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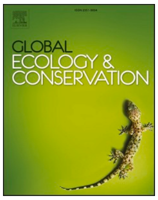

Estimation of habitat suitability and landscape connectivity for Liaoning and Jilin clawed salamanders (Hynobiidae: *Onychodactylus*) in the transboundary region between the People's Republic of China and the Democratic People's Republic of Korea

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ABSTRACT

Human activities and climate change have caused damage to the natural world, leading to increased attention on habitat protection. However, most conservation efforts focus on flagship species, while many other species lack protection and are gradually becoming extinct due to the lack of conservation efforts and public attention. The Liaoning clawed salamander (*Onychodactylus zhaoermii*) and the Jilin clawed salamander (*Onychodactylus zhangyapingi*) are two amphibians endemic to Northeast Asia, but they have not received enough conservation attention, and little is known about their distribution. In this study, we collected field survey and literature data for both species to obtain data on occurrence, and constructed ecological niche models (ENMs) to understand their suitable habitat and potential distribution. The ENMs revealed that the suitable habitat of *O. zhangyapingi* was primarily located within the Yalu River basin, as well as western and eastern mountains of the Democratic People's Republic of Korea (DPR Korea). On the other hand, the suitable habitat for *O. zhaoermii* was mainly distributed in the Xiuyan area of Liaoning in China, the Changbai Mountains, and north of the Tumen River basin. Although there is currently no direct evidence of the species' presence in DPR Korea, the ENM results support their putative presence in the nation, as there are large patches of suitable habitat. In addition, the connectivity model showed the presence of transboundary corridors between patches of suitable habitat, with some nodes (here defined as continuous patches of habitat enabling connection between suitable habitats) located in multiple provinces or within different countries. In addition, the two nodes with the lowest resistance distance value were contiguous with the nodes along the corridors. In our evaluation of the transboundary corridors in the eastern and western parts of the study area, we found that the surfaces located downstream along the Tumen River showed a better quality for corridor. However, the gradual fragmentation and disappearance of the

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landscape may lead the two species to extinction. Therefore, we recommend establishing a transboundary amphibian protection network in the China-DPR Korea river basin and encouraging collaborations for amphibian surveys and applied conservation projects in the Tumen River basin.

1. Introduction

Since humans entered the industrial age, the continuous increase in productivity has been accompanied by the continuous degradation of the natural world (Chu and Karr, 2013). As a result, natural landscapes such as forests and wetlands were gradually eroded by human activities (Scanes, 2018). In addition to the physical transformation of the natural world, the effects of climate change are ever increasing (Fedele et al., 2019); and human activities impact the climate through greenhouse gas emissions and deforestation, which make extreme weather events more frequent (Angélil et al., 2014). Under the direct and indirect influence of human activities and climate change, many species are facing increasingly severe challenges for survival (Hunter, 2007; Luedtke et al., 2023; Pacifici et al., 2017). To address this crisis, governments and non-governmental organizations have begun to implement planned protection for some flagship species' habitats and invested significant resources since the 1980 s, although mainly for mammals and birds (Franco JLdA, 2013). However, compared to charismatic species, many species lack adequate protection due to their low popularity, resulting in more extensive and urgent threats (Costante et al., 2022).

Amphibians are important due to their role as ecosystem health indicators (Halliday, 2008), and they offer valuable insights into evolutionary biology and ecology through their species diversity and widespread distribution (Liedtke et al., 2022). However, with the intensification of human activity and the increasing occurrence of extreme weather, the habitat of many amphibian species is constantly shrinking and becoming increasingly fragmented, resulting in a sharp decline in populations and even in extinctions (Womack et al., 2022). Many amphibian species are becoming threatened and at risk of extinction before we learn about them, such as the focal clade of this study (Borzée, 2024; Wake and Vredenburg, 2008).

The clawed salamanders (genus *Onychodactylus*) are endemic to Northeast Asia, with 12 species currently described (Frost, 2023). The members of the genus are distributed across Northeast China, the Korean Peninsula, Japan, and the Russian Far East (Poyarkov et al., 2012). All members of the genus are lungless, have long aquatic larval stage (Lee et al., 2008; Lee and Park, 2016), and take a long time to reach sexual maturity (Kuzmin, 1995; Poyarkov et al., 2012). In addition, both larvae and adults are highly dependent on clear mountain streams with high level of dissolved oxygen for survival and reproduction (Hong, 2017; Lee and Park, 2016; Park, 2005; Poyarkov et al., 2012). Due to these anatomical and ecological characteristics, habitats of *Onychodactylus* species restricted to clear mountain streams and adjacent forest environments (Kuzmin, 1995; Maslova et al., 2021). Furthermore, several species have small and fragmented geographic distribution (Borzée et al., 2022; Yoshikawa and Matsui, 2013). These combined characteristics make *Onychodactylus* species highly vulnerable to rapid environmental changes (Poyarkov et al., 2012; Shin et al., 2021). Despite the apparent vulnerability and conservation needs in the face of multiple threats, the distribution and ecology of many *Onychodactylus* species are still poorly known due to their elusive behavior and difficulties conducting field surveys in their habitats (Borzée, 2024).

The Liaoning clawed salamander (*Onychodactylus zhaoermii*) and the Jilin clawed salamander (*Onychodactylus zhangyapingi*) are confirmed to occur in limited mountain ranges in northern People's Republic of China (hereafter China). *Onychodactylus zhaoermii* is mainly distributed in the Qianshan Mountains and Liaodong Peninsula in Liaoning, China (Poyarkov et al., 2012), and *O. zhangyapingi* is mainly distributed along the Changbai Mountains in the areas of Tonghua and Baishan, with additional observational records in the Yanji region (Hou and Fei, 1964). While their ecologies are poorly known as in other *Onychodactylus* species, their rarity and conservation needs are reflected in their national protection status. For example, *O. zhaoermii* and *O. zhangyapingi* are designated as class I and class II protected animals in China, respectively (List of wild animals under state priority conservation, 2021).

Although the two species have only been documented from several locations in northern China so far (Poyarkov et al., 2012), they are most likely to range further south on the Korean Peninsula considering the continuous distribution of mountain ranges (Borzée et al., 2021; Poyarkov et al., 2012). Furthermore, the presence of *Onychodactylus* has been documented from across the Democratic People's Republic of Korea (hereafter DPR Korea), including the northern regions close to the border between China, DPR Korea, and Russia (Kim and Han, 2009; Won, 1971). While the species-level identity of *Onychodactylus* from northern DPR Korea remains unclear (Borzée et al., 2021; Poyarkov et al., 2012), they are most likely to be conspecific to either one or both of our study species given geographic proximity. However, conducting field surveys in DPR Korea is currently difficult, making the efforts to better characterize the distribution of our study species extremely difficult. This, in turn, poses significant limitation to conservation efforts aimed to cover the species' entire geographic distribution.

In this context, ecological niche models (ENMs) can be used as a powerful yet convenient tool to estimate suitable habitats for conservation planning (Benito et al., 2009; Booth, 2018; Peterson and Soberón, 2012). The application of ENMs in conservation biology has been demonstrated in numerous studies (Zhu et al., 2013), and various computational tools are readily available (Sillero et al., 2023). Ecological niche models have been applied to other species of *Onychodactylus* to assess the threat of future climate change (e.g., Shin et al., 2021). Applying the same general modeling framework to our study species is appropriate considering the general ecological characteristics shared by all members of the genus. Once suitable habitats are estimated, connectivity between suitable habitat patches through landscape analyses can improve baseline information for conservation efforts. Landscape connectivity analyses allow the identification of key areas and corridors that facilitate gene flow (Bolom-Huet et al., 2022), and landscape matrix plays a crucial role in facilitating or obstructing dispersal (Correa Ayram et al., 2015). Therefore, understanding and maintaining connectivity between habitat patches are crucial for the conservation and management of species, especially those with limited dispersal abilities (Lindenmayer, 2019; Zeller et al., 2020). The reduction in landscape connectivity can have negative impacts on the size and quality of available habitat, cause population fragmentation, and result in the decline of populations and species (Rudnick et al., 2012). Amphibians are often used as model species to assess genetic connectivity in variable landscapes because they are dispersal-limited and highly dependent on patchy habitats (Gamble et al., 2007; Sunny et al., 2021; Watts et al., 2015). In amphibian conservation research, constructing ecological corridors has become a widely used approach, such as in the Natura 2000 sites of Romania (Sahlean et al., 2020).

The lack of known geographical barriers and relevant data, coupled with the absence of clear distribution records for these two species and their unknown extent of distribution in the DPR Korea (Poyarkov et al., 2012), have contributed to the limited understanding of *O. zhaoermii* and *O. zhangyapingi*. This, in turn, has hindered efforts aimed at the conservation of these two elusive amphibians. Therefore, our research aims to: (1) determine the potential distribution ranges of *O. zhaoermii* and *O. zhangyapingi*, and (2) assess the connectivity and quality of corridors between habitat patches for the *Onychodactylus* genus. Furthermore, we hope to provide baseline information to stimulate additional research and conservation of these species.

2. Material and methods

2.1. Study area

Our research area covers the southern Liaoning and Jilin provinces of China, the southern Primorsky region of Russia (south of the range of *Onychodactylus fischeri*), and the northern part of the DPR Korea (Fig. 1). This area includes the Liaodong Peninsula basin, the cross-border basin of the Yalu River, and the cross-border basin of the Tumen River. Most of the research area belongs to a temperate monsoon climate, with the rainy season concentrated in summer. There is currently a nature reserve for *O. zhaoermii* in Anshan, Liaoning Province (Meng, 2013). The adult *O. zhaoermii* are active from April, with both males and females in a reproductive state from

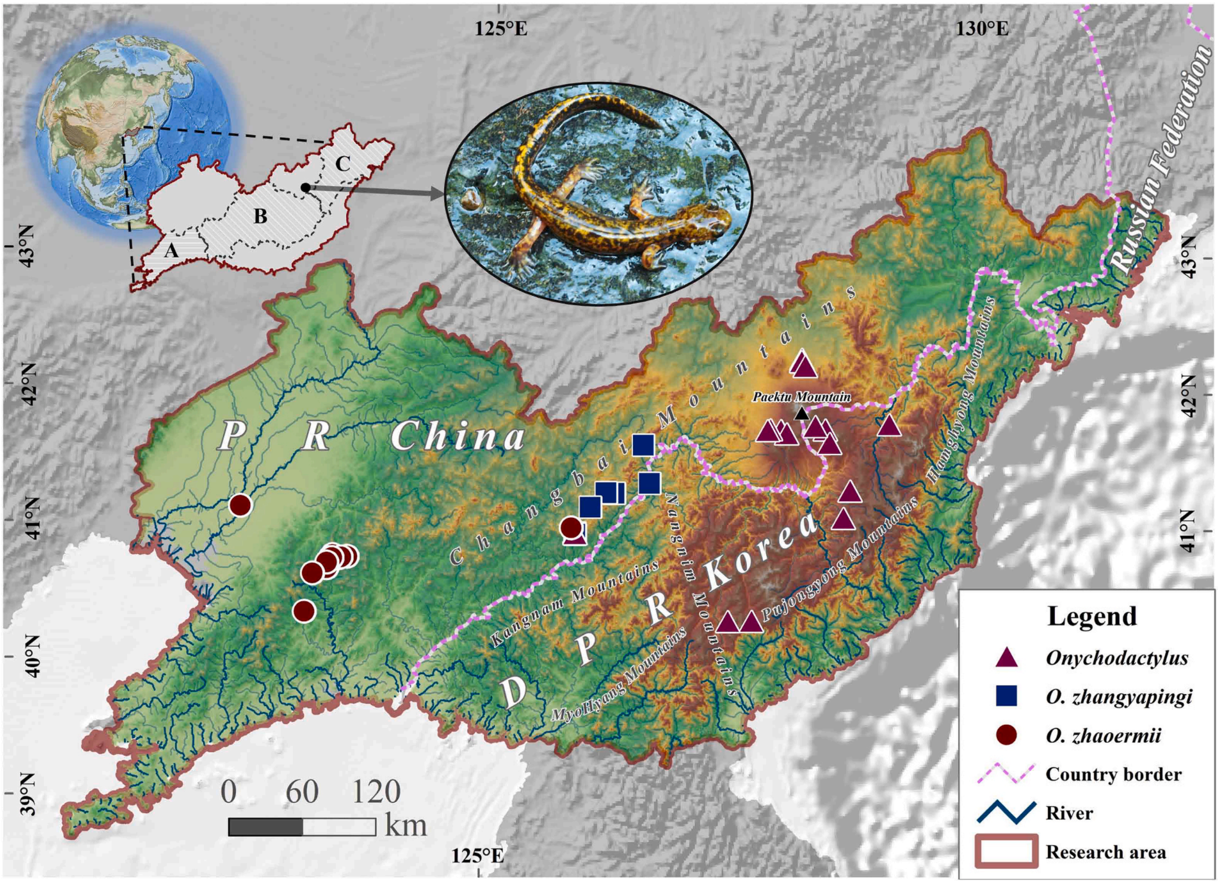

Fig. 1. Research area and Clawed Salamander record points used for modeling. The origin of the sample data includes field sampling, published references, and open data sets. The boundary data came from the College of Geography and Ocean Science, Yanbian University (A: Liaodong Peninsula, B: Yalu River Basin, C: Tumen River Basin). Hillshade from ETOPO1 elevation data. Country border is from GADM (https://gadm.org). *Onychodactylus* photo was taken by Zhengji Piao. Maps are created using ArcMap 10.8.

the beginning of May. The breeding season is expected to start in mid-April when the water temperatures reach at least 6 °C. The hibernation period for *O. zhaoermii* is expected to last from late September until early April (Meng, 2013; Poyarkov et al., 2012; Zhou et al., 2021).

2.2. Occurrence and environmental data

Our field surveys were carried from 2018 to 2021, mainly in Jian in Jilin Province and the surrounding areas of Changbai Mountain. We surveyed the area using opportunistic surveys (Poyarkov et al., 2012) and according to interviews with local residents to determine the possibility of occurrence for the species. The opportunistic surveys were conducted to detected any amphibian species in the focal areas and were conducted following two modalities. Daytime surveys were conducted in the afternoon along streams that were expected to match the ecological requirements of the species (Borzée, 2024). We walked along the stream and flipped the substrate (rocks and logs) where the species was susceptible to be present. The same protocol was used in evenings, coupled with road cruising to survey for the presence of the species on roads during rainy evenings, a method that is known to be adequate for the species, when matching with the migration over ground (Shin et al., 2022)..

We used handheld GPS to record geographic coordinates of all survey locations (Supplementary Fig. S1), and we morphologically identified the species following Poyarkov et al. (2012). A total of 41 presence records were collected through field surveys (n = 14), published literature records (n = 19; Luan, 2018; Lv et al., 2014; Poyarkov et al., 2012; Zhang, 2020; Zhou et al., 2021), and the Global Biodiversity Information Facility (n = 1; https://doi.org/10.15468/dl.qnrmf3; GBIF.org 2023), and a review of records from DPR Korea published in a variety of languages (n = 7; Borzée et al., 2021). While our study area includes a region in Russia, we did not include data points for *O. fischeri* as the species is not known to occur in the study area (Supplementary Table S1).

Considering the environment of the research area, published studies (Do et al., 2022; Lee et al., 2021), and the ecology of *O. zhaoermii* and *O. zhangyapingi* (Borzée, 2024), we initially considered a set of 27 environmental variables for ENM, including terrain factors, climatic factors, natural factors, and anthropogenic factors. The terrain factors include three variables: elevation, slope, and aspect, considering the mountainous habitats of the two study species. The climate factors include 19 bioclimatic variables, considering the sensitivity of *Onychodactylus* to climate variables. Natural factors include two variables: distance to water body and vegetation cover, because both species inhabit cold streams in valleys below the canopy of dense forests, and because their preferred habitat is in coniferous or broadleaf forests (Borzée, 2024). Anthropogenic factors include three variables: distance to artificial areas, human footprint, and distance to cropland, which are considered because all members of the genus *Onychodactylus* are sensitive to human activities. Elevation data were derived from the SRTM 90-meter resolution World DEM database (Jarvis et al., 2008), and slope and

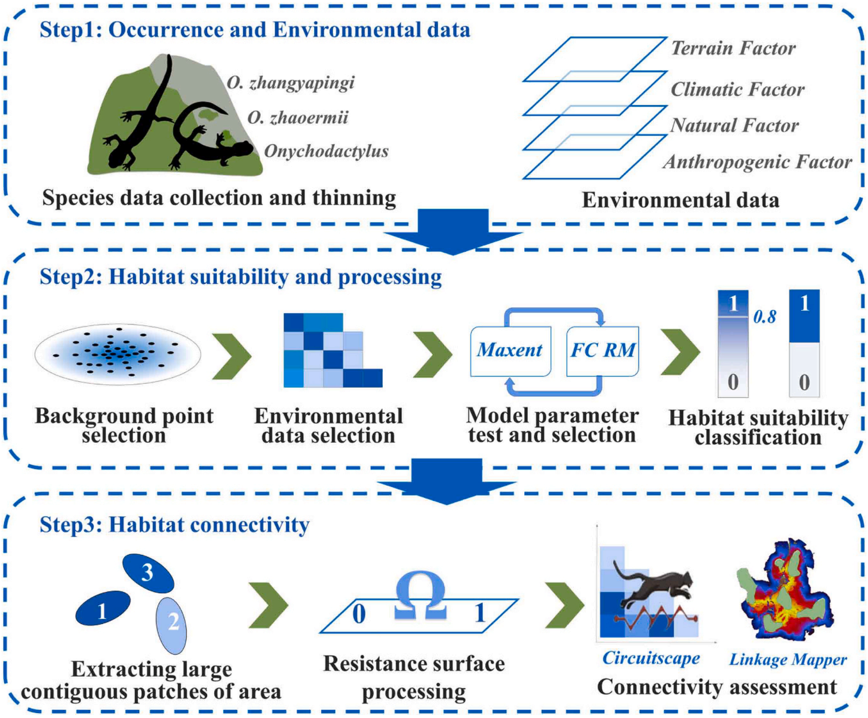

Fig. 2. Research framework for ecological niche model and connectivity modelling in *Onychodactylus* species. Our project had two primary objectives. Firstly, we aimed to determine the potential distribution ranges of *O. zhaoermii* and *O. zhangyapingi* (step 2). Secondly, we evaluated the connectivity between nodes for the *Onychodactylus* genus (step 3). To enhance the logical coherence of the structural diagram and facilitate comprehension, we placed the occurrence points thinning in step 1. This framework can be applied to studies of other species.

aspect data were obtained from the elevation data by using the slope tool and aspect tool respectively in ArcGIS 10.5 (ESRI, Redlands, CA). The aspect is divided into eight directions based on degree measurements. These directions are as follows: north (337.5–22.5°), northeast (22.5–67.5°), east (67.5–112.5°), southeast (112.5–157.5°), south (157.5–202.5°), southwest (202.5–247.5°), west (247.5–292.5°), and northwest (292.5–337.5°). The bioclimatic variables (30 arc-second) were obtained from WorldClim 2.1 (Fick and Hijmans, 2017). The distance to water bodies, distance to artificial areas, and distance to cropland are based on the dataset of Global Land Cover with Fine Classification System at 30 m spatial resolution (GLC_FCS30–2020) (Liu et al., 2020), processed using the Kriging distance tool in ArcGIS10.5. Vegetation cover was obtained through extraction and integration of forest data in the GLC_FCS30–2020 dataset and divided into four categories: 1-coniferous forest, 2-broadleaf forest, 3-other trees, and 4-non trees. Human footprint data was derived from the NASA Socioeconomic Data and Applications Center (Venter et al., 2018). Finally, the resampling tool of ArcGIS10.5 was used to unify the resolution of all environmental data to 1 km. We used the WGS-84 coordinate system for all spatial projections used in this study.

2.3. *Model preparation*

2.3.1. *Occurrence data thinning*

To avoid spatial clustering of occurrence points, we thinned the occurrence data using the R package spThin (Aiello-Lammens et al., 2019). Considering the spatial resolution of the environmental variables, the thinning distance was set to 1 km. After thinning, seven occurrence points were retained for *O. zhangyapingi*, 13 points for *O. zhaoermii* and 15 points for *Onychodactylus* with uncertain species level identification. We divided the occurrence data into three species groupings: *O. zhaoermii*, *O. zhangyapingi*, and aggregated *Onychodactylus* points from the study area (including *O. zhaoermii*, *O. zhangyapingi*, and *Onychodactylus* with uncertain species level identification), and created a model for each grouping.

2.3.2. *Background point selection*

We sampled background points based on occurrence data density (Ahmadi et al., 2023), using the occurrence points that have already been divided into three parts (*O. zhaoermii*, *O. zhangyapingi*, and aggregated *Onychodactylus*) to generate distinct density surfaces. First, we generated a 50-km radius circular buffer around occurrence data, using the R package megaSDM (Shipley et al., 2021). Next, we generated a density grid using the occurrence data, using the density grid limited by the buffer to represent the overall sampling effort within the study area. Finally, from the density grid, we sampled 10,000 background points for each of the three occurrence datasets using the sample function of the R package MASS (Ripley et al., 2023).

2.3.3. *Environmental data selection*

Using the R package SDMtune (Vignali et al., 2020), we used three parts of the occurrence points and the corresponding background points to select the environmental variables. First, we created a Sample With Data (SWD) object for each species grouping based on the background point data and all environment variables initially considered ($n = 27$). Next, we generated a default Maxent model, partitioning 80% of the occurrence data as the training set and 20% of the occurrence points as the testing set. We then applied the “reduceVar” function to the generated default model and retained the environment variables with a percent contribution higher than 3%. This generated a reduced-variable model. Next, we input this reduced-variable model to the "varSel" function to select environment variables with low collinearity. This was done by running a Spearman’s correlation test and setting the correlation threshold at $|\rho| > 0.7$. Therefore, different environmental variables were selected for *O. zhangyapingi*, *O. zhaoermii*, and *Onychodactylus* with uncertain species-level identification (Supplementary Table S2).

2.4. *Habitat suitability and processing*

2.4.1. *Model parameter testing*

We tested the MaxEnt model parameters using the ENMeval package version 2.0 (Kass et al., 2023). To evaluate candidate models for each species, we applied random 10-fold cross-validation for occurrence dataset with $n \geq 25$, and applied “leave-one-out” jackknifing for occurrence dataset with $n < 25$. We tested combinations of six MaxEnt feature classes (FC; L, LQ, H, LQH, LQHP, and LQHPT, where L = linear, Q = quadratic, H = hinge, P = product, T = threshold), and 10 regularization multipliers (RM) ranging from 0.5 to 5 at a 0.5 increment.

2.4.2. *Model selection*

For each of these three models, we selected the lowest $\triangle$AICc (delta.AICc = 0) or used the sequential selection method based on the maximum AUC_{TEST} (area under the receiver operating characteristic curve calculated from testing data) and minimum 10% training omission rate (OR10), resulting in a total of seven outcomes (Supplementary Fig. S2). To further screen the results, we employed the following methods: (1) for *O. zhangyapingi* and *O. zhaoermii*, we selected the prediction result with the smallest geographic distribution range as the species are expected to have restricted geographic range. (2) For *Onychodactylus*, we chose the result covering the area of both *O. zhangyapingi* and *O. zhaoermii*.

We modeled the seven outcomes (Supplementary Fig. S3), using the dismo R package (Hijmans et al., 2022), and then based on these methods, we finally chose three models corresponding to *O. zhangyapingi* (LQH RM = 4), *O. zhaoermii* (L RM = 0.5), and *Onychodactylus* (LQ RM = 0.5) from these model outcomes (Fig. 3). The performance of the model was evaluated using the area under the receiver operating characteristic curve (AUC), and True Skill Statistic (TSS; Allouche et al., 2006), which was calculated by selecting the Maximum Training Sensitivity plus Specificity (MTSS) as the threshold, and the difference between the AUCs calculated from training and testing data ($AUC_{DIFF} = AUC_{TRAIN}$ - AUC_{TEST}; (Warren and Seifert, 2011). The AUC statistic is evaluated based on the following criteria: excellent (0.90–1.00), very good (0.8–0.9), good (0.7–0.8), fair (0.6–0.7), and poor (0.5–0.6) (Duan et al., 2014). The TSS ranges from − 1–1, with a higher value indicating better discrimination (Allouche et al., 2006). The AUC_{DIFF} is a measure used to quantify the difference in performance between the training and testing datasets, where values close to 0 indicate minimal overfitting of models (Shin et al., 2021; Warren and Seifert, 2011). In addition, we assessed variable importance in each model using percent contribution, and plotted the cloglog response curves.

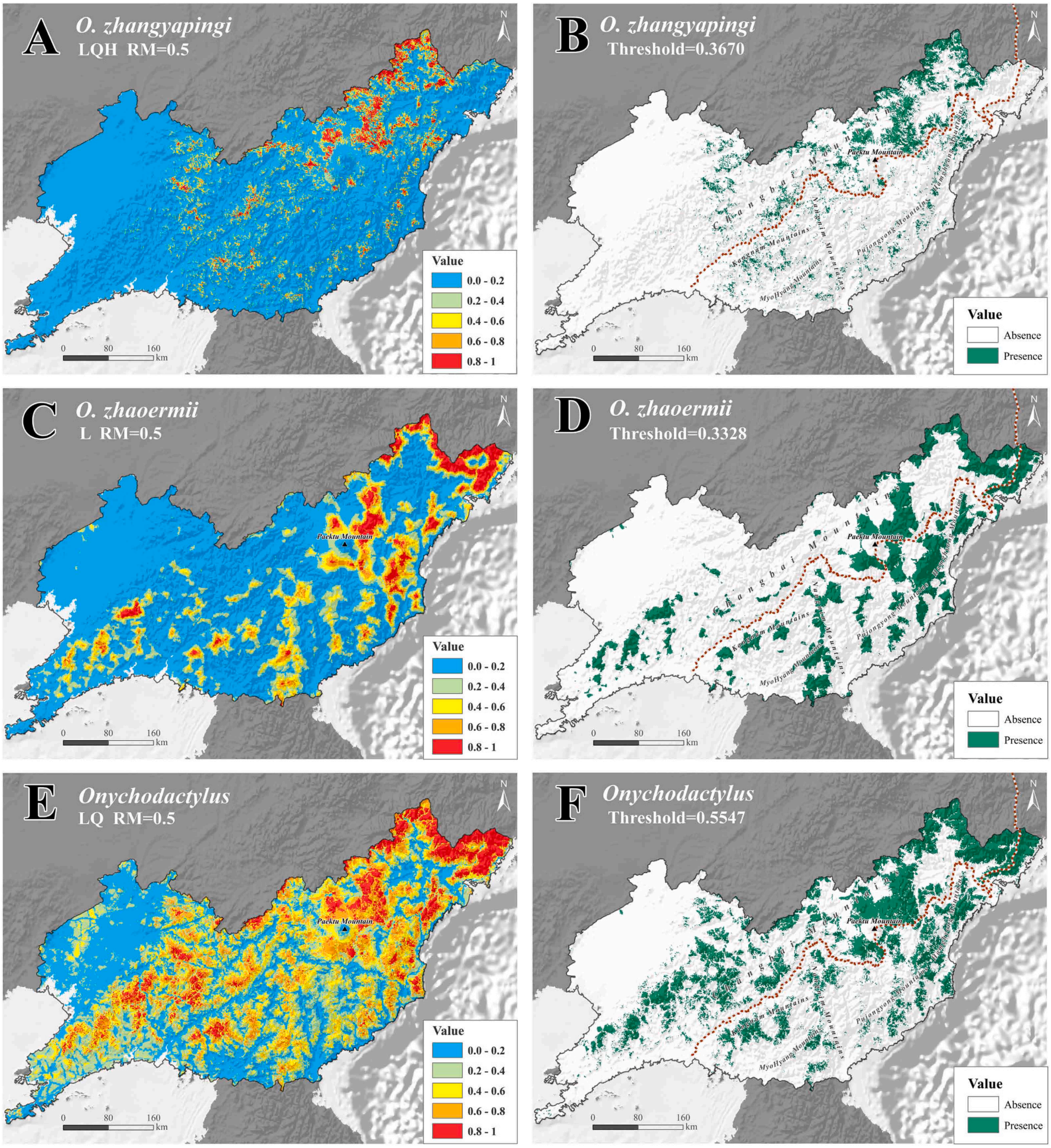

Fig. 3. Habitat suitability distribution and species presence-absence maps for *Onychodactylus* spp. These models were selected from the seven selected models after tuning, based on the methods described in the text. A, C and E are habitat suitability distribution maps: A (AUC = 0.852 ± 0.134; TSS = 0.7251 ± 0.1762; AUC_{DIFF} = 0.1132), C (AUC = 0.845 ± 0.242; TSS = 0.6722 ± 0.0451; AUC_{DIFF} = 0.0363), E (AUC = 0.714 ± 0.153; TSS = 0.3876 ± 0.0230; AUC_{DIFF} = 0.0368); B, D and F are presence/absence maps of habitat suitability distribution.

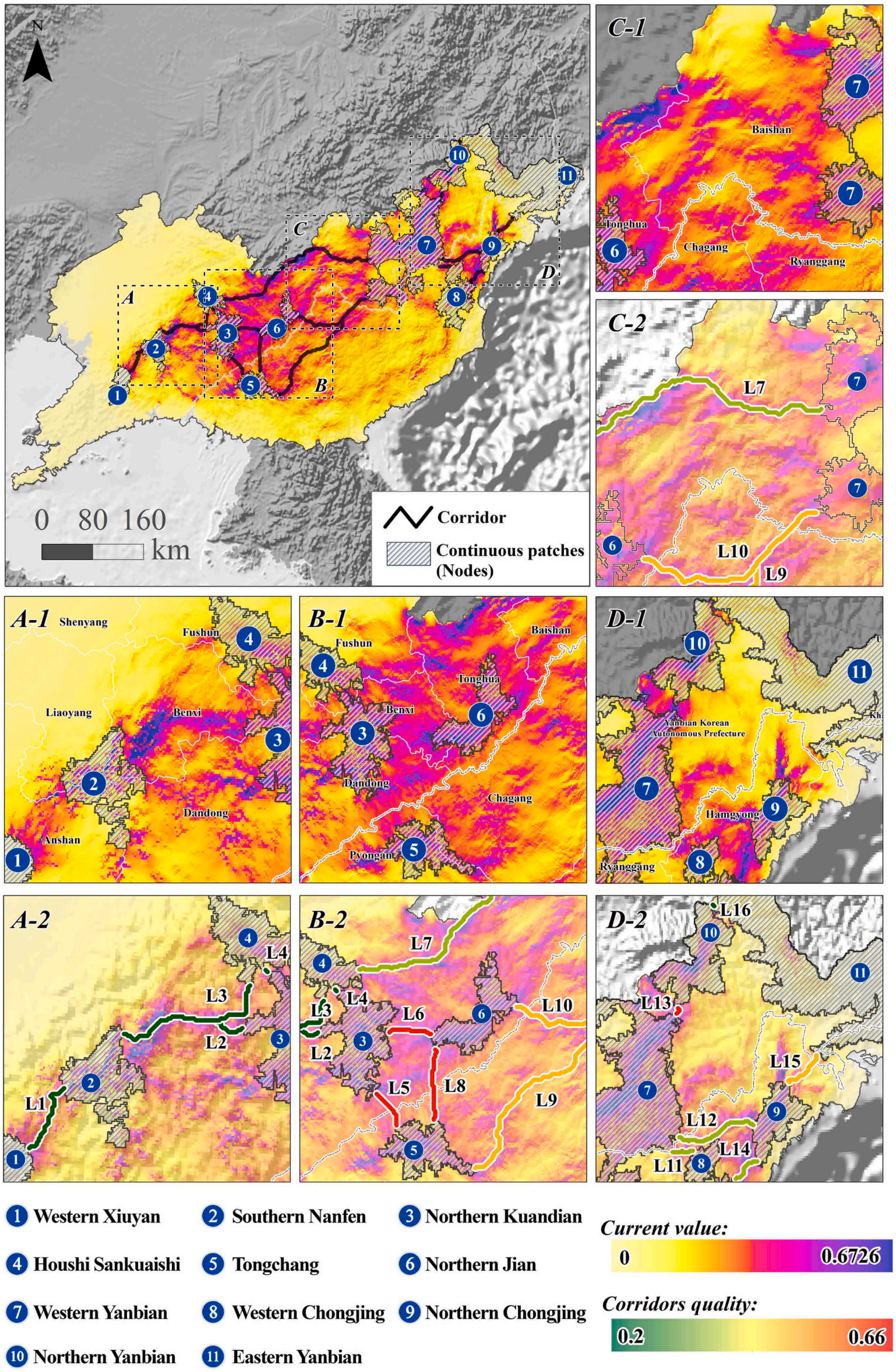

Fig. 4. Corridor connection for *Onychodactylus* species in the transboundary area between China and DPR Korea. We identified 11 continuous patches larger than 1000 km^2 on the presence/absence map of the *Onychodactylus* genus. These nodes are named and indexed with blue circle markers, labeled 1–11 on the map. Our findings reveal that the highest overall current density was 0.6726, concentrated in the purple area, indicating the highest current density and a potential corridor. There are 16 corridors, labeled L1 to L16 on the map, with the black lines showing corridors, while in the submaps, we use the calculation results of the corridors quality to render lines. The redder the color, the higher the cost of movement along the path of least resistance, and the greener the color, The higher the quality of corridors along the least-cost path.

2.4.3. Habitat suitability classification

We used two methods to partition the habitat to evaluate the habitat suitability and the presence/absence of species: (1) Using the equal interval method, the continuous habitat suitability scale was divided into five categories with an interval of 0.2, we defined the area with habitat suitability ≥ 0.8 as the most suitable region (Fig. 3-A, Fig. 3-C, Fig. 3-E). (2) Using the MTSS Cloglog threshold, we reclassified the habitat suitability to describe the presence/absence of species (Fig. 3-B, Fig. 3-D, Fig. 3-F).

2.5. Habitat connectivity

Based on the presence/absence map of the *Onychodactylus* genus, we extracted 11 continuous patches with an area larger than 1000 km^2 as nodes (Fig. 4). Regarding the setting of resistance, we followed the method proposed by Li et al. (2022) and used the following formula to construct the resistance surface:

$$R = 1 - H \tag{1}$$

Where R is resistance surface, and H is the suitability results of the ENMs of the *Onychodactylus* genus. The range of R values is between 0 and 1, with lower resistance in areas with high suitability and higher resistance in areas with low suitability.

To assess the connectivity of the habitat, we first generated a current model using Circuitscape (McRae et al., 2008), taking the 11 nodes and resistance surfaces defined above as input data, and constructed the model in pairwise mode to analyze connectivity between different nodes. Then, we constructed the corridors using Linkage Mapper (McRae and Kavanagh, 2011), the nodes and resistance surfaces were used as input data to construct a network of core areas, calculate cost-weighted distances and least-cost paths.

We analyzed the results in two ways. Firstly, we observe the relationship between high-density current flow directions and the corridors and compare it with the resistance distances values between nodes to support the connection between nodes. Secondly, we calculate the corridor quality, calculated as follows:

$$Q = CWD / LCP \tag{2}$$

Where Q is corridor quality, CWD is the cost-weighted distances between two nodes, and LCP is the Least-cost path lengths between two nodes. The higher values indicate a higher cost of movement along the path of least resistance, while the lower values indicate a higher quality of corridors along the least-cost path (Dutta et al., 2015).

3. Result

3.1. Habitat suitability and processing

The results of final ENMs based on the selected evaluation metrics suggest that the three models performed well, although to varying degrees, and all reached or surpassed the AUC standard. The results for each species grouping are as follows: *Onychodactylus zhangyapingi* ($AUC = 0.852 \pm 0.134$; $TSS = 0.7251 \pm 0.1762$; $AUC_{DIFF} = 0.1132$), *Onychodactylus zhaoermii* ($AUC = 0.845 \pm 0.242$; $TSS = 0.6722 \pm 0.0451$; $AUC_{DIFF} = 0.0363$), and *Onychodactylus* uncertain species identity ($AUC = 0.714 \pm 0.153$; $TSS = 0.3876 \pm 0.0230$; $AUC_{DIFF} = 0.0368$).

For the *O. zhangyapingi* model (Supplementary Table S3), vegetation cover had the highest importance (50.9%), followed by isothermality (17.2%), distance to cropland (8.7%), aspect (8.2%), distance to artificial areas (5.3%), elevation (5.1%), distance to water bodies (2.6%), and slope (2.1%). For the *O. zhaoermii* model (Supplementary Table S4), distance to water bodies had the highest importance (35.2%), followed by mean diurnal range (24.9%), human footprint (19.2%), distance to artificial areas (16.1%), and vegetation cover (4.6%). For the aggregated *Onychodactylus* model (Supplementary Table S5), distance to water bodies had the highest importance (50.1%), followed by vegetation cover (24.7%), human footprint (18.2%), and isothermality (5.3%).

From the response curve, we defined numerical values greater than 0.8 as highly suitable areas (Shin et al., 2021). Suitable habitat in the *O. zhangyapingi* model was characterized by elevation lower than 900 m, slope range of $1^\circ - 7^\circ$, avoiding north and northeast-facing aspects, located 4800 m upstream from water bodies, with an isothermality between 25.7.7 °C and 27.4 °C, mainly surrounded by coniferous and broadleaf forests, and located between 6.17 km and 16.02 km away from areas of human development, and 3.13 km away from cropland (Supplementary Fig. S4). Suitable areas for *O. zhaoermii* were characterized by an area with a human footprint of less than 5, located 24.30 km upstream from lentic water bodies and 10.79 km away from areas of human development, mainly surrounded by coniferous forests (Supplementary Fig. S5). Suitable *Onychodactylus* habitat was characterized by an isothermality range lower than 25 °C, a temperature seasonality lower than 1132, located between 20.92 km and 37.61 km upstream from water bodies, and in areas where the vegetation is mainly composed of coniferous and broadleaf forests (Supplementary Fig. S6).

From the presence/absence binary thresholding, the *O. zhangyapingi* model showed that the suitable habitat is quite fragmented. The larger patches were mainly distributed in the western part of the Tumen River basin, while the fragmented patches were mainly distributed throughout the Yalu River basin and the western and eastern mountains of DPR Korea (Fig. 3-B). The *O. zhaoermii* model showed that suitable patches were relatively intact, mainly distributed in the Xiuyan area of Liaoning, the Changbai Mountains area, and north of the Tumen River basin (Fig. 3-D). For the model generated from aggregated *Onychodactylus* occurrence points, the western region of the study area was more fragmented than the eastern region, and the south was more fragmented than the north (Fig. 3-F).

Table 1

Resistance distances between nodes for *Onychodactylus* spp in the transboundary area between China and DPR Korea. This table presents the resistance distances values between the 11 nodes, a value that represents the landscape barriers faced by the species during migration, a higher value indicates a greater resistance distance between two nodes, disrupted species migration resulting in weaker connectivity. Conversely, a lower value indicates a smaller resistance distance between two nodes, resulting in stronger connectivity.

	Western Xiuyan	Southern Nanfen	Northern Kuandian	Houshi Sankuaishi	Tongchang	Northern Jian	Western Yanbian	Western Chongjing	Northern Chongjing	Northern Yanbian	Eastern Yanbian
Western Xiuyan	0	0.106	0.232	0.239	0.328	0.350	0.552	0.646	0.742	0.740	0.781
Southern Nanfen	0.106	0	0.126	0.134	0.223	0.245	0.448	0.541	0.637	0.635	0.677
Northern Kuandian	0.232	0.126	0	0.021	0.097	0.106	0.317	0.410	0.506	0.504	0.546
Houshi Sankuaishi	0.239	0.134	0.021	0	0.163	0.159	0.366	0.460	0.556	0.554	0.595
Tongchang	0.328	0.223	0.097	0.163	0	0.111	0.279	0.370	0.467	0.465	0.506
Northern Jian	0.350	0.245	0.106	0.159	0.111	0	0.206	0.303	0.398	0.395	0.437
Western Yanbian	0.552	0.448	0.317	0.366	0.279	0.206	0	0.045	0.112	0.047	0.125
Western Chongjing	0.646	0.541	0.410	0.460	0.370	0.303	0.045	0	0.086	0.142	0.161
Northern Chongjing	0.742	0.637	0.506	0.556	0.467	0.398	0.112	0.086	0	0.134	0.094
Northern Yanbian	0.740	0.635	0.504	0.554	0.465	0.395	0.047	0.142	0.134	0	0.018
Eastern Yanbian	0.781	0.677	0.546	0.595	0.506	0.437	0.125	0.161	0.094	0.018	0

3.2. *Habitat connectivity*

The corridor connection results showed that the highest current density in this area was 0.6726. The Westrn Xiuyan node was located in Anshan, and Southern Nanfen node was located at the junction of four cities: Anshan, Liaoyang, Benxi, and Dandong (Fig. 4 A-1). There was a clear current between Western Xiuyan node and Southern Nanfen node (L1; Fig. 4 A-2). The northern Kuandian node was located at the junction of Dandong, Fushun, and Benxi (Fig. 4 B-1). There was a clear current between Southern Nanfen node and Northern Kuandian node (L2; Fig. 4 A-2). Houshi Sankuaishi node was mainly located in Fushun (Fig. 4 B-1). There was a clear current between Southern Nanfen node and Houshi Sankuaishi node (L3; Fig. 4 B-2). There was a clear current between the Northern Kuandian and Houshi Sankuaishi nodes (L4; Fig. 4 B-2). The Northern Jian node panned the cities of Tonghua in Jilin Province and Benxi in Liaoning Province (Fig. 4 B-1). There was a clear current (L6; Fig. 4 B-2), from the Northern Kuandian node to the Northern Jian node. The Western Yanbian node was mainly located in Baishan and the Yanbian Korean Autonomous Prefecture (China), partially including Ryangang Province (Fig. 4 D-1) in DPR Korea. L7 connected the Houshi Sankuaishi node with the Western Yanbian node, while L10 extending eastward from the Northern Jian node to the Western Yanbian node, located in the western part of the Yanbian Korean Autonomous Prefecture (Fig. 4 C-2). L13 connected the Northern Yanbian node with the Western Yanbian node, while L16 connected the Eastern Yanbian and Northern Yanbian nodes (Fig. 4 D-2).

The Tongchang node was located within DPR Korea, encompassing the North Pyongan and Chagang Provinces (Fig. 4 B-1). The Northern Kuandian and Northern Jian nodes, across the Yalu River, were connected to the Tongchang node (corridor L5 and L8; Fig. 4 B-2). The Western Yanbian node was connected with the Tongchang node (L9; Fig. 4 C-2). The Western Yanbian node was connected to the Western and Northern Chongjing nodes (corridor L11 and L12; Fig. 4 D-2). Finally, the Eastern Yanbian node, connected across the Tumen River with the Northern Chongjing node (L15; Fig. 4 D-2).

Based on the results of resistance distances between nodes, the two nodes with the lowest resistance distance value were consistent with the continuous patches along the corridors (Table 1). The corridors quality, had low values between the following patches: Western Xiuyan - Southern Nanfen, Southern Nanfen - Northern Kuandian, Southern Nanfen - Houshi Sankuaishi, Northern Kuandian - Houshi Sankuaishi and Northern Yanbian - Eastern Yanbian, where a low value indicated a higher quality of corridors along the least-cost path. The corridors with high values were between the following patches: Northern Kuandian - Tongchang, Northern Kuandian - Northern Jian, Tongchang - Northern Jian and Western Yanbian - Northern Yanbian, where high values indicated a higher cost of movement along the path of least resistance (Table 2).

4. Discussion

4.1. *Habitat suitability*

The models for *Onychodactylus zhangyapingi*, *Onychodactylus zhaoermii*, and aggregated *Onychodactylus* in the transboundary area between China and DPR Korea are characterized by highly suitable habitat patches. All modeling results show a characteristic distribution along major mountain ranges, especially in the eastern mountainous areas of DPR Korea. From the distribution of occurrence points that we have collected, the westernmost locality of *O. zhaoermii* reaches the Liaodong Peninsula. For *O. zhaoermii*, based on the presence points on the Liaodong Peninsula, the results indicated a relatively large area of high suitability near the Changbai Mountain, which coincide with our *Onychodactylus* occurrence point for which the species-level identity was not determined. On the other hand, the modeling results for *O. zhangyapingi* based on distribution points in the middle reaches of the Yalu River show a relatively high spatial similarity to the distribution of *O. zhaoermii* in the eastern part of the study area, despite the fragmented habitat. Although there is currently no direct evidence to prove the distribution of *O. zhangyapingi* and *O. zhaoermii* in DPR Korea, our models indicate that the

Table 2

Characteristics of the 16 corridors between the 11 nodes in the transboundary area between China and DPR Korea.

Node 1	Node 2	Corridor	Euclidean distance (ED, km)	Cost-weighted distance (CWD, weighted km)	Least-cost path length (LCP, km)	Corridors quality (CWD: LCP)
Western Xiuyan	Southern Nanfen	L1	32.37	12.97	46.23	0.28
Southern Nanfen	Northern Kuandian	L2	58.48	15.89	77.89	0.20
Southern Nanfen	Houshi Sankuaishi	L3	66.99	23.43	93.56	0.25
Northern Kuandian	Houshi Sankuaishi	L4	1.07	0.41	1.52	0.27
Northern Kuandian	Tongchang	L5	26.85	19.58	29.86	0.66
Northern Kuandian	Northern Jian	L6	28.74	18.26	33.37	0.55
Houshi Sankuaishi	Western Yanbian	L7	218.66	97.67	284.09	0.34
Tongchang	Northern Jian	L8	51.86	32.63	55.74	0.59
Tongchang	Western Yanbian	L9	195.88	95.94	228.06	0.42
Northern Jian	Western Yanbian	L10	104.48	60.52	131.16	0.46
Western Yanbian	Western Chongjing	L11	12.12	5.71	17.44	0.33
Western Yanbian	Northern Chongjing	L12	54.20	22.00	69.30	0.32
Western Yanbian	Northern Yanbian	L13	3.58	3.20	5.63	0.57
Western Chongjing	Northern Chongjing	L14	17.89	9.01	25.48	0.35
Northern Chongming	Eastern Yanbian	L15	28.53	13.85	35.67	0.39
Northern Yanbian	Eastern Yanbian	L16	1.07	0.39	1.52	0.26

species most likely occur in the area, and field surveys would be most appropriate to demonstrate their presence. While conducting targeted surveys for our study species is DPR Korea is currently not possible, our results underscore that applied conservation efforts are still valuable urgently required in this region, and transboundary research is most valuable.

4.2. Habitat connectivity

In the overall modeling results, suitable habitat patches were fragmented and very dispersed. Among all the patches, Northern Jian patch is critical, as it includes records of both *O. zhangyapingi* and *O. zhaoermii*. In the corridor analysis, L6, L7, L9, and L10 connect the east and west regions of the study area, indicating the possibility of a contact zone between the two *Onychodactylus* species. However, our results for the corridor between the Northern Kuandian patch, Tongchang patch, and the Northern Jian patch in the western region reflect a high moving cost for the transboundary corridors L5 and L8. In comparison, the corridors L11 and L12 located on the east side of the research area have a better quality. The reason for this difference is probably that the eastern region is more mountainous. L15 is a special transboundary corridor, which connects the Northern Chongjing and Eastern Yanbian patches downstream of the Tumen River. Although the corridor quality of L15 is lower than L11 and L12, it reveals the possibility of crossing the eastern side of the research area.

The loss and fragmentation of habitats increase mortality risks for amphibians with higher dispersal abilities during migration, and may result in isolation and extinction of species with limited dispersal abilities (Cushman, 2006). Given the limited dispersal ability of *Onychodactylus* in general, it can be argued that corridors connecting suitable habitat patches themselves are unlikely to directly contribute to the genetic diversity of populations. However, the flip side of the argument is that maintaining high quality corridors between habitat patches are especially important given that gene flow between populations isolated into different habitat patches are like to be very limited already, even in geographic proximity (Suk et al., 2018). Furthermore, given their vulnerability to environmental shifts, it will be increasing difficult for populations in fragmented habitat patches to track their niches under climate warming (Ashrafzadeh et al., 2019; Velo-Antón et al., 2013). Despite our knowledge of the migration abilities of *O. zhangyapingi* and *O. zhaoermii* are limited, habitat fragmentation within its range emphasizes the urgent need to maximize habitat connectivity for these species. Zhou et al. (2021) also modeled the distribution of *O. zhaoermii*, and the largest suitable area predicted overlaps with the Southern Nanfen node from our results, located at the junction of four counties: Liaoyang, Benxi, Dandong and Anshan.

4.3. Field inventories and research limitations

Field inventories are important, especially for rare species with limited ranges because they provide invaluable baseline data for further research, and well-designed field surveys can provide additional reliable data for ENM (Costa et al., 2009). However, two main reasons remain for the large number of unidentified individuals. The first is the limited molecular identification capacity in the institutions that collected the samples, or permits for transfer. Although we obtained 14 samples in the field, only two could be identified through morphological characteristics, which was reflected in our materials (Supplementary Table S1). The second reason for the lack of species level identification is that the open access dataset we used to build the models did not provide identification at the species level. Most of these samples are from DPR Korea (Borzée et al., 2021). Thus, these unidentified individuals limit the number of input samples we can use in the models for specific species, especially for *O. zhangyapingi* ($n < 10$).

Following their formal species description in 2012 (Poyarkov et al., 2012), only few studies have been conducted on *O. zhangyapingi* and *O. zhaoermii* (Luan, 2018; Wang et al., 2008; Xiong et al., 2016). Conservation research for these two species has mainly focused on *O. zhaoermii*, located to the west of the study area, and thus with a scope restricted to Liaoning Province. The main reason for this unbalanced focus is that the area where *O. zhangyapingi* is distributed is also the distribution range of Amur tiger (*Panthera tigris altaica*), Amur leopards (*Panthera pardus orientalis*) and some large cloven-hoofed animals (Feng, 2013), therefore competing for conservation attention. While the number of the samples we used for models is limited, related research has shown that a small number of occurrences still has the possibility to provide a strong predictive power in ENMs (Breiner et al., 2015; Papeş and Gaubert, 2007; Pearson et al., 2006; Proosdij et al., 2015). Therefore, additional field investigation in the future could improve our results.

4.4. Suggestions for the conservation of Onychodactylus

All members of the genus *Onychodactylus* are under various anthropogenic threats, and they share vulnerability to these threats due to highly conserved ecology. For example, climate change (Borzée et al., 2022; Shin et al., 2021), habitat degradation associated with logging and farming activities (Kuzmin and Maslova, 2005; Poyarkov et al., 2012), roadkill (Shin et al., 2020; Shin et al., 2022; Yun et al., 2021), and poaching (Yoshikawa and Matsui, 2013) have been highlighted as potential threats on the genus. These threats have both direct and indirect effects on the populations, and the consequences are difficult to anticipate for many of the threat factors.

Our results highlight that the ENM predictions of *O. zhangyapingi* are sensitive to croplands and that the species does not occur in their vicinity. Jilin is an agricultural province (Zhang et al., 2023), and the development of agriculture in the Yanbian Korean Autonomous Prefecture results in a great pressure on the environment (Li, 2016). Although the impacts of agricultural activities on the species have not been directly demonstrated, degradation of freshwater qualities and adjacent forest habitats due to human activities have been frequently associated with the population decline in *Onychodactylus* (Borzée et al., 2022; Kuzmin, 1995; Poyarkov et al., 2012; Shin et al., 2021; Suk et al., 2018; Yoshikawa and Matsui, 2013). Therefore, agricultural areas are therefore likely to greatly restrict the suitable habitat and range of *O. zhangyapingi*. It is worth noting that the records of *Onychodactylus* in Yanji, Yanbian Korean Autonomous Prefecture date from 1927 (Hou and Fei, 1964) and that the species has not been observed in the area since. The development of agriculture and the destruction of natural habitats may have resulted in the species being difficult to find in this area. Human disturbances in the study area may eventually decrease in the future with the large-scale human population decline (You et al., 2021). However, this cannot be regarded as a genuine improvement for species conservation in the face of multiple complex threats with short- and long-term negative effects. In addition, the threat from illegal poaching cannot be ruled out (Marshall et al., 2020), although there is currently no evidence of poaching targeting the population of *O. zhaoermii* and *O. zhangyapingi*, and there is no traditional medicinal use of these species in China (Rui et al., 2014),

Overall, our research attempted to fill the research gap in understanding the distribution of these species, although there are some inevitable limitations in our model. Based on this study, we suggest the establishment of a transboundary amphibian protection network in the Yalu and Tumen River basins, especially focused on the protection of corridors in the eastern part of the research area. We also encourage international collaborations for amphibian surveys and applied conservation projects in the western part of the research area.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2023.e02694.

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