Frontiers of Biogeography 2024, 16.2, e62301

RESEARCH ARTICLE

Frontiers of Biogeography
the scientific journal of
the International Biogeography Society

From Korean to northeast Asian endemicity: on the occurrence of *Pelophylax chosenicus* along the Eastern Coastal Yellow Sea

Amaël Borzée[1,2]*, Yucheol Shin[1,3], Yoonhyuk Bae[1],
Daecheol Jeong[4], Hina Amin[5], Mi-sook Min[4]* and Siti N. Othman[1]

[1]Laboratory of Animal Behaviour and Conservation, College of Life Sciences, Nanjing Forestry University, Nanjing, People's Republic of China.

[2]Jiangsu Agricultural Biodiversity Cultivation and Utilization Research Center, Nanjing, Jiangsu Province, 210014, People's Republic of China.

[3]Department of Biological Sciences, College of Natural Science, Kangwon National University, Chuncheon, Republic of Korea.

[4]Research Institute for Veterinary Science and Conservation Genome Resource Bank for Korean Wildlife, College of Veterinary Medicine, Seoul National University, Seoul 08826, Republic of Korea.

[5]Co-Innovation Center for Sustainable Forestry in Southern China, College of Biology and the Environment Nanjing Forestry University, Nanjing 210037, People's Republic of China.

*Correspondence: Amaël Borzée, amaelborzee@gmail.com; Mi-sook Min, minbio@yahoo.co.kr

Abstract

Understanding the distribution of species is a primary requirement to understand their behaviour, conservation, and phylogeography. Over the last decades, the number of species described on the Korean Peninsula has significantly increased, but surveys around the boundaries of the Peninsula are still needed to refine the range of these species. Further surveys, supported by ecological niche models, are especially needed in areas where the environment is similar and connected. We conducted surveys in the continuous landscapes of the Republic of Korea, the Democratic People's Republic of Korea, and the People's Republic of China to determine the distribution of the gold-spotted pond frog, *Pelophylax chosenicus* (Okada, 1931). The surveys were conducted between 2015 and 2021 through the use of visual and call encounters. We supported our surveys with molecular analyses by sequencing the mitochondrial 16S rRNA, 12S rRNA, and Cyt*b* gene fragments to confirm the species identity of the northernmost population in China. As a result, we found the species to be widespread in low-elevation wetlands along the eastern coast of the Yellow Sea, with two isolated populations in the southeast of the Korean Peninsula, and the northernmost population in the vicinity of Dandong in the People's Republic of China. We then determined the importance of landscape types for the species, especially rice paddies, and used ecological niche models to define suitable habitats across the region. As this species is listed as threatened in the Republic of Korea, knowing its exact distribution will be important for conservation practices.

Highlights

- We determined new records of *Pelophylax chosenicus* and suitable habitat at a new locality along the Eastern Coast of the Yellow Sea based on field surveys, molecular genetics, and ecological niche modelling.
- Our analyses support two divergent clades within the species, showing a pattern of single colonisation of the Korean Peninsula from Northeastern China.
- We determined the importance of low-elevation landscapes for the species based on its newly defined range across northeast Asia.
- We highlighted that most of the remaining habitat for the species was made of agricultural wetlands, i.e. rice paddies.
- Our ecological niche models showed that isothermality, precipitation of the driest month, and mean temperature of the wettest quarter were the most important variables explaining the distribution of the species.

Keywords: anuran surveys, ecological niche modelling, molecular barcoding, northeast Asia, range extension, rice paddies, species identification, water frog

e-ISSN: 1948-6596 https://escholarship.org/uc/fb doi:10.21425/F5FBG62301

Introduction

Identifying the distribution of species is a key requirement to understand their diversity and behavioural ecology, but also the threats they face (Manne and Pimm 2001, Richardson and Whittaker 2010). Historically, conducting field surveys was one of the first forms of research effort in the study of biodiversity (Wallace 1876), and determining the distribution and occurrence of species remains an essential prerequisite to understand and protect biodiversity (Wang et al. 2021, Borzée 2023). Data on occurrences are generally based on field surveys, automated monitoring, surveys via citizen science, and literature reviews (Fletcher Jr et al. 2019, Groffen et al. 2022). The raw data can then be complemented through the use of ecological niche models to determine the suitable habitat for the species (Araújo et al. 2019), which may be ground-validated through surveys to find new populations (Mizsei et al. 2016). The use of ecological niche models has been a critical development in ecology as it enables the understanding of species distribution, and prediction of species occurrence across the landscape. This methodology is particularly beneficial over large areas (Synes et al. 2016), or when field surveys are not feasible (Peng et al. 2023). This is the case for taxa distributed across the Korean Peninsula and the northeast People's Republic of China (hereafter China), in which the species' distribution in the Democratic People's Republic of Korea (hereafter DPR Korea) can only rarely be surveyed (Borzée et al. 2021).

The genus *Pelophylax* Fitzinger, 1843 is widespread in Eurasia, likely originating from the western Palearctic (Pyron 2014), with the East Asian clades having diverged about 6.2 mya (Liu et al. 2010). The genus is almost continuously distributed across the Palearctic, and some species are also found in the dry landscapes of central Asia. In northeast Asia, the *Pelophylax nigromaculatus* (Hallowell, 1861) and *Pelophylax plancyi* (Lataste, 1880) species complexes (following Liu et al. 2010) have diverged about 4.8 mya, but they have a history of complex hybridisation, with cytonuclear discordance in numerous populations, likely in relation to glacial cycling (Komaki et al. 2015). The genus is widespread across numerous landscapes as species have broad ecological requirements: some species can breed in most types of wetlands (Garcia et al. 2017; e.g. *P. nigromaculatus* in northeast Asia, Borzée et al. 2021), and they express traits associated with the successful invasions of new habitats (Wang et al. 2016, Wang et al. 2017, Bae et al. 2022). Niche segregation between the two species complexes is also likely to occur based on landscape use (Borzée 2024), prey preference, and microhabitat use (Eom et al. 2007, Borzée et al. 2019b, Nakanishi et al. 2020), with the *P. plancyi* complex expected to have more stringent ecological requirements.

Pelophylax chosenicus was first described in 1931 (but see Okada 1926) and the species can be estimated to have been abundant at the beginning of the 20th century (Okada 1928, Okada 1931, Shannon 1956). Hybridisation with sympatric *Pelophylax* species has been known for a long time (Nishioka 1972, Nishioka and Okumoto 1983), although the behavioural ecology of the species has been studied for less than 30 years (Yoon et al. 1998). Attention to the conservation needs for the species is more recent (Shim 2003, Ra et al. 2008a, Park et al. 2009), and work to date has provided important insights to guide further research (Do et al. 2021). *Pelophylax chosenicus* is closely related to *P. plancyi* (Ryu and Hwang 2011, Zhou et al. 2023), and the time of divergence between the two clades is so far unresolved, although it is likely to be relatively recent (Liu et al. 2010). In addition, the species are morphologically distinct, with male *P. plancyi* having clearly visible vocal sacs (Fei et al. 2012) and male *P. chosenicus* generally lacking vocal sacs, or having internal vocal sacs (Kim et al. 2019), despite some exceptions possibly related to hybridisation with *P. nigromaculatus* as males of the latter species have large vocal sacs and the two species hybridise (Komaki et al. 2015, Borzée 2024).

Pelophylax chosenicus is distributed along the western coast of the Korean Peninsula, until an unknown northern boundary in China. Following multiple publications on northward range extension (Borzée et al. 2017b, Borzée et al. 2018b, Son and Borzée 2020, Zhou et al. 2023), and modelling results showing that the species likely extends further north than surveyed (Borzée et al. 2021), more information is needed on the distribution of the species, and especially in the coastal area in China. Thus, this study was conducted to understand the distribution of *P. chosenicus* through field surveys and ecological niche modelling, relying on molecular tools to identify the northernmost population at the species level.

Materials and Methods

Field surveys

Surveys were conducted between 2015 and 2021, mixing both standardised transects and opportunistic observations. Standardised surveys were conducted separately in the Republic of Korea (R Korea hereafter), DPR Korea, and China. The surveys in R Korea were conducted in conjunction with surveys conducted for hylid populations (Borzée et al. 2017c, Borzée et al. 2018a) as *Pelophylax chosenicus*, the target species, generally shares its breeding habitat with *Dryophytes suweonensis* and *D. flaviventris* (Borzée et al. 2020a). The surveys were conducted between late April and early July, matching the breeding season of the species (Seo et al. 2014, Groffen et al. 2022). Survey sites were broadly selected to match the habitat types where the species occurs, including both natural and agricultural wetlands. Each site was surveyed through an aural transect, and the presence and absence of the species were binary encoded for each site (0 = absence; 1 = presence). The time of day and weather patterns were selected to match with the activity windows of the species (Yang et al. 2000). The exact details of the protocol can be found in Borzée et al. (2017a).

In addition, opportunistic survey transects were conducted across the nation, always matching with the breeding season of the species and in potentially adequate habitats (survey sites in Fig. 1 and GPS coordinates in Table S2).

Surveys in DPR Korea were conducted opportunistically in 2017 and 2018, followed by surveys in 2019 relying on the same protocol as the one used in R Korea. The methodology and data points are presented in a countrywide review (Borzée et al. 2021). Surveys in China were conducted in June 2018, following the same protocol as used in R Korea, but within an area geographically restricted to the regions surrounding the city of Dandong. Additional opportunistic survey transects were conducted at four sites along the coast and further along the border between China and DPR Korea (Fig. 1 and GPS coordinates in Table S2).

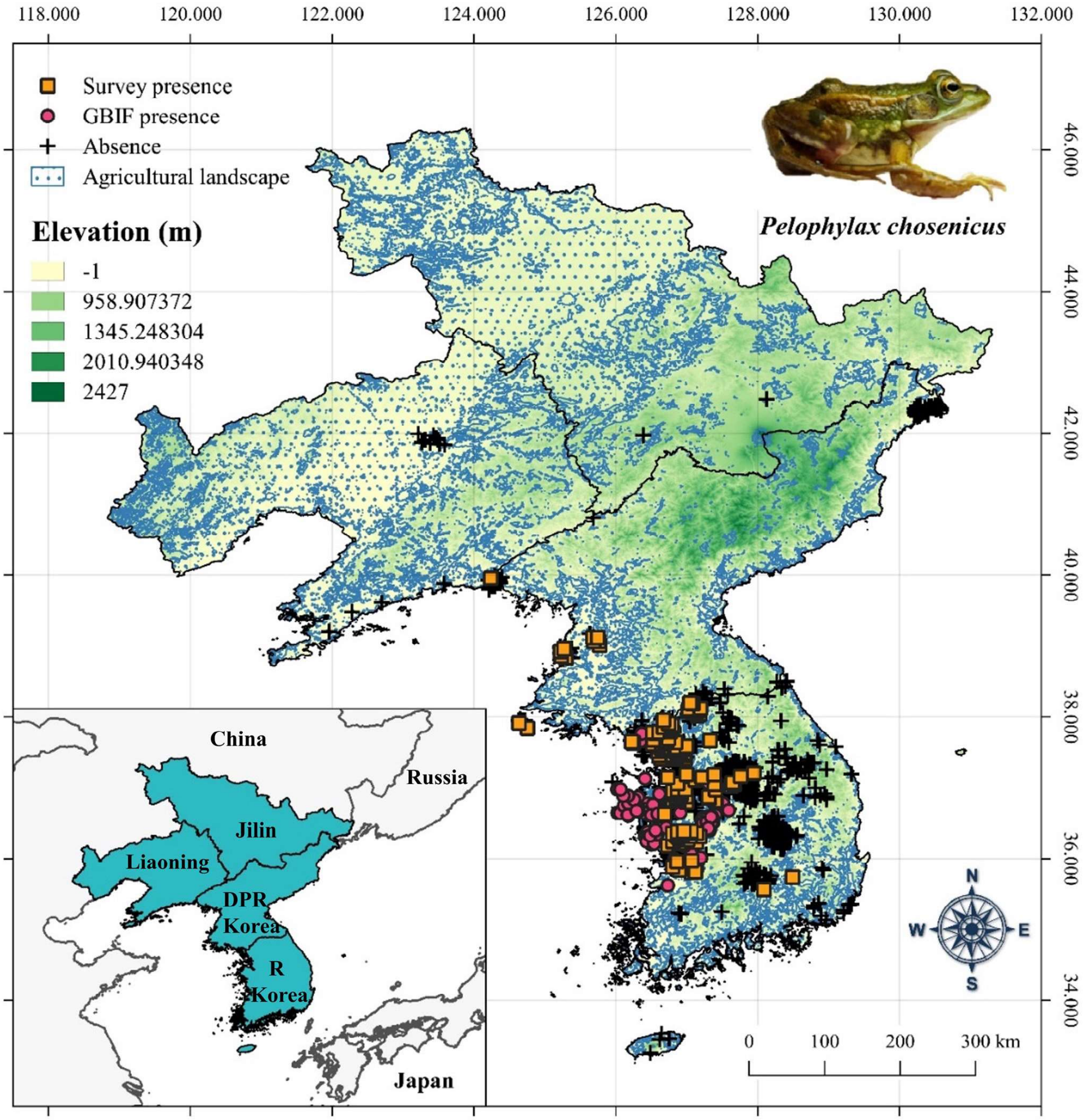

Figure 1. Spatial distribution of presence (*n* = 403; 273 field survey points and 130 from GBIF and one museum datapoint) and putative absence points from field surveys (*n* = 1280) for *Pelophylax chosenicus* across the study area. The presence points are divided into unique survey-based data and occurrence data derived from the Global Biodiversity Information Facility (GBIF.org; DOI: https://doi.org//10.15468/dl.6kvymf). The agricultural landscapes are represented as areas with an agricultural landscape cover greater than 50%. The location of the study area (blue polygon) in northeast Asia is shown on the inset map. Map computed with QGIS3 (QGIS Development Team (2022). QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org).

The GPS coordinates were only recorded at the starting point of all transects, and as no transect was longer than 500 m it did not impact the coordinate accuracy of subsequent analyses. In total, we conducted 1674 surveys. While the probability of detecting the species should be close to the highest value possible with the protocol used (Petitot et al. 2014, Başkale and Çapar 2016), and specifically because of spending at least 5 min at each site, we consider each transect where the species was not detected as a putative absence point later in the manuscript. The dataset was also complemented by a museum datapoint (Shin et al. 2020), resulting in an additional presence point (37.6678°N, 127.3264°E).

Sampling ethics and molecular identification

To further verify the occurrence of *P. chosenicus* in China, we identified the six individuals sampled during our survey in Dandong, China through barcoding and phylogenetic analyses. All six individuals were captured on the spot during the survey, and orally swabbed (Dryswab™ ENT, Medical Wire, Wiltshire, UK) following non-invasive methods, ethically guided and permitted by the Experimental Animal Welfare and Ethics Committee of Nanjing Forestry University (IACUC approval number: 20-220-11). The individuals were released back to the sampling point within 5 min of capture, and the buccal swabs were kept in dry conditions with desiccation beads, and then frozen at -20°C until DNA extraction. We extracted the genomic DNA using the DNeasy Blood and Tissue Extraction Kit (Qiagen, Hilden, Germany), following the manufacturer's protocol. We determined the concentration of each DNA sample using a NanoDrop™ 2000/2000c. To complement the dataset, we also added eight *P. chosenicus* individuals sampled in R. Korea (sample information in Table S1).

For all samples, we isolated and amplified three of the most phylogenetically informative mitochondrial markers commonly used for barcoding of northeast Asian *Pelophylax*: 16S rRNA, 12S rRNA, and Cytochrome b (Cyt*b*) using polymerase chain reactions (PCR). The primer pairs targeted a 510 bp-long 16S rRNA gene fragment (Sumida et al. 2002) with the primers FS01 (5'-AACGCTAAGATGAACCCTAAAAAGTTCT-3') and R16 (5'-ATAGTGGGGTATCTAATCCCAGTTTGTTTT-3'), a 380 bp-long 12S rRNA gene fragment using the primers L1091 (5' (5'AAAAAGCTTCAAACTGGGATTAGATACCCCACTAT3') and H1478 (5'TGACTGCAGAGGGTGACGGGCGGTGT3') adapted from Kocher et al. (1989), and a 658 bp-long Cyt*b* gene fragment using the primers B104F (5'AACATCTCTGCATGATGAAACTTCGG-3') and B829R (5'ATTGAGCGAAGGATGGCGTAGGCGAA-3') adapted from Liu et al. (2010). We prepared the PCR reaction with a total volume of 20 µL per tube for each DNA template, and each sample contained 35 to 50 ng/µL of DNA. The final concentrations of our PCR reactions were 0.125 µM for each forward and reverse primer, 1x Ex Taq Buffer (Takara; Shiga, Japan), 1.875 mM of magnesium chloride ($MgCl_2$), 0.2 mM of dNTPs Mix (Takara; Shiga, Japan), 0.1 unit/µL of Ex taq (HR001A, Takara; Shiga, Japan), and we added double-distilled water to make up the final volume. We conducted the PCR amplifications using a SimpliAmpTM Thermal Cycler (Applied Biosystems, USA), under the following thermal conditions: initial denaturation for 5 min at 95°C; 35 cycles of denaturation at 94°C for 1 min, annealing at 55°C for 1 min, extension at 72°C for 1 min, followed by a final extension at 72°C for 10 min. To screen the PCR products, we ran the electrophoreses on a 1.5% agarose gel loaded with 3 µL of PCR amplicons and 1 uL of TopGreen Nucleic Acid 6x Loading Dye (GenomicBase, Republic of Korea). The PCR amplicons were sent for purification and Sanger sequencing for both forward and reverse directions to Cosmogenetech (Cosmogenetech Co., Ltd., Seoul, Republic of Korea) and Tsingke Biotech Co., Ltd. (Beijing, China). We deposited all newly generated sequences in GenBank (accession numbers in Table S2).

To confirm the identity of the individuals sampled in Dandong, we then reconstructed the phylogeny of the species using different combinations of independent and concatenated datasets of 16S rRNA (*n* taxa = 93), 12S rRNA (*n* taxa = 101), and Cyt*b* (*n* taxa = 170) gene fragments. The taxa in the analyses included the sympatric and congeneric species in the region: *P. nigromaculatus, P. plancyi, P. chosenicus, P. mongolius, P. hubeiensis,* and *P. fukienensis*; along with five outgroup taxa consist of the western Palearctic *P. bedriagae* and *P. lessonae,* and three Asian ranids; *Glandirana emeljanovi*, *G. rugosa*, and *Amolops granulosus* (Table S1). To align the sequences, we first retrieved the sequences for ingroups and outgroups from BLASTn and GenBank (accession numbers in Table S1; originating from Min et al. 2008, Zhang et al. 2008, Liu et al. 2010, Ryu and Hwang 2011, Jeong et al. 2013, Komaki et al. 2015, Hofman et al. 2016, Jiang et al. 2017, Eo et al. 2019, Huang et al. 2019, Tokumoto et al. 2019, Oike et al. 2020, Margaryan et al. 2021, Zhou et al. 2022b, and Zhou et al. 2022a). We analysed and trimmed the DNA sequences using Geneious Prime version 2022.1 (http://www.geneious.com, Kearse et al. 2012), and aligned the sequences using Clustal Omega (Sievers et al. 2011) with the default settings in the same Geneious Prime program. The final alignments used for the phylogenetic analyses were 890 bp-long for the concatenated 12S rRNA and 16S rRNA gene fragments (*n* sequence = 75), 658 bp-long for the Cyt*b* gene fragment (*n* sequence = 170), and 1,548 bp-long for the concatenated 12S rRNA, 16S rRNA and Cyt*b* gene fragments (*n* sequence = 70).

Finally, we reconstructed the phylogeny using the Bayesian Inference (BI) method in MrBayes version 3.2.6 (Huelsenbeck and Ronquist 2001). We determined the best nucleotide substitution model using PartitionFinder version 2.1.1 (Lanfear et al. 2017) and obtained SYM+G as the best model for the concatenated 16S rRNA and 12S rRNA gene fragments and HKY+I+G as the best nucleotide substitution model for the Cyt*b* gene fragment. In addition, we obtained GTR+I+G as the best model for the concatenated dataset for the three gene fragments, based on the five partitions we recovered using the fixed single position strategy for the non-coding 16S rRNA and 12S rRNA gene fragments, and the three codon positions strategy for the protein coding Cyt*b*. In MrBayes version 3.2.5 (Huelsenbeck and Ronquist 2001), we analysed the input NEXUS files for each independent and concatenated datasets. For each dataset input file, we included information about the best fit nucleotide substitution model, and we ran the analysis by sampling the Markov chain Monte Carlo (MCMC) for ten million generations. We sampled the Markov chain every 1000 generations and discarded the first 10% of the generations as burn-in. We evaluated the adequacy of the sampling and the convergence of the trees generated from the analyses by confirming that the average standard deviation of split frequencies had reached < 0.01 at the end of each analysis. To verify whether each tree reached stationarity, we evaluated the effective sample size (ESS) of each posterior distribution using TRACER version 1.7.1 (Rambaut et al. 2018), confirming ESS > 400 across all runs.

Additionally, due to the availability of sequences for *P. plancyi,* the clade most closely related to *P. chosenicus*, in the alignment of Cyt*b* (*n* = 170), we analysed the maternal genealogies by generating the haplotype data using DNAsp version 6 (Rozas et al. 2017). Here we assigned all sequences to their respective clades based on the resolved phylogenetic tree. Finally, we computed the number of haplotype group and haplotype diversity. We then inferred the haplotype network using the TCS method (Clement et al. 2002) embedded in PopART version 1.7 (Leigh and Bryant 2015).

Landscape features

To analyse the landscape features used by *P. chosenicus*, we combined the data obtained from our field surveys with records from the Global Biodiversity Information Facility (GBIF; DOI: https://doi.org//10.15468/dl.6kvymf.), matching the dataset extracted through the *megaSDM* package in R (Shipley et al. 2022), by running the 'OccurrenceCollection' function. The combined datasets resulted in a total of 403 occurrence points (Fig. 1). In addition to using presence points, we used the 1280 putative absence points recorded from our surveys to compare landscape features between presence and absence points (Fig. 1). We spatially thinned the occurrence data using a thinning distance of 500 m, resulting in 273 unique presence points and 922 putative absence points. Finally, we extracted landscape types at these spatially thinned presence and absence sites. To do so, we downloaded the 500-m resolution global land cover raster from the Global Land Cover by National Mapping Organizations (GLCNMO version 3; Kobayashi et al. 2017; available from https://globalmaps.github.io/glcnmo.html). The raster cells for this dataset were classified into 14 different landscape types (broadleaf deciduous forest, broadleaf evergreen forest, cropland, other vegetation mosaic, herbaceous vegetation, mixed forest, needleleaf deciduous forest, needleleaf evergreen forest, open canopy forest, paddy field, shrub, sparse vegetation, urban, water bodies), including several landcover types that are suitable habitats for *P. chosenicus* (e.g., natural and agricultural wetlands based on the literature: Borzée 2024; Table S2). Finally, we conducted a Chi-square goodness of fit test to determine the relationship between the type of landscape for each of the presence (*n* = 273) and putative absence datasets (*n* = 922). Further, due to the expected reliance of the species on rice paddies based on empirical data, we binary encoded the presence of rice paddies for each site (Table S2) and tested for a difference between species occurrence and rice paddies through a third chi-square test.

Ecological niche modelling

To generate ecological niche models (ENMs) for *P. chosenicus*, we initially considered a set of 27 environmental variables, including 19 bioclimatic variables and elevation data downloaded from the WorldClim 2.0 database (Fick and Hijmans 2017; https://www.worldclim.org/), six consensus land cover variables (cultivated area, forest cover, herbaceous vegetation cover, open water bodies, shrub cover, urban areas) and slope data downloaded from EarthEnv (Tuanmu and Jetz 2014, Amatulli et al. 2018; http://www.earthenv.org/). The selection of the six land cover layers is based on the habitat feature analyses of presence points. All environmental layers were downloaded as 1-km spatial resolution rasters. To define the model calibration area (Soberón and Peterson 2005), we generated a 50-km radius circular buffer (~ 0.45 dd) around each occurrence point using the 'BackgroundBuffers' function of the *megaSDM* package (Shipley et al., 2021). We then masked the environmental layers to the boundaries of the calibration area using R packages *raster* (Hijmans 2021) and *rgdal* (Bivand et al. 2021) and used the masked rasters for downstream niche modelling.

We further spatially thinned the initial occurrence dataset (*n* = 405) using the thinning distance of 1km. This resulted in a total of 273 occurrence points used for model calibration. To generate the background dataset, we implemented a target group background sampling to account for the differences in spatial sampling efforts between China, DPR Korea, and R Korea (Barber et al. 2022). To do so, we first downloaded all amphibian occurrence points recorded from within the boundaries of the calibration area from GBIF via the *megaSDM* package (no DOI is assigned to the dataset when extracted through the package). Then, we converted these points to a density raster representing the spatial sampling efforts of amphibian occurrence points within the modelling extent. We used this raster for spatial bias correction in the model calibration process.

Using the R package *SDMtune* (Vignali et al. 2020), we implemented a data-driven variable selection approach to select environmental variables with high importance and low collinearity. First, using 80% of the occurrence points (*n* = 218), 8,000 target group background points, and all 27 environmental variables masked to the calibration area, we trained a Maximum

Entropy (MaxEnt) model in default settings and 10 permutations. We used the 'varImp' function to check the importance of each variable. We then used the 'reduceVar' function to generate a reduced-variable model, applying a percent contribution threshold of 1 and removing variables below this threshold. Next, we used the 'varSel' function on the reduced-variable model to further remove highly collinear variables. The threshold for this step was the Spearman's correlation coefficient of 0.7. In both steps of variable reduction, we used the True Skill Statistic (TSS; Allouche et al. 2006) calculated from the testing dataset to compare the performance of models before and after variable removal. After this step, the following eight environmental variables were retained for model calibration: isothermality (bio3), mean temperature of wettest quarter (bio8), precipitation of driest month (bio14), cultivated landscape cover, herbaceous vegetation cover, open water bodies, urban areas, and slope.

We optimized the MaxEnt model parameters using the *ENMeval* package (version 2.0.0; Kass et al. 2021). Using the eight selected environmental variables, all occurrence points, and 10,000 target group background points as inputs and applying a 10-fold cross-validation, we tested the combinations of six MaxEnt feature classes (L, LQ, H, LQH, LQHP, LQHPT) and regularization multipliers (RM) ranging from 0.5 to 8 at the increment of 0.5. Among the candidate ENMs output from the *ENMeval* run, we selected the optimal model generated with an H feature combined with a regularization multiplier of 0.5, as this model had both the highest test AUC (area under the receiver operating characteristic curve) and the lowest 10% omission rate (Kass et al. 2021).

Based on the selected optimal model parameters, we projected the final ENM on a 10-fold cross-validation using MaxEnt version 3.4.1 via the *dismo* R package (Hijmans et al. 2020). We used cloglog output and used jackknife tests to assess the importance of each variable. The ENMs were first projected across the calibration area, and then projected across the entire study area. We evaluated the final model based on the following criteria: 1) AUC, 2) TSS (Allouche et al. 2006), using Maximum Test Sensitivity plus Specificity threshold (= 0.4154) for calculation, 3) AUC_{DIFF} (difference between training and validation AUC; Warren and Seifert 2011), 4) comparisons with the known distribution of *P. chosenicus* (NIBR 2019), and 5) comparisons with null models (Bohl et al. 2019, Kass et al. 2021). For comparisons with null models, we used the 'ENMnulls' function of the *ENMeval* package (Kass et al. 2021) to simulate 100 iterations of null models with the same parameterization as the empirical model (H feature with RM value of 0.5). The AUC, TSS, and comparisons with null models were used to assess the model's predictive abilities, AUC_{DIFF} was used to assess the degree of model overfitting, and comparisons with known distributions were used to visually assess the consistency between the predicted and actual distributions.

To identify the suitable habitat for *P. chosenicus* across our study range, we applied one "liberal" threshold (= 0.2578; 10-percentile training presence; P10) and one "strict" threshold (= 0.4154; Maximum Test Sensitivity plus Specificity; MTSS) to convert the continuous suitability outputs of ENMs into binary presence/absence maps. To generate binary maps, we used the 'ecospat.binary.model' function of the *ecospat* R package (Di Cola et al. 2017). We used R version 4.1.0 (R Core Team 2021) for all the analyses.

Results

Species distribution

We documented a total of 1195 independent datapoints (thinned from the 1674 surveys conducted), including 394 presence points (273 after thinning; complemented with 130 datapoints from GBIF (after thinning) and one datapoint from the museum), and a total of 1280 putative absence points (922 after thinning; Fig. 1). In R Korea, we found the species to be ranging from Buan in the south, along with two isolated inland populations, and continuously present from Buan northwards through the continuous landscape in the lowlands of the nation, interrupted only by the Chilgap hills and the Seoul-Incheon urban area. All presence datapoints collected in DPR Korea were in the lowlands, and the species is expected to be similarly continuously distributed along the west coast of the Korean Peninsula until the border with China. In China, the only presence points recorded were in the vicinity of Dandong, close to the border with DPR Korea.

Molecular identifications, phylogenetic relationship, and haplotype network

Out of the six *Pelophylax* sampled in Dandong, four individuals clustered within *P. chosenicus* (18PcC002-18PcC005; Figs. 2-4; accession numbers in Table S2, though note that 18PcC400 did not amplify for all gene fragments). One of the individuals (18PpC001) did not belong to the *P. chosenicus* clade (Figs. 2-4), but based on the focal gene fragment, it was instead related to either *P. plancyi* distributed in central China (see Cyt*b* tree) or *P. nigromaculatus* distributed from northeast to central China (see concatenated trees; Figs. 2 and 3). The concatenated trees inferred from the 12S and 16S rRNA fragments recovered four individuals sampled in Dandong within a polyphyletic clade containing *P. chosenicus*, *P. nigromaculatus* and *P. plancyi* (890 bp; *n* = 75; posterior probability (PP) = 88%; Fig. 2). Within the polyphyletic clade, *P. chosenicus* was distributed across the Korean Peninsula and southern Liaoning Province, here referred to as Eastern Coastal Yellow Sea, while *P. nigromaculatus* and *P. plancyi* were distributed across the Chinese Mainland (Fig. 2).

The concatenated tree for the three mitochondrial gene fragments (12S rRNA, 16 rRNA, and Cyt*b*; 1548 bp; *n* = 70; Fig. 3) provided a better resolution of the phylogenetic relationships within the genus, resolving two distinctive clades within *P. chosenicus*, one restricted to the Korean Peninsula and southern Liaoning Province (Clade II, Eastern Coastal Yellow Sea; PP = 70%; Fig. 3) and one distributed on the Korean

Peninsula but also including a *P. plancyi* individual from Anhui, China (Clade I; PP = 99%; Fig. 3). Two of the individuals sampled in Dandong formed a subclade (PP = 91%; Fig. 3), and all four clustered within the *P. chosenicus* clade restricted to the Eastern Coastal Yellow Sea (PP = 70%; Fig. 3).

The Cyt*b* tree supported the same phylogenetic clustering, with the five individuals within the monophyletic *P. chosenicus* clade distributed on the Korean Peninsula and Eastern Coastal Yellow Sea (Clade B; PP = 86%; Fig. 4). The haplotype network for the same Cyt*b* fragment (658 bp; *n* = 70) resulted in 80 haplotype groups with a haplotype diversity of 0.964 (Fig. 4B).

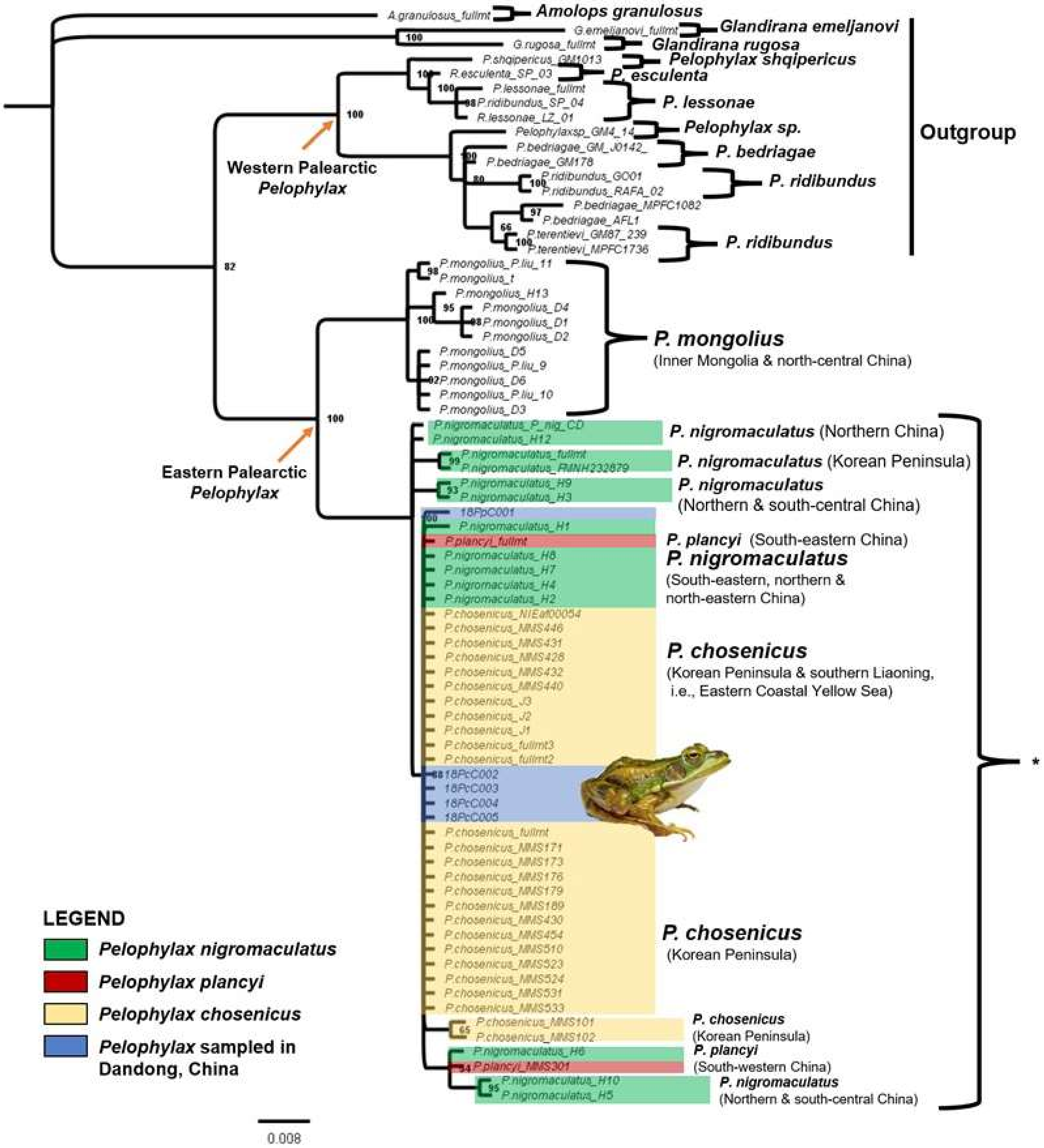

Figure 2. Phylogenetic tree for *Pelophylax* individuals sampled in Dandong in relation to sympatric species. Phylogeny reconstructed using the concatenated 12S rRNA and 16S rRNA gene fragments (890 bp; *N* = 75). The percentage of posterior probability is indicated for each node. Individuals are colour-coded only when the species is sympatric with *P. chosenicus*. The asterisk symbol (*) represents polyphyletic clade including *P. chosenicus*, *P. nigromaculatus*, and *P. plancyi*.

Here, the six *Pelophylax* individuals sampled from Dandong grouped into three distinct haplotype groups consisting of: (a) an individual clustered within the haplotype group 36, sharing ancestry with *P. plancyi* from Sichuan and Hunan (*n* haplotype = 3; Fig. 4B), (b) two individuals within the *P. chosenicus* haplotype group restricted to Dandong (haplotype 57; *n* haplotype = 2; Fig. 4B), with shared ancestry with the *P. chosenicus* haplotype groups originating from Liaoning and the Korean Peninsula (haplotype 57; Fig. 4B), and (c) three individuals clustering with the *P. chosenicus* haplotype group restricted to the Korean Peninsula (haplotype group 59; *n* haplotype = 12; Fig. 4B).

Landscape features

Based on 273 presence points, the highest number of occurrences was recorded in agricultural landscapes (*n* = 146; cropland and rice paddies combined), followed by urban areas (*n* = 53), deciduous broadleaf forests (*n* = 15), open canopy forests (*n* = 12), vegetation mosaics (*n* = 11), mixed forests (*n* = 9), water bodies (*n* = 9), evergreen needleleaf forests (*n* = 5), shrubs (*n* = 5), deciduous needleleaf forests (*n* = 4), herbaceous vegetation (*n* = 3), and sparse vegetation (*n* = 1). The extent of occurrence of *P. chosenicus* was significantly different across land cover types (chi-square test; $\chi^2 = 406.38$; df = 12; $p < 0.001$; Fig. 5).

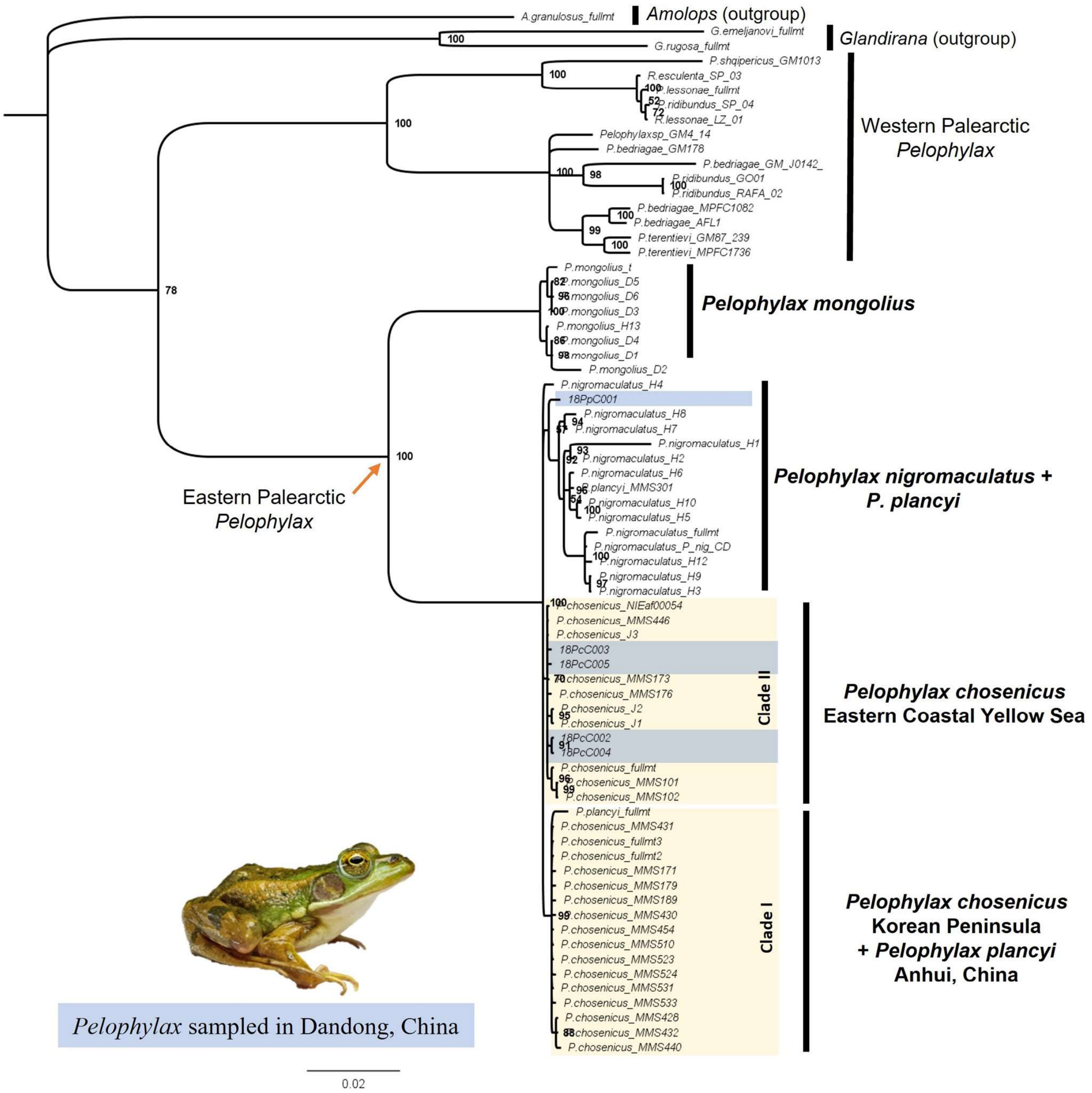

Figure 3. Phylogenetic tree for the *Pelophylax chosenicus* individuals sampled in Dandong in relation to sympatric and congeneric species from the Eastern Palearctic. Phylogeny reconstructed using 1548 bp concatenated 16S rRNA, 12 rRNA, and Cyt*b* gene fragments (*n* = 70). The percentage of the posterior probability is indicated for each node, and the individuals newly sampled in this study are highlighted in dark blue. *P. chosenicus* clades are in yellow.

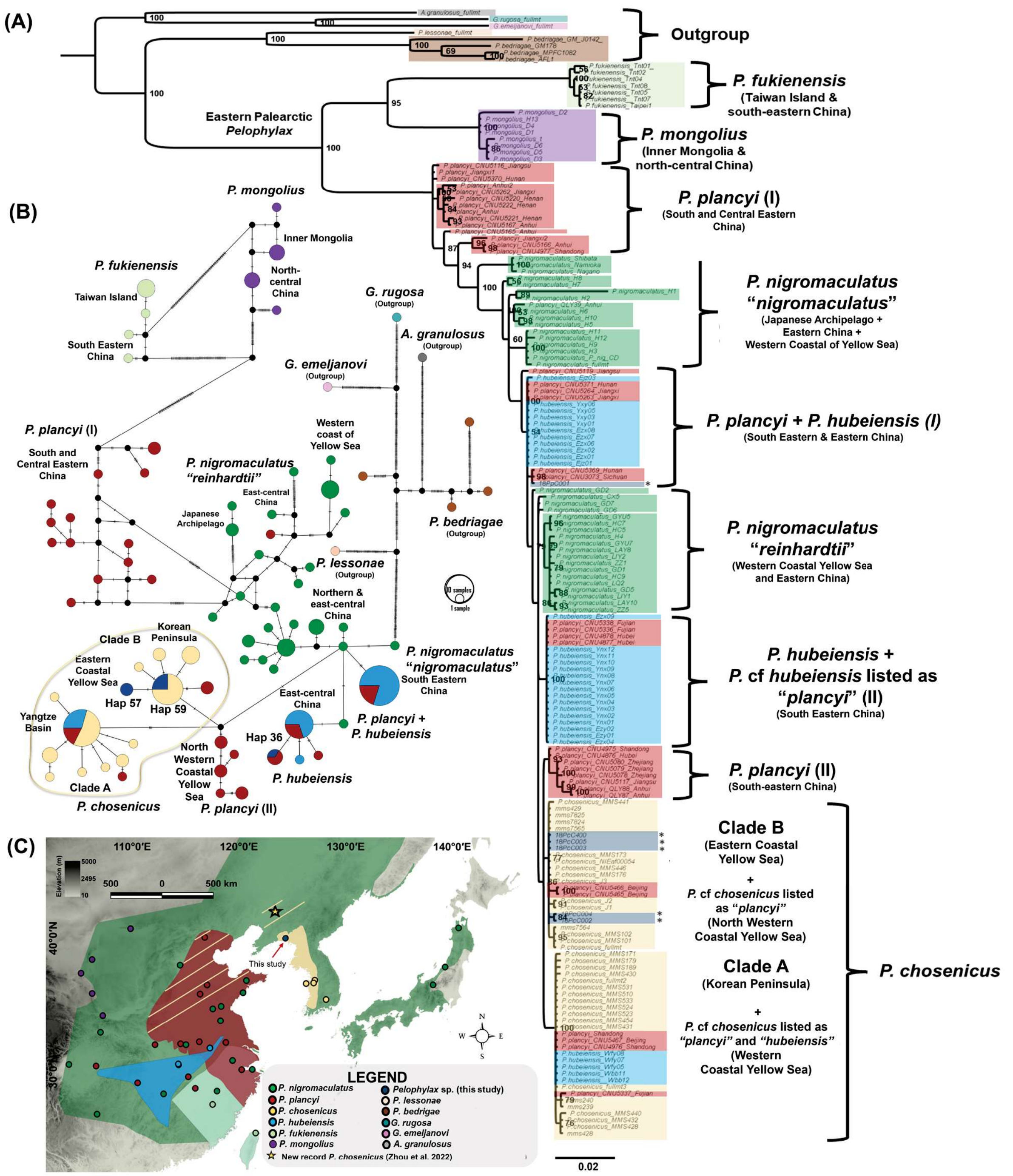

Figure 4. Phylogenetic relationships and haplotype network inferred from the Cyt*b* gene fragment for *Pelophylax chosenicus* individuals sampled in Dandong and their sympatric and congeneric species from the Eastern Palearctic. (A) Phylogenetic tree reconstructed using 648 bp from the Cyt*b* gene fragment (n = 170). The percentage of the posterior probability is indicated for each node, and the individuals sampled in Dandong are highlighted in dark blue and marked with an asterisk (*). (B) Haplotype network based on the same Cyt*b* fragment (n = 170) together with the selected outgroup taxa. The colours used to code the haplotypes match the colours used for the phylogenetic tree. Hatch marks between two haplotypes indicate mutation events. Solid black circles indicate missing haplotypes. The size of haplotype groups is standardized to the scale provided in the network. (C) Distribution map with the sampling locations and ranges based on the IUCN Red List of Threatened Species for all selected species. All colours match with the clades and haplotype groups.

For the 922 putative absence points (after thinning), the highest number of absence points was recorded in agricultural landscapes (*n* = 467), followed by deciduous broadleaf forest (*n* = 111), vegetation mosaics (*n* = 76), urban areas (*n* = 76), open canopy forests (*n* = 60), mixed forests (*n* = 40), shrubs (*n* = 25), water bodies (*n* = 21), evergreen broadleaf forests (*n* = 14), herbaceous vegetation (*n* = 12), evergreen needleleaf forests (*n* = 10), deciduous needleleaf forests (*n* = 8), and sparse vegetation (*n* = 2). The area of putative absence points was significantly different across land cover types ($\chi^2 = 1237.4$; df = 13; $p < 0.001$; Fig. 5).

Finally, we found that 70 out of the 273 presence points (25.67%) were located in rice paddies, while 198 out of the 922 putative absence points (21.47%) were located in rice paddies, a significant difference between the presence and putative absence points ($\chi2 = 343.83$; df = 1; $p < 0.001$).

Ecological niche modelling

The two statistical evaluation metrics indicated high predictive performance of the final ENM (AUC = 0.820 ± 0.027 SD; TSS = 0.553 ± 0.008 SD), while the AUC_{DIFF} value (= 0.023) indicated low model overfitting. In addition, the comparisons of test AUC scores with 100 null ENMs indicated a significantly higher predictive performance of the empirical models (Mann-Whitney *U*-test: $W = 4800$; $p < 0.001$; Fig. 6). Furthermore, the plotted continuous habitat suitability model and binary presence/absence maps generated from both P10 (“liberal”) and MTSS (“strict”) thresholds were consistent with the known distribution of *P. chosenicus* across the Korean Peninsula (NIBR 2019). Therefore, we considered the final ENM to be suitable as a representation of habitat suitability for *P. chosenicus* across the geographical extent of our study.

Based on percent contribution, isothermality (bio3) had the highest contribution to the model, followed by slope, precipitation of driest month (bio14), mean temperature of wettest quarter (bio8), cultivated landscape cover, urban landscape cover, herbaceous vegetation cover, and the cover of open water bodies (Table 1). Based on permutation importance, isothermality (bio3) had the highest contribution, followed by precipitation of driest month (bio14), mean temperature of wettest quarter (bio8), cultivated landscape cover, slope, herbaceous vegetation cover, the cover of open water bodies, and urban landscape cover (Table 1). According to the response curves, the suitable habitats for *P. chosenicus* across our study area were characterized by isothermality between 22 and 28, mean temperature of wettest quarter above 22°C, precipitation of driest months above 25mm, slope below approximately 15°, cultivated landscape cover greater than 40%, herbaceous vegetation cover approximately below 52%, cover of open water bodies greater than 20%, and cover of urban areas approximately below 85% (Fig. 7).

Both continuous and binary MaxEnt outputs showed areas of high habitat suitability across the western coast of the Korean Peninsula, in agreement with previous model-based range predictions for the species (Borzée et al. 2021). The areas of suitable habitat predicted by the ENM were highly consistent with the known distribution across R Korea (NIBR 2019; Fig. 8; Fig. 9), and the expected distribution in DPR Korea and China (Borzée 2024). Our ENM predictions showed that the narrow areas of highly suitable habitat along the western coast of the Korean Peninsula continued into the southern coastal regions of Dandong in Liaoning Province, China (Fig. 8). Across central Liaoning Province, there was another broad area of predicted suitable habitat continuing into northern Jilin Province. Both P10 (“liberal”) and the MTSS (“strict”) thresholds consistently predicted such patterns of suitable habitats, while the former tended to predict broader areas to be suitable for *P. chosenicus* (Fig. 9).

Discussion

Here we report the presence of *Pelophylax chosenicus* in China, identified through phylogenetic and haplotype analyses, highlighting the continuity of the population with *P. chosenicus* on the Korean Peninsula (Figs. 2-4). We also clarify the divergence within *P. chosenicus* (Min et al. 2008), segregated into two distinctive clades (Clade I and A and II and B; in Figs. 3 and 4 respectively), with our samples clustering within the clade ranging on the Korean Peninsula and further north along the Eastern Coastal Yellow Sea (Clade B; Fig. 4).

Table 1. Percent contribution and permutation importance of environmental variables used to predict current habitat suitability of *Pelophylax chosenicus*. Based on 273 occurrence points compiled from survey results and the Global Biodiversity Information Facility (GBIF; data in Table S1).

Variable	Percent contribution	Permutation importance
Isothermality (bio3)	33.3	46.2
Slope	31.9	2.0
Precipitation of driest month (bio14)	20.5	23.1
Mean temperature of wettest quarter (bio8)	7.1	22.7
Cultivated landscape	3.8	5.1
Urban landscape	2.3	0.2
Herbaceous vegetation	0.7	0.3
Open water bodies	0.5	0.3

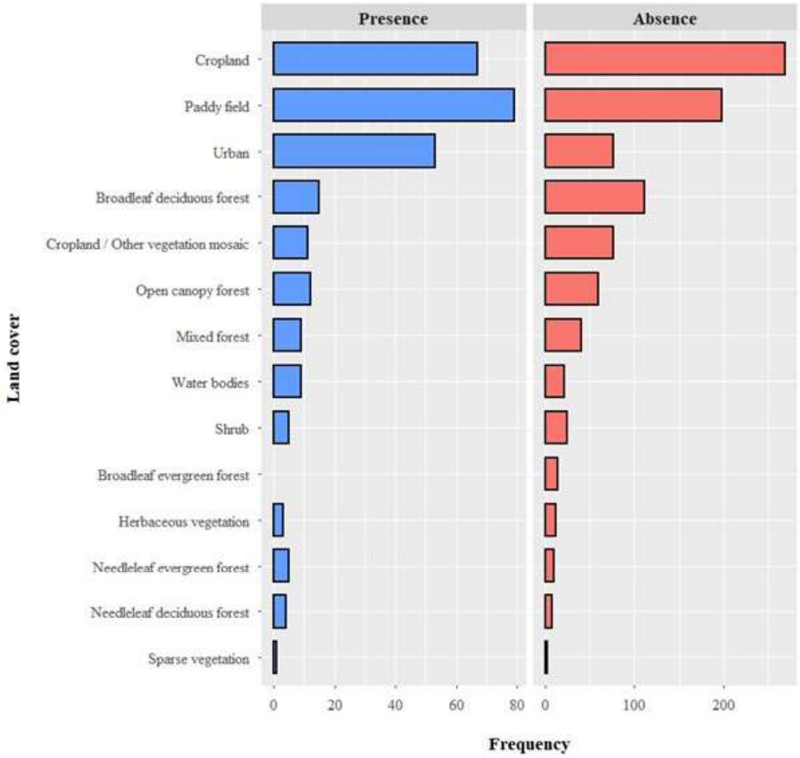

Figure 5. Landscape characteristics at presence (*n* = 273) and putative absence (*n* = 922) sites for *Pelophylax chosenicus*. The distribution of presence and putative absence sites were significantly different across land cover types (chi-square tests; $p < 0.001$). For both presence and absence datasets, agricultural landscapes (croplands and rice paddies combined) account for the highest recorded frequency among landscape types, but the frequency of rice paddies is significantly different between presence and putative absence sites (chi-square test; $p < 0.001$).

In addition, our samples assigned to *P. chosenicus* clustered with individuals assigned to *P. plancyi* ranging across the North Eastern Coastal Yellow Sea (Beijing, Shandong), and the Yangtze Basin. Furthermore, the clade assigned to *P. plancyi* (*P. plancyi* II; Fig. 4) is more closely related to *P. chosenicus*, and re-assigning the samples from this clade to *P. chosenicus* would remove the polyphyly within *P. chosenicus*, and result in a clear boundary between the two species. This taxonomic update would result in *P. chosenicus* distributed around the Yellow Sea, but not south of the Shandong Peninsula and thus not including the type locality of *P. plancyi*. In contrast, *P. plancyi* would be ranging further south, from the northern boundaries of the Yangtze Basin, and thus segregating the two clades along river basins already known to have shaped phylogenetic patterns in ranids (Shen et al. 2022).

Clade diversity but a single colonisation of the Korean Peninsula

The phylogeny and haplotype network based on the Cyt*b* fragment also demonstrated a high divergence within *P. nigromaculatus*, *P. plancyi* and *P. hubeiensis,* resulting in polyphyletic and multiple intra-specific clades, in opposition to the strongly structured clades of *P. mongolius* and *P. fukienensis* (Fig. 4).

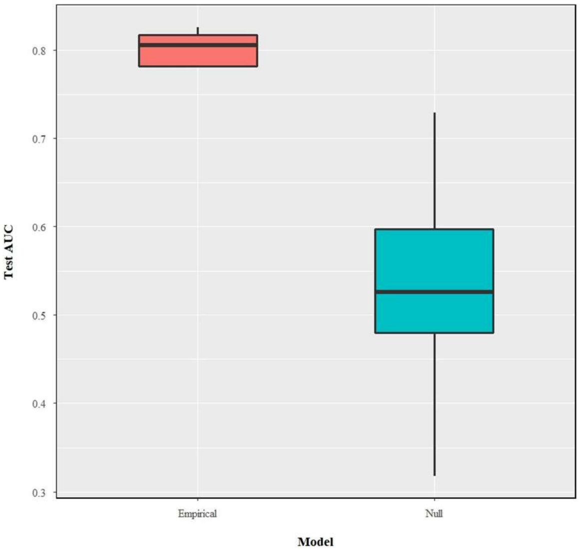

Figure 6. The distribution of test AUC values between the empirical MaxEnt models of *Pelophylax chosenicus* (*n* = 48) and null models (*n* = 100). The empirical models have significantly higher test AUC values compared to the null models (Mann-Whitney *U*-test: $W = 4800$; $p < 0.001$).

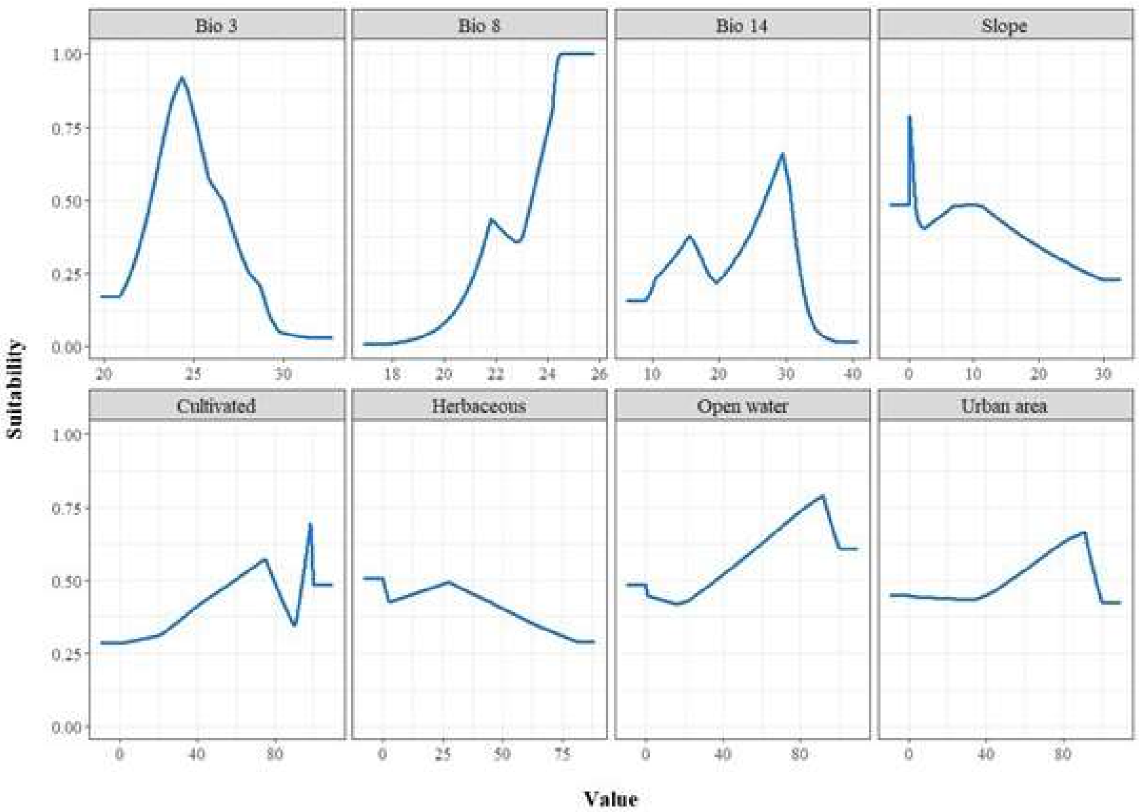

Figure 7. Response curves of *Pelophylax chosenicus* to environmental variables used in ecological niche modelling. See Table 1 for the contribution value of each variable. Based on 273 occurrence points compiled from survey results and the Global Biodiversity Information Facility (GBIF; data in Table S1).

This pattern was most likely induced by widespread secondary contacts in multiple refugia (Zhang et al. 2008; Fig. 4), and the blurring of genetic boundaries by the trade of the genus (Wang et al. 2016; Wang et al. 2017), making phylogenetic relationships difficult to interpret. Our results for *P. nigromaculatus* recovered the demonstrated clade divergence (Komaki et al. 2015) here associating "*reinhardtii*" with the lineage on continental Asia (Peters 1867) and "*nigromaculatus*" with the lineage in Japan (Hallowell 1861 "1860"). In contrast, *P. hubeiensis* predominantly ranges within the central Yangtze Basin (Hubei; Clade II; Fig. 3 and 4), but the polyphyletic nature of the species hints at the need for further studies.

However, we did not recover any paraphyly within the focal *P. chosenicus* clade and, presumably, the multiple secondary contacts were not as prominent for this species due to its distribution on the Eastern Coastal Yellow Sea. The divergence within *P. chosenicus* may be the result of a single colonisation of the Korean Peninsula, similarly to other northeast Asian anurans that colonised the northern latitudes before becoming isolated on the Korean Peninsula (e.g. *Bufo stejnegeri*; Fong et al. 2020).

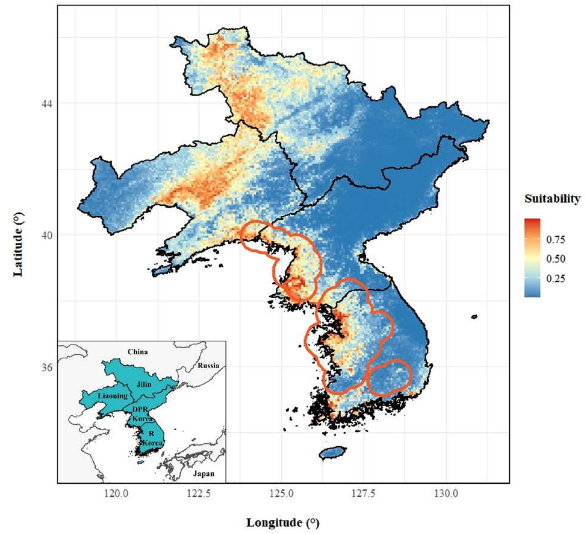

Figure 8. MaxEnt habitat suitability model for *Pelophylax chosenicus* based on eight environmental variables and 273 occurrence points (AUC = 0.820 ± 0.027 SD; TSS = 0.553 ± 0.008 SD; $\text{AUC}_{\text{DIFF}} = 0.023$). The model was first trained on the calibration area (circular polygon) and then projected across the entire study extent encompassing the Korean Peninsula and Jilin and Liaoning provinces in China.

Suitability of habitats for the species in northeast Asia

We identified suitable habitats throughout eastern DPR Korea using ENMs and we confirm the presence of two inland populations in R Korea, one south of Daegu and the other in the vicinity of Hapcheon. The southernmost population reported in Buan, R Korea, may not be the southernmost one, based on the modelling results, as suitable habitat is found further south than the southernmost confirmed presence. However, the current known distribution is not entirely unexpected as it generally matches with the southern distribution boundary of the Korean endemic *Dryophytes flaviventris* (Borzée et al. 2020b). The presence of the two inland populations in R Korea is also in agreement with the modelling results and confirms the likely presence of other inland populations throughout the Korean Peninsula. The additional datapoint in Shenyang, Liaoning Province, China, published during the review process of this manuscript demonstrates the validity of our results (Zhou et al. 2022a; Fig. 1).

Our modelling results predict the presence of the species in the plains west of the Bohai Bay, and further surveys in the area are needed, although the species would have to have dispersed across a landscape that is a range delineation boundary for other species, such as *Rana huanrenensis* (IUCN SSC Amphibian Specialist Group 2019). This type of movement is however not impossible as dispersal across the Yellow Sea has happened in some species, including *Rana coreana* (Borzée 2024). Both surveys and modelling results support the absence of *P. chosenicus* on the east coast of the Korean Peninsula and further north, in line with the data already published (NIBR 2019, Borzée 2024) and available through the citizen science platform iNaturalist (https://www.inaturalist.org/observations?place_id=any&subview=map&taxon_id=66318), a credible platform for amphibian species identification (Borzée et al. 2019c). Further surveys in eastern Korea, Jilin Province in China, and the Russian Primorye are thus unlikely to detect the presence of the species, but additional surveys are needed in Jeolla Province in R Korea, along the whole west coast of DPR Korea, and in all the lowlands of Liaoning in China.

In terms of landscape use, *P. chosenicus* was found to be significantly more often present in croplands, deciduous broadleaf forests, and urban areas. It is important to understand the link between the drivers of settlement for historical human populations, their transformation into the current urban area, and the match with the lowlands used by species, similar to *Dryophytes suweonensis* (Borzée et al. 2017c) but also amphibians in general (Small and Cohen

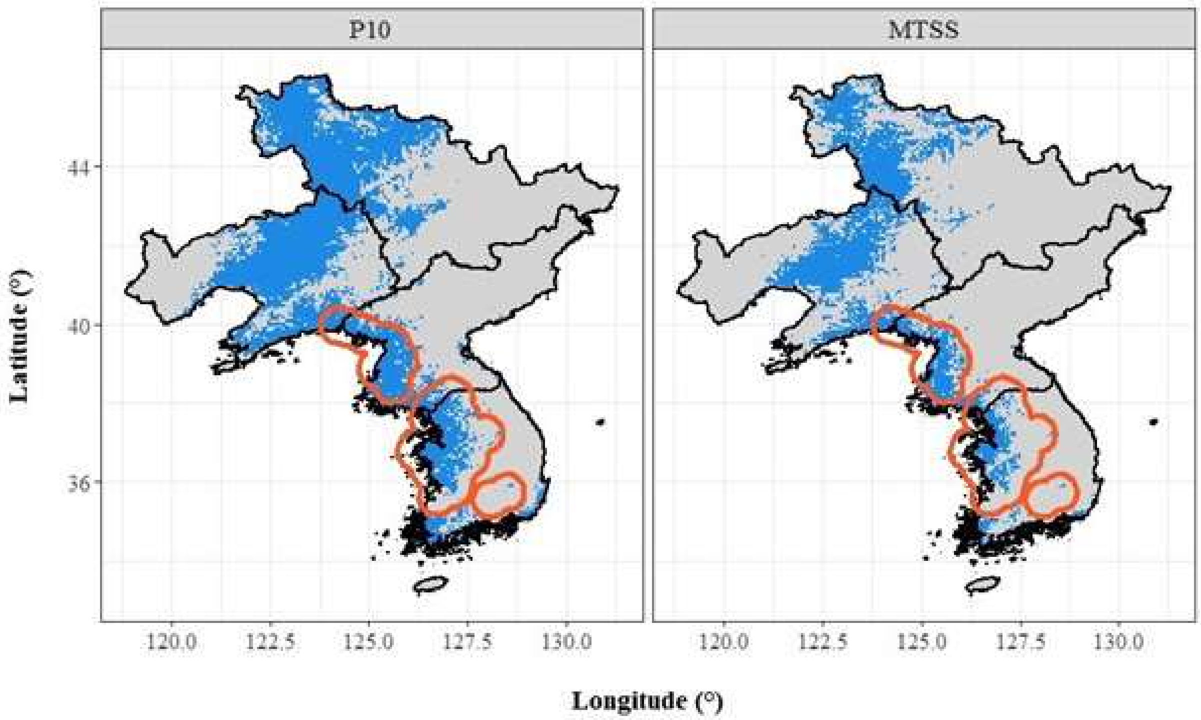

Figure 9. Binary presence/absence maps for *Pelophylax chosenicus*. Generated from MaxEnt model outputs by applying one “liberal” threshold (= 0.2578; 10 percentile training presence; P10) and one “strict” threshold (= 0.4154; Maximum Test Sensitivity plus Specificity; MTSS). While both thresholds generally predicted similar areas of presence both within the calibration area (circular polygon) and across the entire study area, the more liberal P10 threshold predicted broader areas of presence. The four areas on the two maps delineated by administrative boundaries are (from the north west): Liaoning and Jilin Provinces in China, DPR Korea and R Korea.

2004), and the connection with high biodiversity (Dambrine et al. 2007). The sites with putative absence were generally agricultural landscapes, followed by deciduous broadleaf forests, vegetation mosaics, and urban areas. The overlap in the landscape features where the species was found and putatively absent is representative of the broad scale of the sampling effort, within and outside of the range of the species, and highlights that landscape variables are not limiting the distribution of the species. In contrast, the distribution of *P. chosenicus* is likely restricted by other variables such as elevation or climate, similar to other anuran species (Otto et al. 2007). The significant difference in presence and putative absence in relation to rice paddies is important as the species relies on this type of landscape for its survival, as expected due to the high rate of conversion of natural wetlands into agricultural wetlands in R Korea (Lee and Miller-Rushing 2014, Park et al. 2021b, Borzée et al. 2019a), but it also relies on other types of landscapes, and even wetlands in urban areas (Sung et al. 2007, Ra et al. 2008b, Ra et al. 2010).

In general, our modelling results were well supported, and the empirical models were better supported than the null models, highlighting the validity of our results. In addition, the two binary thresholds used did not show extensive variations in the predicted suitable habitat for the species. Isothermality was the most important variable, representative of daily temperature fluctuations in comparison with yearly variations, and highlighting that the range of the species was not determined by landscape use only, similarly to the Chinese giant salamander as its range is also restricted by isothermality (Zhang et al. 2020). Slope was the second most important variable (<15°) for habitat suitability, generally matching with lowlands in our focal landscape, a variable also associated with the occurrence of the syntopic *D. suweonensis* and *D. flaviventris* (Borzée et al. 2020b), and also associated with the Chinese giant salamander (Zhang et al. 2020). Next in the list of important variables was the precipitation of the driest month, with habitat suitability being associated with rain regimes matching with light rain (> 25mm), followed by a mean temperature of the wettest quarter (>22°C), matching with relatively high temperature for temperate areas, and the breeding season of the species (Seo et al. 2014). Finally, vegetation cover with cultivated landscape over > 40%, herbaceous vegetation cover approximately below 52% and cover of urban areas approximately below 85% were related to habitat suitability. These last variables also highlight that while the species can live in agricultural wetlands, likely due to their ancestral presence in habitats being transformed, they are also present in other areas. The strong overlap with urban areas could be related to the ability of the species to cope with development, although it is more likely related to the expectation that *P. chosenicus* can be relatively long lived (15 years for the closely related *P. nigromaculatus*, Kashiwagi et al. 2005), in connection with the fact that urban development in R Korea is relarively recent (Lee and Miller-Rushing 2014, Lee et al. 2018); and that individuals in urban areas are remnant populations as the species is sensitive to pollution (Byeon 2010, Borzée et al. 2018c).

Understanding the distribution and landscapes for the conservation of species

While our results can be seen in a positive light as we define a broader range than previously known for *P. chosenicus*, these are not genuine improvements in the status of the species, but additional information on a species that is listed as Vulnerable and decreasing in the IUCN Red List of Threatened Species (IUCN SSC Amphibian Specialist Group 2021). The species faces multiple threats (Cheong et al. 2009, Ra and Park 2011, Ra et al. 2016), but habitat loss remains the main pressure as most low elevation wetlands have been converted to rice agriculture, and are now being transformed into dry agriculture or for the production of other manufactured goods for economic reasons (e.g. in the boundaries of Seoul; Park et al. 2021b). However, the threats need to be better understood as the species is not strictly bound to rice paddies, unlike other threatened species in the same landscape (NIBR 2019), but it is sensitive to agrochemical pollution (Borzée et al. 2018c). In addition, the species is under threat due to climate change both because of the shift in climate for current natural habitats (Gerick et al. 2014, Kim et al. 2021), but also because of the delay in the flooding of rice paddies where the species breeds in agricultural wetlands (Chuang et al. 2018). It is important to note that conservation efforts are ongoing in R Korea, with a translocation program initiated by the National Institute of Ecology of Korea (Park et al. 2021a), and several conservation plans and recommendations available (Yang and Koo 2016, Ra et al. 2019, Yoo et al. 2019). In addition, the species is not likely to be threatened in DPR Korea (Borzée et al. 2021). Further surveys are needed in China to better understand the distribution of the species, and the threats to it within this part of the range.

Acknowledgements

We are grateful to Yikweon Jang for the help provided over the years and to Desiree Andersen for the help during fieldwork in China. This work was supported by the Foreign Youth Talent Program (QN2023014004L) from the Ministry of Science and Technology to AB, and partially supported by the grant from the National Institute of Biological Resources (NIBR), funded by the Ministry of Environment (MOE) of the Republic of Korea (NIBR201703204) to MSM. We are also grateful to the Handling editor, Rob Whittaker, and L. Lee Grismer and another anonymous reviewer for the comments provided to our manuscript.

Author Contributions

AB conceptualised the study, conducted the investigation, methodology, formal analysis and software, was involved in funding acquisition and wrote the original draft; YS conducted the methodology, software, formal analysis, validated the data and wrote the original draft; YB conducted the methodology and validated the data; DJ conducted the methodology and was involved in writing; HA was involved in writing; MSM conducted the methodology, validated the data, was involved in funding acquisition and manuscript writing; SNO conducted the methodology, software, formal analysis, validated the data and wrote the original draft. All authors were involved in reviewing and editing of the manuscript.

Data Accessibility Statement

The sequences generated from this study have been deposited to the GenBank (https://www.ncbi.nlm.nih.gov/) under specific accession numbers. The distribution data are available in the Global Biodiversity Information Facility (gbif.org; DOI: 10.15468/dl.6kvymf). The complete MaxEnt distribution modelling workflow in R is available from GitHub (https://github.com/yucheols/Pelophylax_chosenicus_SDM). A preprint of this work has been deposited at the following: https://www.biorxiv.org/content/10.1101/2022.03.23.485556v1. The supporting data for molecular phylogeny and landscape modelling can be found in the supplementary material as Table S1 and Table S2.

Supplemental Material

The following materials are available as part of the online article at https://escholarship.org/uc/fb
Table S1. Information on molecular samples used to reconstruct the phylogenetic trees in this study.
Table S2. Dataset on presence and absence points for Pelophylax chosenicus used in this study.

References

Allouche, O., Tsoar, A. & Kadmon, R. (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). Journal of Applied Ecology, 43, 1223-1232. https://doi.org//10.1111/j.1365-2664.2006.01214.x

Amatulli, G., Domisch, S., Tuanmu, M.-N., Parmentier, B., Ranipeta, A., Malczyk, J. & Jetz, W. (2018) A suite of global, cross-scale topographic variables for environmental and biodiversity modeling. Scientific Data, 5, 180040. https://doi.org//10.1038/sdata.2018.40

Araújo, M.B., Anderson, R.P., Barbosa, A.M., Beale, C.M., Dormann, C.F., Early, R., Garcia, R.A., Guisan, A., Maiorano, L. & Naimi, B. (2019) Standards for distribution models in biodiversity assessments. Science Advances, 5, eaat4858. https://doi.org//10.1126/sciadv.aat4858

Bae, Y., Park, J., Othman, S.N., Jang, Y. & Borzée, A. (2022) Record of invasive *Rana huanrenensis* Fei, Ye, and Huang, 1990 and *Pelophylax nigromaculatus* (Hallowell, 1861) on Ulleung Island, Republic of Korea. BioInvasion Records, 11, 278-286. https://doi.org//10.3391/bir.2022.11.1.28

Barber, R.A., Ball, S.G., Morris, R.K.A. & Gilbert, F. (2022) Target-group backgrounds prove effective at correcting sampling bias in Maxent models. Diversity and Distributions, 28, 128-141. https://doi.org//10.1111/ddi.13442

Başkale, E. & Çapar, D. (2016) Detection probability and habitat selection of the Beyşehir Frog, *Pelophylax caralitanus* (Arikan 1988), in southwestern Anatolia, Turkey. Russian Journal of Herpetology, 23, 205-214

Bivand, R., Keitt, T. & Rowlingson, B. (2021) rgdal: bindings for the 'Geospatial' Data Abstraction Library. R package version, 1.5-23, https://CRAN.R-project.org/package=rgdal

Bohl, C.L., Kass, J.M. & Anderson, R.P. (2019) A new null model approach to quantify performance and significance for ecological niche models of species distributions. Journal of Biogeography, 46, 1101-1111. https://doi.org//10.1111/jbi.13573

Borzée, A., Kosch, T.A., Kim, M. & Jang, Y. (2017a) Introduced bullfrogs are associated with increased *Batrachochytrium dendrobatidis* prevalence and reduced occurrence of Korean treefrogs. PLoS ONE, 12, e0177860. https://doi.org//10.1371/journal.pone.0177860

Borzée, A., Bae, Y.H., Groffen, J. & Jang, Y. (2017b) *Pelophylax chosenicus* (Gold-spotted Pond Frog). Herpetological Review, 48, 79-80

Borzée, A., Kim, K., Heo, K., Jablonski, P.G. & Jang, Y. (2017c) Impact of land reclamation and agricultural water regime on the distribution and conservation status of the endangered *Dryophytes suweonensis*. PeerJ, 5, e3872. https://doi.org/10.7717/peerj.3872

Borzée, A., Andersen, D. & Jang, Y. (2018a) Population trend inferred from aural surveys for calling anurans in Korea. PeerJ, 6, e5568. https://doi.org/10.7717/peerj.5568

Borzée, A., Bae, Y.H. & Seliger, B. (2018b) *Pelophylax chosenicus* (Gold-spotted Pond Frog). Herpetological Review, 49, 709

Borzée, A., Kyong, C.N., Kil, H.K. & Jang, Y. (2018c) Impact of water quality on the occurrence of two endangered Korean anurans: *Dryophytes suweonensis* and *Pelophylax chosenicus*. Herpetologica, 74, 1-7. https://doi.org//10.1655/Herpetologica-D-17-00011

Borzée, A., Struecker, M.-Y., Yi, Y., Kim, D. & Kim, H. (2019a) Time for Korean wildlife conservation. Science, 363, 1161-1162. https://doi.org//10.1126/science.aaw9023

Borzée, A., Ren, J., Li, J.-T., Groffen, J., Jang, Y. & Messenger, R.K. (2019b) Microhabitat segregation between Black-spotted Pond Frogs, *Pelophylax nigromaculatus*, and Gold-striped Pond Frogs, *P. plancyi* (Anura: Ranidae). Reptiles & Amphibians: Conservation and Natural History, 26, 119–120

Borzée, A., Baek, H.J., Lee, C.H., Kim, D.Y., Song, J.-Y., Suh, J.-H., Jang, Y. & Min, M.-S. (2019c) Scientific publication of georeferenced molecular data as an adequate guide to delimit the range of Korean *Hynobius* salamanders through citizen science. Acta Herpetologica, 14, 27-33. https://doi.org//10.13128/Acta_Herpetol-24102

Borzée, A., Oh, S., Sin, E. & Jang, Y. (2020a) Spring voices in Korean rice fields: the effect of abiotic variables and syntopic calls on the calling activity of the treefrog *Dryophytes suweonensis*. Asian Herpetological Research, 11, 335–341. https://doi.org//10.16373/j.cnki.ahr.190046

Borzée, A., Messenger, K.R., Chae, S., et al. (2020b) Yellow sea mediated segregation between North East Asian *Dryophytes* species. PLoS ONE, 15, e0234299. https://doi.org//10.1371/journal.pone.0234299

Borzée, A., Litvinchuk, S.N., Ri, K., et al. (2021) Update on distribution and conservation status of amphibians in the Democratic People's Republic of Korea: conclusions based on field surveys, environmental modelling, molecular analyses and call properties. Animals, 11, 2057. https://doi.org//10.3390/ani11072057

Borzée, A. (2023) A 13-step framework for a better integration of streamlined conservation research. Integrative Conservation, 2, 156-164. https://doi.org//10.1002/inc3.28

Borzée, A. (2024) Continental Northeast Asian Amphibians: Origins, Behavioral Ecology, and Conservation. Academic Press, Elsevier. Amsterdam, Netherlands.

Byeon, C.W. (2010) Water purification and ecological restoration effects of the Keumeo stream sustainable structured wetland biotop (SSB) System established on the floodplain of Kyungan stream. Journal of the Korean Society of Environmental Restoration Technology, 13, 23-35

Cheong, S.W., Sung, H.C., Park, D.S. & Park, S.R. (2009) Population viability analysis of a Gold-spotted Pond Frog (*Rana chosenica*) population: implications for effective conservation and re-introduction. Korean Journal of Environmental Biology, 27, 73-81

Chuang, M.F., Borzée, A. & Jang, Y. (2018) Impact of environmental variables on the breeding phenology of a South Korean treefrog, *Dryophytes suweonensis*. International Long Term Ecological Research Network, Tunghai University, Taiwan.

Clement, M., Snell, Q., Walker, P., Posada, D. & Crandall, K. (2002) TCS: Estimating gene genealogies. Parallel and Distributed Processing Symposium, International Proceedings, 2, 184

Dambrine, É., Dupouey, J.L., Laüt, L., Humbert, L., Thinon, M., Beaufils, T. & Richard, H. (2007) Present forest biodiversity patterns in France related to former Roman agriculture. Ecology, 88, 1430-1439. https://doi.org//10.1890/05-1314

Di Cola, V., Broennimann, O., Petitpierre, B., et al. (2017) ecospat: an R package to support spatial analyses and modeling of species niches and distributions. Ecography, 40, 774-787. https://doi.org//10.1111/ecog.02671

Do, M.S., Son, S.J., Choi, G., Yoo, N., Koo, K.S. & Nam, H.K. (2021) Anuran community patterns in the rice fields of the mid-western region of the Republic of Korea. Global Ecology and Conservation, 26, e01448. https://doi.org//10.1016/j.gecco.2020.e01448

Eo, S.H., Lee, B.-J., Park, C.-D., Jung, J.-H., Hong, N. & Lee, W.-S. (2019) Taxonomic identity of the *Glandirana emeljanovi* (Anura, Ranidae) in Korea revealed by the complete mitochondrial genome sequence analysis. Mitochondrial DNA Part B, 4, 961-962. https://doi.org//10.1080/23802359.2019.1579074

Eom, J.H., Lee, J.H., Ra, N.Y. & Park, D.S. (2007) Preferred feeding sites and prey of the adult Gold-spotted pond frog, *Rana plancyi chosenica*. Journal of Ecology and Environment, 30, 357-361. https://doi.org//10.5141/JEFB.2007.30.4.357

Fei, L., Ye, C. & Jiang, J. (2012) Colored atlas of Chinese amphibians and their distributions. Sichuan Science and Technology Press. Chengdu, People's Republic of China.

Fick, S.E. & Hijmans, R.J. (2017) WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. International Journal of Climatology, 37, 4302-4315. https://doi.org//10.1002/joc.5086

Fletcher Jr, R.J., Hefley, T.J., Robertson, E.P., Zuckerberg, B., McCleery, R.A. & Dorazio, R.M. (2019) A practical guide for combining data to model species distributions. Ecology, 100, e027. https://doi.org//10.1002/ecy.2710

Fong, J.J., Yang, B.-T., Li, P.-P., Waldman, B.S. & Min, M.-S. (2020) Phylogenetic systematics of the water toad (*Bufo stejnegeri*) elucidates the evolution of semi-aquatic toad ecology and Pleistocene glacial refugia. Frontiers in Ecology and Evolution, 7, 523. https://doi.org//10.3389/fevo.2019.00523

Garcia, V.O.S., Ivy, C. & Fu, J. (2017) Syntopic frogs reveal different patterns of interaction with the landscape: a comparative landscape genetic study of *Pelophylax nigromaculatus* and *Fejervarya limnocharis* from central China. Ecology and Evolution, 7, 9294-9306. https://doi.org//10.1002/ece3.3459

Gerick, A.A., Munshaw, R.G., Palen, W.J., Combes, S.A. & O'Regan, S.M. (2014) Thermal physiology and species distribution models reveal climate vulnerability of temperate amphibians. Journal of Biogeography, 41, 713-723. https://doi.org//10.1111/jbi.12261

Groffen, J., Andersen, D. & Borzée, A. (2022) Breeding phenology and landscape use in all amphibian species from the Republic of Korea based on citizen science data and governmental biodiversity surveys. Frontiers in Environmental Science, 10, 846481. https://doi.org//10.3389/fenvs.2022.846481

Hallowell, E. (1861 "1860") Report upon the Reptilia of the North Pacific Exploring Expedition, under command of Capt. John Rogers, U.S. N. . Proceedings of the Academy of Natural Sciences of Philadelphia, 12, 480–510

Hijmans, R.J., Phillips, S., Leathwick, J. & Elith, J. (2020) dismo: Species Distribution Modeling. R package version 1.3-3, https://CRAN.R-project.org/package=dismo

Hijmans, R.J. (2021) raster: Geographic Data Analysis and Modeling. R package version, 3.4-13, https://CRAN.R-project.org/package=raster

Hofman, S., Pabijan, M., Osikowski, A., Litvinchuk, S.N. & Szymura, J.M. (2016) Phylogenetic relationships among four new complete mitogenome sequences of *Pelophylax* (Amphibia: Anura) from the Balkans and Cyprus. Mitochondrial DNA, 27, 3434–3437. https://doi.org//10.3109/19401736.2015.1025266

Huang, A., Luo, H., Luo, S., et al. (2019) The complete mitogenome of the granular torrent frog, *Amolops granulosus* (Anura: Ranidae). Mitochondrial DNA Part B, 4, 2643-2644. https://doi.org//10.1080/23802359.2019.1643800

Huelsenbeck, J.P. & Ronquist, F. (2001) MRBAYES: Bayesian inference of phylogenetic trees. Bioinformatics, 17, 754-755

IUCN SSC Amphibian Specialist Group (2019) *Rana huanrensis*. The IUCN Red List of Threatened Species 2019, e.T58619A63855773. https://doi.org//10.2305/IUCN.UK.2019-1.RLTS.T58619A63855773.en

IUCN SSC Amphibian Specialist Group (2021) *Pelophylax chosenicus*. The IUCN Red List of Threatened Species, e.T58577A110101963. https://doi.org//10.2305/IUCN.UK.2021-3.RLTS.T58577A110101963.en

Jeong, T.J., Jun, J., Han, S., Kim, H.T., Oh, K. & Kwak, M. (2013) DNA barcode reference data for the Korean herpetofauna and their applications. Molecular Ecology Resources, 13, 1019-1032. https://doi.org//10.1111/1755-0998.12055

Jiang, L., Zhao, L., Liu, Y., Leng, Z., Zhao, L. & Ruan, Q. (2017) The complete mitochondrial genome sequence of the Dark-spotted frog *Pelophylax nigromaculatus* (Amphibia, Anura, Ranidae). Mitochondrial DNA Part A: DNA Mapping, Sequencing, and Analysis, 28, 236–237. https://doi.org//10.3109/19401736.2015.1115857

Kashiwagi, K., Shinkai, T., Kajii, E. & Kashiwagi, A. (2005) The effects of reactive oxygen species on amphibian aging. Comparative Biochemistry and Physiology Part C: Toxicology & Pharmacology, 140, 197-205. https://doi.org//10.1016/j.cca.2005.02.001

Kass, J.M., Muscarella, R., Galante, P.J., Bohl, C.L., Pinilla-Buitrago, G.E., Boria, R.A., Soley-Guardia, M. & Anderson, R.P. (2021) ENMeval 2.0: Redesigned for customizable and reproducible modeling of species' niches and distributions. Methods in Ecology and Evolution, 12, 1602– 1608. https://doi.org//10.1111/2041-210X.13628

Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., Cooper, A., Markowitz, S. & Duran, C. (2012) Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. Bioinformatics, 28, 1647-1649. https://doi.org//10.1093/bioinformatics/bts199

Kim, H.-T., Kim, H., Jeon, G. & Kim, D. (2019) Arrow guide of amphibians and reptiles. Econature. Seoul, Republic of Korea.

Kim, H., Adhikari, P., Chang, M. & Seo, C. (2021) Potential distribution of amphibians with different habitat characteristics in response to climate change in South Korea. Animals, 11, 2185. https://doi.org//10.3390/ani11082185

Kobayashi, T., Tateishi, R., Alsaaideh, B., Sharma, R.C., Wakaizumi, T., Miyamoto, D., Bai, X., Long, B.D., Gegentana, G. & Maitiniyazi, A. (2017) Production of global land cover data - GLCNMO2013. Journal of Geography and Geology, 9, 1-15. https://doi.org//10.5539/jgg.v9n3p1

Kocher, T.D., Thomas, W.K., Meyer, A., Edwards, S.V., Pääbo, S., Villablanca, F.X. & Wilson, A.C. (1989) Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. Proceedings of the National Academy of Sciences USA, 86, 6196-6200. https://doi.org//10.1073/pnas.86.16.6196

Komaki, S., Igawa, T., Lin, S.M., Tojo, K., Min, M.S. & Sumida, M. (2015) Robust molecular phylogeny and palaeodistribution modelling resolve a complex evolutionary history: glacial cycling drove recurrent mtDNA introgression among *Pelophylax* frogs in East Asia. Journal of Biogeography, 42, 2159-2171. https://doi.org//10.1111/jbi.12584

Lanfear, R., Frandsen, P.B., Wright, A.M., Senfeld, T. & Calcott, B. (2017) PartitionFinder 2: new methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. Molecular Biology and Evolution, 34, 772-773. https://doi.org//10.1093/molbev/msw260

Lee, J.K., Chung, O.-S., Park, J.-Y., Kim, H.-J., Hur, W.-H., Kim, S.-H. & Kim, J.-H. (2018) Effects of the Saemangeum Reclamation Project on migratory shorebird staging in the Saemangeum and Geum Estuaries, South Korea. Bird Conservation International, 28, 238-250. https://doi.org//10.1017/S0959270916000605

Lee, S.-D. & Miller-Rushing, A.J. (2014) Degradation, urbanization, and restoration: a review of the challenges and future of conservation on the Korean Peninsula. Biological Conservation, 176, 262-276. https://doi.org//10.1016/j.biocon.2014.05.010

Leigh, J. & Bryant, D. (2015) PopART: full-feature software for haplotype network construction. Methods in Ecology and Evolution, 6, 1110–1116

Liu, K., Wang, F., Chen, W., Tu, L., Min, M.-S., Bi, K. & Fu, J. (2010) Rampant historical mitochondrial genome introgression between two species of green pond frogs, *Pelophylax nigromaculatus* and *P. plancyi*. BMC Evolutionary Biology, 10, 201. https://doi.org//10.1186/1471-2148-10-201

Manne, L.L. & Pimm, S.L. (2001) Beyond eight forms of rarity: which species are threatened and which will be next? Animal Conservation, 4, 221-229. https://doi.org//10.1017/S1367943001001263

Margaryan, A., Noer, C.L., Richter, S.R., et al. (2021) Mitochondrial genomes of Danish vertebrate species generated for the national DNA reference database, DNAmark. Environmental DNA, 3, 472– 480. https://doi.org//10.1002/edn3.138

Min, M.-S., Park, S.K., Che, J., Park, D.S. & Lee, H. (2008) Genetic diversity among local populations of the gold-spotted pond frog, Rana plancyi chosenica (Amphibia: Ranidae), assessed by mitochondrial cytochrome b gene and control region sequences. Animal Systematics, Evolution and Diversity, 24, 25-32. https://doi.org//10.5635/kjsz.2008.24.1.025

Mizsei, E., Üveges, B., Vági, B., Szabolcs, M., Lengyel, S., Pfliegler, W.P., Nagy, Z.T. & Tóth, J.P. (2016) Species distribution modelling leads to the discovery of new populations of one of the least known European snakes, *Vipera ursinii graeca*, in Albania. Amphibia-Reptilia, 37, 55-68

Nakanishi, K., Honma, A., Furukawa, M., Takakura, K.-I., Fujii, N., Morii, K., Terasawa, Y. & Nishida, T. (2020) Habitat partitioning of two closely related pond frogs, *Pelophylax nigromaculatus* and *Pelophylax porosus brevipodus*, during their breeding season. Evolutionary Ecology, 34, 855-866. https://doi.org//10.1007/s10682-020-10061-1

NIBR (2019) Red Data Book of Republic of Korea. Volume 2: Amphibians and Reptiles. National Institute of Biological Resources, Ministry of Environment. Incheon, Republic of Korea.

Nishioka, M. (1972) Nucleo-cytoplasmic hybrids between *Rana brevipoda* and *Rana plancyi chosenica*. Scientific report of the Laboratory for Amphibian Biology of Hiroshima University, 1, 259-275. https://doi.org//10.15027/287

Nishioka, M. & Okumoto, H. (1983) Reproductive capacity and progeny of amphidiploids between *Rana nigromaculata* and *Rana plancyi chosenica*. Scientific report of the Laboratory for Amphibian Biology of Hiroshima University, 6, 141-181. https://doi.org//10.15027/352

Oike, A., Mochizuki, M., Tojo, K., Matsuo, T., Nakamura, Y., Yasumasu, S., Ito, E., Arai, T. & Nakamura, M. (2020) A phylogenetically distinct group of *Glandirana rugosa* found in Kyushu, Japan. Zoological Science, 37, 193-202. https://doi.org//10.2108/zs190007

Okada, Y. (1926) A study on the distribution of tailess batrachians of Japan. Annotationes Zoologicae Japonenses, 11, 137-144

Okada, Y. (1928) Frogs in Korea. Journal of the Chosen Biological Society, 6, 15-46

Okada, Y. (1931) The tailless bactracians of the Japanese Empire. Journal of the Imperial Agricultural Experiment Station, Nishigahara, Tokyo, 29, 1-215

Otto, C.R., Snodgrass, J.W., Forester, D.C., Mitchell, J.C. & Miller, R.W. (2007) Climatic variation and the distribution of an amphibian polyploid complex. Journal of Animal Ecology, 76, 1053-1061. https://doi.org//10.1111/j.1365-2656.2007.01300.x

Park, C., Kwon, K., Yoo, N., Lee, J., Kang, D., Park, J., Yoo, J., Kim, K. & Yoon, J. (2021a) Post-release monitoring after reintroduction of captive-reared Korean endangered frog, *Pelophylax chosenicus*. Proceedings of the National Institute of Ecology of the Republic of Korea, 2, 114-119. https://doi.org//10.22920/PNIE.2021.2.2.114

Park, D.-S., Park, S.-R. & Sung, H.-C. (2009) Colonization and extinction patterns of a metapopulation of Gold-spotted Pond Frogs, *Rana plancyi chosenica*. Journal of Ecology and Environment, 32, 103-107. https://doi.org//10.5141/JEFB.2009.32.2.103

Park, I.-K., Park, D. & Borzée, A. (2021b) Defining conservation requirements for the Suweon Treefrog (*Dryophytes suweonensis*) using species distribution models. Diversity, 13, 69. https://doi.org//10.3390/d13020069

Peng, Y., Li, Y., Cao, G., Li, H., Shin, Y., Piao, Z., Perez, F., Zhu, W. & Borzée, A. (2023) Estimation of habitat suitability and landscape connectivity for Liaoning and Jilin clawed salamanders (Hynobiidae: *Onychodactylus*) in the transboundary region between the People's Republic of China and the Democratic People's Republic of Korea. Global Ecology and Conservation, 48, e02694. https://doi.org//10.1016/j.gecco.2023.e02694

Peters, W.C.H. (1867) Über Fledertheire (*Pteropus gouldii*, *Rhinolophus deckenii*, *Vespertilio lobipes*, *Vesperugo temminckii*) und Amphibien (*Hypsilurus godeffroyi*, *Lygosoma scutatum*, *Stenostoma narisostre*, *Onychocephalus unguirostris*, *Ahaetulla polylepis*, *Pseudechis scutellatus*, *Hoplobatrachus reinhardtii*, *Hyla coriacea*). Monatsberichte der Königlichen Preussische Akademie des Wissenschaften zu Berlin, 1867, 703–712

Petitot, M., Manceau, N., Geniez, P. & Besnard, A. (2014) Optimizing occupancy surveys by maximizing detection probability: application to amphibian monitoring in the Mediterranean region. Ecology and Evolution, 4, 3538-3549. https://doi.org//10.1002/ece3.1207

Pyron, R.A. (2014) Biogeographic analysis reveals ancient continental vicariance and recent oceanic dispersal in amphibians. Systematic Biology, 63, 779–797. https://doi.org//10.1093/sysbio/syu042

R Core Team (2021) R: a language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.

Ra, N.-Y., Sung, H.-C. & Park, D. (2008a) Characteristics of *Rana plancyi chosenica* habitats and potential factors involved in the decline of the species. The Korean Research Society of Herpetologists, 8, 14

Ra, N.-Y., Sung, H.-C. & Park, D. (2016) Current status of the gold-spotted pond frog, Rana plancyi chosenica, and its habitat distributions in Korea. The Korean Research Society of Herpetologists, 13-14. https://www.earticle.net/Article/A281134

Ra, N.-Y., Bae, S., Min, S.-H., Son, H., Baek, S.-J. & Geum, J.-W. (2019) Recovery process of the Endangered Gold-Spotted Pond Frog(Pelophylax chosenicus) in the Du-ung Wetland. The Korean Research Society of Herpetologists, 18, https://www.earticle.net/Article/A361215

Ra, N.Y., Sung, H.C., Cheong, S., Lee, J.H., Eom, J. & Park, D. (2008b) Habitat use and home range of the endangered Gold-spotted pond frog (*Rana chosenica*). Zoological science, 25, 894-903. https://doi.org//10.2108/zsj.25.894

Ra, N.Y., Park, D., Cheong, S., Kim, N.S. & Sung, H.C. (2010) Habitat associations of the endangered Gold-spotted pond frog (*Rana chosenica*). Zoological Science, 27, 396-401. https://doi.org//10.2108/zsj.27.396

Ra, N.Y. & Park, D. (2011) Saving the Gold-spotted pond frog in South Korea. FrogLog, 98, 15

Rambaut, A., Drummond, A.J., Xie, D., Baele, G. & Suchard, M.A. (2018) Posterior summarization in Bayesian phylogenetics using Tracer 1.7. Systematic Biology, 67, 901–904. https://doi.org//10.1093/sysbio/syy032

Richardson, D.M. & Whittaker, R.J. (2010) Conservation biogeography–foundations, concepts and challenges. Diversity and Distributions, 16, 313-320. https://doi.org/10.1111/j.1472-4642.2010.00660.x

Rozas, J., Ferrer-Mata, A., Sánchez-DelBarrio, J., Guirao-Rico, S., Librado, P., Ramos-Onsins, S. & Sánchez-Gracia, A. (2017) DnaSP 6: DNA sequence polymorphism analysis of large data sets. Molecular Biology & Evolution, 34, 3299-3302. https://doi.org//10.1093/molbev/msx248

Ryu, S.H. & Hwang, U.W. (2011) Complete mitochondrial genome of the Seoul frog *Rana chosenica* (Amphibia, Ranidae): Comparison of *R. chosenica* and *R. plancyi*. Mitochondrial DNA, 22, 53–54. https://doi.org//10.3109/19401736.2011.603313

Seo, M., Lee, B., Park, C., Oh, H., Kim, H., Lee, K., Kang, C., Gil, H. & Park, J. (2014) Threatened wildlife at a glance. National Institute of Biological Resources. Incheon, Republic of Korea.

Shannon, F.A. (1956) The Reptiles and Amphibians of Korea. Herpetologica, 12, 22-49

Shen, H., Xu, M., Yang, X., Chen, Z., Xiao, N. & Chen, X. (2022) A new Brown frog of the genus *Rana* (Anura, Ranidae) from North China, with a taxonomic revision of the *R. chensinensis* species group. Asian Herpetological Research, 13, 145–158. https://doi.org//10.16373/j.cnki.ahr.210062

Shim, J.H. (2003) Study on the In Extu and restoration strategy planning for the protected wildlife Anura (*Rana plancyi chosenica* Okada) in Korea. Korean Journal of Nature Conservation, 1, 63-74. https://doi.org//10.30960/kjnc.2003.1.4.63

Shin, Y., Jang, Y., Allain, S.J.R. & Borzée, A. (2020) Catalogue of herpetological specimens of the Ewha Womans University Natural History Museum (EWNHM), Republic of Korea. ZooKeys, 965, 103-139. https://doi.org//10.3897/zookeys.965.52976

Shipley, B.R., Bach, R., Do, Y., Strathearn, H., McGuire, J.L. & Dilkina, B. (2022) megaSDM: integrating dispersal and time-step analyses into species distribution models. Ecography, 2022, https://doi.org//10.1111/ecog.05450

Sievers, F., Wilm, A., Dineen, D., et al. (2011) Fast, scalable generation of high-quality protein multiple sequence alignments using Clustal Omega. Molecular Systems Biology, 7, 539. https://doi.org//10.1038/msb.2011.75

Small, C. & Cohen, J.E. (2004) Continental Physiography, Climate, and the Global Distribution of Human Population. Current Anthropology, 45, 269-277

Soberón, J. & Peterson, A.T. (2005) Interpretation of models of fundamental ecological niches and species' distributional areas. Biodiversity Informatics, 2, 1. https://doi.org//10.17161/bi.v2i0.4

Son, E. & Borzée, A. (2020) *Pelophylax chosenicus* (Gold-spotted Pond Frog), Geographic distribution note. Herpetological Review, 51, 134

Sumida, M., Kondo, Y., Kanamori, Y. & Nishioka, M. (2002) Inter-and intraspecific evolutionary relationships of the rice frog *Rana limnocharis* and the allied species *R. cancrivora* inferred from crossing experiments and mitochondrial DNA sequences of the 12S and 16S rRNA genes. Molecular Phylogenetics and Evolution, 25, 293-305. https://doi.org//10.1016/S1055-7903(02)00243-9

Sung, H.C., Cha, S.M., Cheong, S.W., Park, D.S. & Park, S.R. (2007) Monitoring local populations and breeding migration patterns of the Gold-spotted pond frog, *Rana chosenica*. Journal of Ecology and Environment, 30, 121-126. https://doi.org//10.5141/JEFB.2007.30.2.121

Synes, N.W., Brown, C., Watts, K., White, S.M., Gilbert, M.A. & Travis, J.M. (2016) Emerging opportunities for landscape ecological modelling. Current Landscape Ecology Reports, 1, 146-167

Tokumoto, Y., Ramamonjisoa, N., Zheng, X.J. & Natuhara, Y. (2019) 16S rDNA sequences of 8 frog species and rhod sequences of two *Pelophylax* spp. in Aichi prefecture. Japan. Bulletin of Nagoya Biodiversity Center, 6, 15–22

Tuanmu, M.-N. & Jetz, W. (2014) A global 1-km consensus land-cover product for biodiversity and ecosystem modeling. Global Ecology and Biogeography, 23, 1031-1045. https://doi.org//10.1111/geb.12182

Vignali, S., Barras, A., Arlettaz, R. & Braunisch, V. (2020) SDMtune: an R package to tune and evaluate species distribution models. Ecology and Evolution 10, 11488– 11506. https://doi.org//10.1002/ece3.6786

Wallace, A.R. (1876) The geographical distribution of animals. Harvard University Press. Cambridge, USA.

Wang, S., Liu, C., Zhu, W., Gao, X. & Li, Y. (2016) Tracing the Origin of the Black-spotted Frog, *Pelophylax nigromaculatus*, in the Xinjiang Uyghur Autonomous Region. Asian Herpetological Research, 7, 69–74. https://doi.org//10.16373/j.cnki.ahr.150071

Wang, S., Fan, L., Liu, C., Li, J., Gao, X., Zhu, W. & Li, Y. (2017) The origin of invasion of an alien frog species in Tibet, China. Current Zoology, 63, 615–621. https://doi.org//10.1093/cz/zow117

Wang, Z., Zeng, J., Meng, W., Lohman, D.J. & Pierce, N.E. (2021) Out of sight, out of mind: public and research interest in insects is negatively correlated with their conservation status. Insect Conservation and Diversity, 14, 700-708. https://doi.org//10.1111/icad.12499

Warren, D.L. & Seifert, S.N. (2011) Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. Ecological Applications, 21, 335-342. https://doi.org//10.1890/10-1171.1

Yang, D.S. & Koo, B.H. (2016) A study on the improvement plan for a habitat of "Gold-spotted pond frog (*Pelophylax chosenicus*)" in danger of regional extinction in the urban area - case on the abandoned railroad site on Su-in line. Journal of the Korean Society of Environmental Restoration Technology, 19, 95-107. https://doi.org//10.13087/kosert.2016.19.2.95

Yang, S.Y., Kim, J.B., Min, M.S., Suh, J.H. & Kang, Y.J. (2000) Monograph of Korean Amphibia. Academy Book. Seoul.

Yoo, N., Do, M.S., Nam, H.K., Choi, G., Son, S.J. & Yoo, J.C. (2019) Habitat characteristics of anuran species inhabiting rice fields of western mid-south Korea - in the case of Daeho reclamation agricultural land by farming practices. Korean Journal of Ecology and Environment, 52, 366-377. https://doi.org//10.11614/KSL.2019.52.4.366

Yoon, I.B., Kim, J.I. & Yang, S.Y. (1998) Study on the food habits of *Rana nigromaculata* Hallowell and *Rana plancyi chosenica* Okada (Salientia; Ranidae) in Korea. Korean Journal of Environmental Biology, 16, 69-76

Zhang, H., Yan, J., Zhang, G. & Zhou, K. (2008) Phylogeography and demographic history of Chinese black-spotted frog populations (*Pelophylax nigromaculata*): evidence for independent refugia expansion and secondary contact. BMC Evolutionary Biology, 8, 1

Zhang, Z., Mammola, S., Liang, Z., Capinha, C., Wei, Q., Wu, Y., Zhou, J. & Wang, C. (2020) Future climate change will severely reduce habitat suitability of the Critically Endangered Chinese giant salamander. Freshwater Biology, 65, 971-980. https://doi.org//10.1111/fwb.13483

Zhou, S., Zhang, Z., Wang, H., Miao, Q., Xu, S., Guan, P. & Shi, J. (2022a) New record species of anura from China: *Pelophylax chosenicus*. Chinese Journal of Zoology, 57, 440–446

Zhou, S., He, L., Ma, S., Xu, S., Zhai, Q., Guan, P., Wang, H. & Shi, J. (2022b) Taxonomic status of *Rana nigromaculata mongolia* and the validity of *Pelophylax tenggerensis* (Anura, Ranidae). Zootaxa, 5165, 486-500. https://doi.org//10.11646/zootaxa.5165.4.2

Zhou, S.B., Zhang, Q.Y., Hu, Z.Q., Xia, Z.Y., Miao, Q., Guan, P. & Shi, J.S. (2023) The validity of *Pelophylax chosenicus* (Okada, 1931) and *P. hubeiensis* (Fei & Ye, 1982)(Amphibia, Ranidae). Herpetozoa, 36

Submitted: 14 October 2023
First decision: 6 January 2024
Accepted: 13 February 2024

Edited by Minh Le and Robert J. Whittaker