the climatic variables of the point and the reference layer, while $S < 0$, indicates that at least one climatic variable at the point is beyond the reference range, and the greater the negative value, the higher the degree of climate anomaly.[85] In this case, the mobility-oriented parity approach (MOP)[87] is similar to MESS in detecting strict extrapolation, however, MOP keeps the maximum extrapolation value of 0 (strict extrapolation) to limit SDM projections outside training condition ranges, making it impossible to evaluate extrapolation degree beyond the training conditions.[88] Therefore, we used MESS as it is sufficiently informative but more flexible than MOP to identify areas of past or future climates with no modern analog. This is crucial for our interpretation of the projected climate suitability model for *H. chinensis* as it is a cosmopolitan species with a large-scale distribution.

In order to evaluate the performance of the model under climate conditions, we calculated the corrected Akaike information criterion (AICc), the area under the receiver operating characteristic curve (AUC) and the true skill statistic (TSS). Despite the existence of alternatives such as Sorensen and Jaccard indices, the AUC and TSS are more relevant for our study since we calibrated the SDMs for the present time, and our models focused on a species with a wide geographic distribution. Additionally, both AUC and TSS are still accurate descriptive statistics to evaluate the performance of the models,[13,89] effective for models' evaluation,[90] and still relevantly used by other high-impact studies.[13,89]

First, we calculated the AICc,[91] since the AUC does not account for the goodness-of-fit of the model and model complexity, or the increase of false absences due to the use of background data.[92] AICc balances the goodness of fit and the number of parameters of the model, which allows selecting models with optimal complexity.[91] Second, we calculated the AUC and TSS using the testing dataset.[93] AUC is a threshold independent statistic that represents the ability of a model to discriminate between presences and absences of species occurrences from the study area.[94] TSS is considered to be the most practical measure of model performance to distinguish between presence and absence, which scale spans from −1 to 1, with higher values indicating better model performance.[95] Using AUC and TSS to evaluate ENMs can improve the accuracy of model results.[96]

Incorporating dispersal constraints and predicting suitable distribution

We used the paleoclimate data to project the optimal model onto past climates using MaxEnt. To project the future distribution under a variety of climate scenarios accounting for dispersal constraints, we used the cellular automation model as implemented in the MigClim package in R.[33] The MigClim package is a function library that enables the implementation of species-specific dispersal constraints into projections of species distribution models under environmental change and/or landscape fragmentation scenarios.[33,97] For example, Lemes et al.[98] examined how animal-plant interactions and dispersal limitations might affect the responses of Brazil nut-dependent frogs (*Adelphobates castaneoticus, Osteocephalus castaneicola* and *Rhinella castaneotica*) to climate change. The result showed that when dispersal limitation was included in the models, the suitable range of all three frog species was reduced considerably by the end of the century.[98] The finding demonstrated the effectiveness of MigClim in modeling terrestrial habitat for both invertebrates and vertebrates. In the MigClim model, we input three types of data: (1) the species' initial distribution (a binary map of *H. chinensis* initial distribution); (2) habitat suitability maps; and (3) barriers (land use types that inhibit the dispersal of target species). In accordance with the habitat characteristics of *H. chinensis*, we set agricultural wetlands and ponds to 0, the weakest resistance to dispersion, indicating areas where *H. chinensis* can spread. We assigned a value of 1 to other land types modified or degraded by humans, representing barriers to dispersal. Land use and land cover were downloaded from Casearth (www.data.casearth.cn).[99] We considered unlimited dispersal to be ecologically valid here, not because the species can disperse by itself without restriction, but because it is heavily traded across East Asia for human consumption, and individuals escape and establish populations regularly.[57,69]

We constructed our MigClim models with the following parameters based on *H. chinensis* and the model parameter requirements[97]: rcThreshold = 500; encChgSteps = 5; dispSteps = 20; iniMatAge = 1; dispKernel = c(1); propagate production = c(0.02, 0.1, 0.5,0.9); lddFreq = 0.05; lddMinDist = 2; lddMaxDist = 3; replicates = 5. Finally, we organized the number of pixels that *H. chinensis* can occupy under different climate scenarios from our results into a table (Table 2). All calculations were performed in R v. 4.3.1 (R Core Team, 2023).

Overlap of suitable habitats

We assessed the extent to which potentially suitable habitats for *H. chinensis* overlap with agricultural wetlands under current climate conditions because the reproduction, growth, and development of *H. chinensis* and many other anurans overlaps with the growing season of agricultural crops.[45,100] However, environmental changes in agricultural wetlands may force frogs out of rice paddies or ponds due to the effects of modern farming practices, such as pesticide use[100] and the construction of cement ditches.[101] The extent of overlap between *H. chinensis* and agricultural wetlands under the current climate conditions was assessed by comparing existing habitat suitability maps with agricultural wetlands ecosystem maps. We extracted agricultural wetlands from land use and land cover data. The proportion of occurrences from the agricultural wetlands compared to non-agricultural wetlands was 1:7, with 319 datapoints in dry agricultural landscapes. We binarized the habitat suitability map and the agricultural wetlands map and transformed them into presence-absence map using the reclassification function of ArcGIS 10.6 (ESRI, 2012). Then, we superimposed the converted presence-absence maps of *H. chinensis* and agricultural wetlands to determine areas of overlap. We calculated the number of suitable pixels from the overlapped map between habitat suitability of *H. chinensis* under the current climate the and presence-absence map of agricultural wetlands.