Behind the mountains and over the sea: the Changbai Mountain Range provided *Rana coreana* with a Chinese residence permit all along

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#### ABSTRACT

The Changbai Mountain Range is generally perceived as a barrier to amphibian distribution, but it might not be playing this role anymore. *Rana coreana* was first described as a Korean endemic species, split from *Rana amurensis*, which ranges at more northern latitude. The species was then found on the Shandong peninsula in China, where it was first described as *Rana kunyuensis*, before being synonymised with *R. coreana*. So far, the contact zone with *R. amurensis* was expected to be in the vicinity of Pyongyang in DPR Korea, west of the Baekdu Mountain Range. However, the species is known from a population further north, and during surveys in Dalian in Liaoning Province, China, we found *R. coreana* on the southern slopes of the Laoling Mountain Range facing the Yellow Sea. Our phylogenetic analyses based on mitochondrial ribosomal markers showed the individual to cluster with *R. coreana* samples from the Korean Peninsula. In addition, our ecological niche models showed the presence of suitable habitats outside of the known range of the species, deserving further investigation. The habitat of the species at this new locality is similar to the one known in the three range nations, and highlights the need for more surveys in northeast China as the barrier formed by the Changbai Range is more porous than originally expected.

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# Introduction

The Korean Peninsula is often considered a functional island for animal species due to its isolation by seas on the East, South, and West, and by the Changbai Mountain Range to the north (Fu and Wen 2023). In the context of biogeography, this isolation has been reinforced by geological events, primarily the orogenesis of the mountain chain (Yang et al. 2017), but also the permafrost line roughly reaching the same latitude during ice ages (Yi and Kim 2010; Aizawa et al. 2012; Kim et al. 2013), and the variation in sea level around the peninsula (Li et al. 2014). As a result, many species are indeed endemic to the Korean peninsula (Nam et al. 2018; Yoon et al. 2018; Chung et al. 2023).

For amphibians, many species have a distribution pattern following the Baedudaegan Massif, ranging latitudinally along the peninsula (Borzée 2024). Some species are restricted to the lowlands between the highlands and the coastal area (e.g. *Dryophytes suweonensis*, Borzée et al. 2017; Pelophylax chosenicus, Borzée et al. 2024), while others are restricted to higher elevations (e.g. Bufo stejnegeri, Fong et al. 2020; Onychodactylus koreanus, Borzée et al. 2022) and others are present in most of the suitable areas along the range (e.g. Pelophylax nigromaculatus; Komaki et al. 2015). However, most species range out of the Korean Peninsula, and the Changbai Mountain does not reflect its presence into genetic divergence (e.g. Dryophytes japonicus; Dufresnes et al. 2016), or is ever straddled by species (e.g. Onychodactylus zhangyapingi, Peng et al. 2023). However, it is fair to highlight the past impact of the mountain range on speciation patterns in species such as Bombina orientalis (Fong et al. 2016), and Rana dybowskii and Rana uenoi (Yang et al. 2017). Finally, some species that were thought to be endemic to the Korean Peninsula have later been found to be also occurring in Liaoning in the People's Republic of China (hereafter China; e.g. P. chosenicus; Borzée et al. 2024).

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Here we focus on the Korean Brown Frog, Rana coreana, a species thought to be restricted to the Korean Peninsula and to the Shandong Peninsula in China until 2022 (Zhou et al. 2022). The species was described in 2006 (Song et al. 2006), and although the type locality is unclear and is only presumed to be in Songdo in Incheon, or in Seungnam in Suweon, both in the Republic of Korea (Okada 1928). The species diverged from Rana amurensis about 10 million years ago (Zhou et al. 2017), and the population first described as Rana kunyuensis on the Shandong Peninsula was later synonymised with R. coreana (Zhou et al. 2015). The species is common, although not continuously distributed in the Republic of Korea (hereafter R Korea), and it is not present on Jeju and other islands (Borzée 2024). It is confirmed northwards up to Pyongyang latitude in the Democratic People's Republic of Korea (hereafter DPR Korea; Borzée et al. 2021) and in Shenyang, Liaoning, in the People's Republic of China (hereafter China; Zhou et al. 2022). This manuscript highlights the presence of numerous adequate landscapes further north than traditionally accepted, and the absence of apparent barriers to genetic exchange between the Korean and Liaoning populations.

# **Materials and methods**

### Field surveys

We surveyed the area between Dandong and Dalian on 15 June 2024 through rapid assessments using call surveys, following the protocol from Borzée and Jang (2015) and Borzée et al. (2017). The sites were selected along the lowlands south of the Laoling Mountain Range of the Liaodong Peninsula in Liaoning, facing the Yellow Sea to detect the presence of *P. chosenicus*. Each survey point consisted of a minimum of five minutes listening to the calls of amphibians in the area.

# **Field identification**

Upon encountering a *Rana* roadkill (Figure 1) between two pre-selected sites, the body was photographed and stored in 99% alcohol for further analyses. To identify the species based on morphology, we followed the identification criteria from Borzée (2024), focusing on the presence of a continuous white strip on the totality of the upper lip and red smooth spots on the ventral and lateral sides, a criteria valid during the breeding season (Borzée et al. 2023).

## **Phylogenetic analysis**

We extracted the tissue from the right leg of the individual, dried it to remove any alcohol left from preservation,



**Figure 1.** Individual *R. coreana* found in Dalian (39.518369°N, 122.339219°E) on 15 July 2024. The species can be identified through the characteristic un-interrupted white stripe covering the totality of the upper lip, supported by the half-webbed toes. The individual had been victim of a collision with a car before encounter.

and extracted DNA using the DNAeasy Blood and Tissue Kit (Qiagen Pvt. Ltd, Hilden, Germany), using the protocols provided by the manufacturer. The Polymerase Chain Reaction (PCR) amplification was performed by Tsingke Co., Ltd., Wuhan, People's Republic of China to obtain the 410-bp long 12S rRNA gene fragment (primers: FS01-RANA12SF-AACGCTAAGATGAACCC-TAAAAAGTTCT and R16-RANA12SR-ATAGTGGGGTATC-TAATCCCAGTTTGTTTT) and the 550-bp long 16S rRNA gene fragment (primers: F51-RANA16S-CCCGCCTGTTTAC-CAAAAACA and R51-RANA16S-GGTCTGAACTCAGAT-CACGTA; Sumida et al. 2002), followed by Sanger sequencing of both strands. The sequences generated by this study, for both 12S rRNA and 16S rRNA gene fragments were deposited to Genbank under accession numbers PQ032572 and PQ008571, respectively.

To identify the species through phylogenetic analyses, we first trimmed and complemented the raw sequences of the individual for both the 12S rRNA and 16S rRNA gene fragments using the Geneious Alignment tool in Geneious Prime v. 2023.2.1 (Kearse et al. 2012). Independently, we aligned the sequences of each gene fragment with the homologous sequences available in Genbank (https://www.ncbi. nlm.nih.gov/genbank/). We then concatenated the sequence alignments of the two gene fragments using Geneious Prime v. 2023.2.1. The final concatenated alignment included 89 taxa (815 bp), among which six related Rana species from northeast Asia as ingroup: R. amurensis, R. coreana, R. dybowskii, R. huanrenensis, and R. taihangensis. Additionally, we added R. zhenhaiensis (n = 3) as outgroup (details in Table S1). Prior the reconstruction of the phylogeny, we identified the best-fit partitioning scheme and substitution models for the concatenated 12S rRNA and

16S rRNA dataset using Partition Finder v.2.1.1 (Lanfear et al. 2012). As both fragments were non-coding RNA, we obtained K80+I as the best substitution model for both subsets of partition. We then integrated the information for the best substitution model in our concatenated alignment dataset (.Nexus) to reconstruct the Bayesian phylogenetic tree in Mr. Bayes v. 3.2.7 (Ronquist et al. 2012). We ran the analysis using the Monte Carlo Markov Chain (MCMC) algorithm, with 4 chains, 10,000,000 iterations, and a burn-in of 1000. To ensure the convergence and robustness of the phylogenetic analysis, we optimised the value of split frequencies (<0.05), the parameter space and the pattern of randomness of the MrBayes at the end of its run.

#### Ecological niche models

Finally, we used ecological niche models to determine other areas where the species might be present. The data used for this analysis originated from GBIF (DOI: http://10.15468/DL.XTTPF9, accessed 9 July 2023) and from the literature for datapoints in DPR Korea (Borzée et al. 2021), along with the new datapoint collected here (details in Table S2). When filtering GBIF data, we removed all data without coordinates and duplicates. To reduce the sampling bias, we thinned occurrence points within 4 km distance using spThin package (Aiello-Lammens et al. 2015) and using the bias files created by the MASS package (Venables and Ripley 2002) in R version 4.2.1 (R Core Team 2024). We decided to rely on the 19 bioclimatic variables (Worldclim 2.1; Fick and Hijmans 2017) and elevation (2.5 arc-minute resolution) only, after the removal of highly correlated variables (Pearson's r > 0.8; Bradie and Leung 2017), as very little has been published on the ecological preferences of the species for both the Korean Peninsula and China, and pre-selecting variables based on the literature would likely bias the models towards either of the populations. We retained six variables for the final models: annual mean temperature (bio 1), isothermality (×100; bio 3), temperature annual range (bio 7), annual precipitation (bio 12), precipitation seasonality (coefficient of variation; bio 15), and elevation. We ran MaxEnt version 3.4.4 (Elith et al. 2011; Phillips et al. 2017) with default setting (Phillips and Dudík 2008) and used the cross-validate run type option with ten replicates. For the model evaluation, we calculated the area under the curve (AUC) and the true skill statistic (TSS; Allouche et al. 2006; Somodi et al. 2017). To visualise the potential suitable habitat, we used ArcGIS pro 3.3.0 (ESRI, Redlands, CA, USA).

### Results

## **Field identification**

The individual we collected in Dalian, China, (Voucher ID: 24RcC001: 39.518369°N, 122.339219°E; Figure 2) on 15 July 2024 had a white uninterrupted stripe covering the totality of the upper lip, but did not have red spots on either of the ventral or lateral sides. It did not show prominent dorsolateral stripes either, a morphological cue that does not seem valid in the northern part of the range of the species (Song et al. 2006; Wang et al. 2017). In addition, the individual had half-webbed toes, another criterion matching with *R. coreana* (Song et al. 2006; Zhao et al. 2017; Othman et al. 2022).

The new site is 330 km west from the closest known site in DPR Korea and 240 km south of the site known in China. There are no barriers to the dispersion of the species between these sites. The habitat between these sites, and along the western coast of the Korean Peninsula and in Liaoning, China, is characterised by lowland riparian wetlands transformed into rice paddies in their large majority, backed by low-elevation hills covered by chestnut-dominated broadleaved forests, where the species is majorly present around 120 m above sea level (Andersen et al. 2022).

#### **Molecular analyses**

The phylogenetic tree (Figure 2) showed that the sample collected from Dalian clustered with the *R. coreana* clade (Bayesian posterior probability [BPP] of 100%). The individual specifically clustered with *R. coreana* individuals originating from both the Korean and Shandon Peninsulas with a BPP of 81%.

### **Ecological niche models**

The model was supported by AUC values greater than 0.7 and TSS values greater than 0.5, an adequately fitting set of value (Phillips et al. 2006). The variables contributing the most to the distribution of *R. coreana* was elevation for both the percentage of contribution (30.3%) and the permutation importance (57.1%; Table 1). The habitat suitability results were thresholded using the maximum training sensitivity plus specificity (MTSS) value, equal to 0.63, to classify the MaxEnt output raster files into suitable and unsuitable habitats (Figure 3).



**Figure 2.** Phylogenetic tree for the identification of the Rana individual sampled in Dalian, China, using 12S rRNA and 16S rRNA gene fragments (815 bp). We included 86 individuals as ingroup, originating from congeneric Rana species distributed across northeast Asia. We used three *R. zhenhaiensis* individuals from Nanjing as outgroup. The numbers indicated on each node represent the percentage of Bayesian Posterior Probability (BPP) support for each clade. The focal individual clusters within the clade containing *R. coreana* from the Korean and Shandong Peninsulas.

**Table 1.** Variable per cent contribution and permutation importance from selected MaxEnt habitat suitability model for *R. coreana* based on the six variables retained for the model.

Variables	Per cent contribution	Permutation importance
Elevation	30.3	57.1
Annual precipitation (bio 12)	27.1	32
Precipitation seasonality (coefficient of variation; bio 15)	21.1	2.2
Temperature annual range (bio 7)	13.3	0
Isothermality (×100; bio 3)	7.7	8.7
Annual mean temperature (bio 1)	0.5	0

As expected, all points from GBIF fell within the areas with the highest habitat suitability for *R. coreana*. Generally, the suitable habitat for the species is clustered around the Yellow Sea, especially in low coastal plains, reaching the edge of the Songliao plains in the north, and the southern edge of the Shandong Peninsula to the south (Figure 3). Our model also predicts suitable habitat in Jiangsu and along the eastern coast of the Korean Peninsula, where the species has not been found.



**Figure 3.** Suitable habitat for *R. coreana* around the Yellow Sea, highlighting the potential for unknown populations at the southern tip of Liaoning, along the Laoliang Mountain Range (deep red). The new locality in Dallian is 330 km west of the closest known locality in DPR Korea.

#### Discussion

This first record of *R. coreana* in Dalian, Liaoning, China, highlights not only a broader-than-expected and betterconnected range for the species, but also the need for further surveys for all amphibian species potentially present in the area. This is not unexpected in view of the known locality in Shenyang (Zhou et al. 2022), and based on the literature as this area is in need of amphibian conservation research (Button and Borzée 2021), which includes field surveys (Borzée 2023). In fact, this is the second species which was expected not to range into China from the Korean Peninsula, but is found further north at low elevation in Liaoning (e.g. P. chosenicus; Borzée et al. 2024). However, we caution against surveying all the suitable habitat highlighted by our model as the species is not present in some areas, likely due to competitive exclusion (Anderson et al. 2002). Namely, these areas are in Jiangsu, where R. coreana would likely be competing with Rana zhenhaiensis, and along the northern coast of the Korean Peninsula and Eastern Russia, where it would likely compete with *R. amurensis*.

This finding further raises questions about the current impact of the Changbai Mountain Range as a barrier to dispersion northward of the Korean Peninsula. While it is true that the highest mountain reaches 2744 m of elevation, and R. coreana could have reached northern localities before the orogenesis of the mountain chain (Wang et al. 2003; Liu et al. 2015), the low plains on the west of the peninsula connect with that south of the Laoling Mountain Range in Liaoning, and allow for continued exchange among populations. In addition, the Yellow Sea was only a paleoriver-bed 21,000 years ago (Ryu et al. 2008), and while of comparatively large proportion and preventing some geneflow (Borzée et al. 2020), the plains that are now tidal flats were exposed and allowing further connectivity along the Peninsula and the land further north.

For *R. coreana*, the discovery of this population means that the species has a much broader and better-

connected range than originally described, and is therefore less threatened than currently assessed (IUCN SSC Amphibian Specialist Group 2022). This is not the result of a decrease in threats, but because of its presence across an area that is less developed and urbanised than the once-thought 'core' population in R Korea (Borzée 2024). It, however, raises guestions about the validity of the finding of Kim and Han (2009) and Borzée et al. (2021), which states that the species only reaches Pyeongyang's latitude in DPR Korea, and that R. amurensis is present further north. It however reinforces the idea that Korean species are indeed in need of reinvigorated conservation research (Borzée et al. 2019), especially in view of threats due to climate change (Jung et al. 2024). Surveys in the Laoling Mountain Range in Liaoning have failed to detect R. amurensis, and it is therefore possible that a misidentification of the species in past-surveys, mistakenly quoted in recent work, restricted the distribution of *R. coreana* further south than it really ranges, while R. amurensis is present from further north only. As a result, this publication sparks curiosity about the distribution of the species in northeast China, but also that of all amphibians and other species.

## **Disclosure statement**

No potential conflict of interest was reported by the author(s).

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## Data availability statement

Sequence generated in this study has been submitted to GenBank (https://www.ncbi.nlm.nih.gov/) under specific accession number.

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# References

Aiello-Lammens ME, Boria RA, Radosavljevic A, Vilela B, Anderson RP. 2015. Spthin: an R package for spatial thinning of species occurrence records for use in ecological niche models. Ecography. 38:541–545. doi:10.1111/ecog.01132.

- Aizawa M, Kim Z-S, Yoshimaru H. 2012. Phylogeography of the Korean pine (*Pinus koraiensis*) in northeast Asia: inferences from organelle gene sequences. J Plant Res. 125:713–723. doi:10.1007/s10265-012-0488-4.
- Allouche O, Tsoar A, Kadmon R. 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). J Appl Ecol. 43:1223–1232. doi:10.1111/j. 1365-2664.2006.01214.x.
- Andersen D, Chuang M-F, Choe M, Kim A, Kwon S, Jang Y, Borzée A. 2022. Elevational distribution of amphibians: resolving distributions, patterns, and species communities in the Republic of Korea. Zool Stud. 61:25.
- Anderson RP, Peterson AT, Gómez-Laverde M. 2002. Using niche-based GIS modeling to test geographic predictions of competitive exclusion and competitive release in South American pocket mice. Oikos. 98:3–16. doi:10.1034/j.1600-0706.2002.t01-1-980116.x.
- Borzée A. 2023. A 13-step framework for better integration of streamlined conservation research. Integr Conserv. 2:156–164. doi:10.1002/inc3.28.
- Borzée A. 2024. Continental Northeast Asian amphibians: origins, behavioral ecology, and conservation. Amsterdam: Academic Press, Elsevier.
- Borzée A, Jang Y. 2015. Description of a seminatural habitat of the endangered Suweon treefrog, *Hyla suweonensis*. Anim Cells Syst. 19:216–220. doi:10.1080/19768354.2015. 1028442.
- Borzée A, Kim K, Heo K, Jablonski PG, Jang Y. 2017. Impact of land reclamation and agricultural water regime on the distribution and conservation status of the endangered *Dryophytes suweonensis*. PeerJ. 5:e3872. doi:10.7717/peerj. 3872.
- Borzée A, Litvinchuk SN, Ri K, Andersen D, Nam TY, Jon GH, Man HS, Choe JS, Kwon S, Othman SN, 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 (Basel). 11:2057. doi:10. 3390/ani11072057.
- Borzée A, Messenger KR, Andersen CS, Groffen D, Kim YI, An J, Othman AJ, Ri S, Nam TY, Bae Y, et al. 2020. Yellow sea mediated segregation between North East Asian *Dryophytes* species. PLoS One. 15:e0234299. doi:10.1371/ journal.pone.0234299.
- Borzée A, Rodriguez M, Bhatri N, Other-Authors M, Angulo A, Othman SN. 2023. Policy recommendations for the Rana trade towards the Republic of Korea. Front Environ Sci. 11:1097849. doi:10.3389/fenvs.2023.1097849.
- Borzée A, Shin Y, Bae Y, Jeong D, Amin H, Min M-S, Othman SN. 2024. From Korean to northeast Asian endemicity: on the occurrence of *Pelophylax chosenicus* along the Eastern Coastal Yellow Sea. Front Biogeogr. 16:e62301. doi:10. 21425/F5FBG62301.
- Borzée A, Shin Y, Poyarkov NA, Jeon JY, Baek HJ, Lee CH, An J, Hong YJ, Min M-S. 2022. Dwindling in the mountains: description of a critically endangered and microendemic *Onychodactylus* species (Amphibia, Hynobiidae) from the Korean Peninsula. Zool Res. 43:750–755. doi:10.24272/j. issn.2095-8137.2022.048.
- Borzée A, Struecker M-Y, Yi Y, Kim D, Kim H. 2019. Time for Korean wildlife conservation. Science. 363:1161–1162. doi:10.1126/science.aaw9023.

- Bradie J, Leung B. 2017. A quantitative synthesis of the importance of variables used in MaxEnt species distribution models. J Biogeogr. 44:1344–1361. doi:10.1111/jbi.12894.
- Button S, Borzée A. 2021. An integrative synthesis to global amphibian conservation priorities. Glob Chang Biol. 27:4516–4529. doi:10.1111/gcb.15734.
- Chung GY, Jang H-D, Chang KS, Choi HJ, Son DC. 2023. A checklist of endemic plants on the Korean Peninsula II. Korean J Plant Taxon. 53:79–101. doi:10.11110/kjpt.2023.53.2.79.
- Dufresnes C, Litvinchuk SN, Borzée A, Jang Y, Li J-T, Miura I, Perrin N, Stöck M. 2016. Phylogeography reveals an ancient cryptic radiation in East-Asian tree frogs (*Hyla japonica* group) and complex relationships between continental and island lineages. BMC Evol Biol. 16:253. doi:10.1186/ s12862-016-0814-x.
- Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates CJ. 2011. A statistical explanation of MaxEnt for ecologists. Divers Distrib. 17:43–57. doi:10.1111/j.1472-4642.2010.00725.x.
- Fick SE, Hijmans RJ. 2017. Worldclim 2: new 1-km spatial resolution climate surfaces for global land areas. Int J Climatol. 37:4302–4315. doi:10.1002/joc.5086.
- Fong JJ, Li P-P, Yang B-T, Zhou Z-Y, Leaché AD, Min M-S, Waldman B. 2016. Influence of geology and human activity on the genetic structure and demography of the Oriental fire-bellied toad (*Bombina orientalis*). Mol Phylogenet Evol. 97:69–75. doi:10.1016/j.ympev.2015.12.019.
- Fong JJ, Yang B-T, Li P-P, Waldman BS, Min M-S. 2020. Phylogenetic systematics of the water toad (*Bufo stejnegeri*) elucidates the evolution of semi-aquatic toad ecology and Pleistocene glacial refugia. Front Ecol Evol. 7:523. doi:10. 3389/fevo.2019.00523.
- Fu J, Wen L. 2023. Impacts of Quaternary glaciation, geological history and geography on animal species history in continental East Asia: a phylogeographic review. Mol Ecol. 32:4497–4514. doi:10.1111/mec.17053.
- IUCN SSC Amphibian Specialist Group. 2022. Rana coreana (amended version of 2019 assessment). The IUCN Red List of Threatened Species 2022: e.T89108544A219751493. https:// dx.doi.org/10.2305/IUCN.UK.2022-2.RLTS.T89108544A2197514 93.en
- Jung J-H, Choi S, Suh J-H, Do MS. 2024. Spatial distributional prediction of Korean Brown Frogs (*Rana uenoi, R. huanrenensis* and *R. coreana*) according to climate change. Curr Herpetol. 43:135–147.
- 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. doi:10.1093/bioinformatics/ bts199.
- Kim L, Han G. 2009. Chosun animal encyclopedia, herpetology volume. Roh H, editor. Pyongyang: Science and Technology.
- Kim SI, Park SK, Lee H, Oshida T, Kimura J, Kim YJ, Nguyen ST, Sashika M, Min MS. 2013. Phylogeography of Korean raccoon dogs: implications of peripheral isolation of a forest mammal in East Asia. J Zool. 290:225–235. doi:10.1111/jzo.12031.
- Komaki S, Igawa T, Lin SM, Tojo K, Min MS, 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. J Biogeogr. 42:2159–2171. doi:10.1111/ jbi.12584.

- Lanfear R, Calcott B, Simon Y, Guindon S. 2012. Partitionfinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. Mol Phylogenet Evol. 29:1695–1701. doi:10.1093/molbev/mss020.
- Li G, Li P, Liu Y, Qiao L, Ma Y, Xu J, Yang Z. 2014. Sedimentary system response to the global sea level change in the East China Seas since the last glacial maximum. Earth-Sci Rev. 139:390–405. doi:10.1016/j.earscirev.2014.09.007.
- Liu JQ, Chen SS, Guo ZF, Guo WF, He HY, You HT, Kim HM, Sung GH, Kim H. 2015. Geological background and geodynamic mechanism of Mt. Changbai volcanoes on the China– Korea border. Lithos. 236:46–73.
- Nam G, Lee B, Kwak M, Lim C, Kim C, Han K, Go E. 2018. Inventory and management of endemic species of Korea Incheon. Republic of Korea: National Institute of Biological Resources.
- Okada Y. 1928. Frogs in Korea. J Chosen Biol Soc. 6:15-46.
- Othman SN, Shin Y, Kim H-T, Chuang M-F, Bae Y, Hoti J, Zhang Y, Jang Y, Borzée A. 2022. Evaluating the efficiency of popular species identification analytical methods, and integrative workflow using morphometry and barcoding bioinformatics for taxonomy and origin of traded cryptic brown frogs. Glob Ecol Conserv. 38:e02253.
- 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. Glob Ecol Conserv. 48:e02694.
- Phillips S, Anderson R, Dudík M, Schapire R, Blair M. 2017. Opening the black box: an open-source release of Maxent. Ecography. 40:887–893. doi:10.1111/ecog.03049.
- Phillips SJ, Anderson RP, Schapire RE. 2006. Maximum entropy modeling of species geographic distributions. Ecol Modell. 190:231–259. doi:10.1016/j.ecolmodel.2005.03.026.
- Phillips SJ, Dudík M. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography. 31:161–175. doi:10.1111/j.0906-7590. 2008.5203.x.
- R Core Team. 2024. R version 4.2.1. Vienna: R Foundation for Statistical Computing. https://www.R-project.org/.
- Ronquist F, Teslenko M, Pvd M, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP. 2012. Mrbayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Syst Biol. 61:539–542. doi:10.1093/sysbio/sys029.
- Ryu E, Lee S-J, Yang D-Y, Kim J-Y. 2008. Paleoenvironmental studies of the Korean peninsula inferred from diatom assemblages. Quat Int. 176-177:36–45. doi:10.1016/j.quaint.2007. 05.015.
- Somodi I, Lepesi N, Botta-Dukat Z. 2017. Prevalence dependence in model goodness measures with special emphasis on true skill statistics. Ecol Evol. 7:863–872. doi:10.1002/ ece3.2654.
- Song J-Y, Matsui M, Chung K-H, Oh H-S, Zhao W. 2006. Distinct specific status of the Korean brown frog, *Rana amurensis coreana* (Amphibia: Ranidae). Zoolog Sci. 23:219–224. doi:10.2108/zsj.23.219.
- 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. Mol Phylogenet Evol. 25:293–305. doi:10.1016/S1055-7903(02)00243-9.

- Venables W, Ripley B. 2002. Modern applied statistics with S. 4th ed. New York: Springer.
- Wang C, Qian L, Zhang C, Guo W, Pan T, Wu J, Wang H, Zhang B. 2017. A new species of *Rana* from the Dabie Mountains in eastern China (Anura, Ranidae). Zookeys. 724:135–153. doi:10.3897/zookeys.724.19383.
- Wang Y, Li C, Wei H, Shan X. 2003. Late Pliocene recent tectonic setting for the Tianchi volcanic zone, Changbai Mountains, northeast China. J Asian Earth Sci. 21:1159– 1170.
- Yang B-T, Zhou Y, Min M-S, Matsui M, Dong B-J, Li P-P, Fong JJ. 2017. Diversity and phylogeography of Northeast Asian brown frogs allied to *Rana dybowskii* (Anura, Ranidae). Mol Phylogenet Evol. 112:148–157. doi:10.1016/j.ympev.2017. 04.026.
- Yi S, Kim S-J. 2010. Vegetation changes in western central region of Korean Peninsula during the last glacial (ca.

21.1-26.1 cal kyr BP). Geosci J. 14:1-10. doi:10.1007/ s12303-010-0001-9.

- Yoon JD, Kim JH, Park SH, Jang MH. 2018. The distribution and diversity of freshwater fishes in Korean Peninsula. Korean J Ecology and Environment. 51:71–85. doi:10.11614/KSL. 2018.51.1.071.
- Zhao H, Yang J, Wang C, Li P, Murphy RW, Che J, Yuan Z. 2017. A new species of the genus *Rana* from Henan, central China (Anura, Ranidae). Zookeys. 694:95–108. doi:10.3897/ zookeys.694.12513.
- Zhou S, Yu M-Z, Miao Q, Zhai Q, Xu S, Guan P. 2022. *Rana coreana* found in Shenyang, Liaoning. Chin J Zool. 57:944–950.
- Zhou Y, Wang S, Zhu H, Li P, Yang B, Ma J. 2017. Phylogeny and biogeography of South Chinese brown frogs (Ranidae, Anura). PLoS One. 12:e0175113.
- Zhou Y, Yang B-T, Li P-P, Min M-S, Fong JJ, Dong B-J, Zhou Z-Y, Lu Y-Y. 2015. Molecular and morphological evidence for *Rana kunyuensis* as a junior synonym of *Rana coreana* (Anura: Ranidae). J Herpetol. 49:302–307. doi:10.1670/13-111.