Niche evolution and diversification in Middle Eastern stream salamanders (*Paradactylodon*): vulnerability to future climate change

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Abstract. The relict genus *Paradactylodon* is narrowly distributed in temperate forests throughout the Middle East region, including *P. mustersi* in Afghanistan, *P. persicus*, and *P. gorganensis* in northwestern and northeastern Iran. Recent phylogenetic analyses suggest that the Iranian *Paradactylodon* populations may belong to a single species, *P. persicus*. In this study, we addressed how climatic niche conservatism and/or niche divergence may have affected the evolution of all *Paradactylodon* species using ecological niche models and multivariate niche analyses to identify niche overlap and assess equivalency and similarity tests. We also used an ensemble of ten algorithms to predict *Paradactylodon* species distributions for recent (1970-2000) and future (2081-2100) climate conditions. The results show that future climate change may cause the loss of 80 to 97% of these species’ suitable habitat, especially at lower elevations. The niche divergence hypothesis was supported by the results of niche equivalency tests on *P. persicus* vs. *P. gorganensis* (and vice versa) with moderate overlap (D = 0.23, I = 0.41) and *P. persicus* vs. *P. mustersi* (and vice versa) with little overlap (D = 0.05, I = 0.06). Meanwhile, the niche similarity test for the niche conservatism hypothesis revealed significant results for *P. persicus* vs. *P. gorganensis*, *P. mustersi* vs. *P. persicus*, and *P. persicus* + *P. gorganensis* (as a single species) vs. *P. mustersi*. Due to these complex evolutionary ecological patterns and allopatric distributions, we recommend that *P. gorganensis* be considered a valid subspecies.

Keywords: conservation, niche conservatism, niche divergence, species distribution models.

Introduction

Understanding how niche conservatism and/or niche divergence play a role in lineage diversification allows us to understand how new species arise and evolve (Kozak and Wiens, 2006; Wellenreuther, Larson and Svensson, 2012). Niche conservatism, or a clade’s or species’ tendency to conserve many aspects of its ancestral ecological niches across evolutionary time, is important for allopatric speciation (Wiens et al., 2010). This process results in vicariant populations as a result of local adaptations and genetic isolation by geographical barriers (Wiens and Graham, 2005). On the other hand, during isolation processes, niche divergence, or the differential adaptation of a clade or species to new environments, may induce population differentiation (Graham et al., 2004; Rundle and Nosil, 2005; Hu et al., 2015; Posso-Terranova and Andrés, 2016). The mechanism by which this occurs is well understood, and it involves either...
dispersion into a new habitat or fragmentation of a continuous habitat, which increases geographical isolation and, in turn, the ecological difference (Coyne and Orr, 2004). These competing theories of niche evolution suggest that geographical and climatic gradients, as well as habitat heterogeneity, including various habitats in an altitudinal gradient, are important selection pressures (Hua and Wiens, 2013). However, there is little research on how niche conservatism versus niche divergence contributes to lineage diversification within species that cross heterogeneous habitats and geographical boundaries.

Evolutionary biologists and ecologists are fundamentally interested in quantifying climate niche differentiation among parapatric and closely related species because this quantification raises questions about the “mechanistic underpinnings of broad-scale geographic patterns” and provides a solid basis for further observations and experimental studies (e.g., Pearman et al., 2008; Chase and Leibold, 2009; Wiens et al., 2010; Rodríguez-Rodríguez et al., 2020; Tran et al., 2021; Vaissi, 2022; Scherz et al., 2023). The development of ecological niche models in combination with geographic information systems and multivariate analyses in environmental (E)-space has renewed interest in ecological niches (Kozak, Graham and Wiens, 2008; Broennimann et al., 2012). Ecological niche models make it possible to quantify niches at unprecedented spatial and temporal scales since they are deeply rooted in niche theory (Pearman et al., 2008). Ecological niche models have the potential to be widely employed to address complex ecological and evolutionary concerns by evaluating niche similarities between species and projecting how taxa will adapt to environmental changes (Soberón, 2007; Guisan et al., 2014). On the other hand, multivariate statistics enable direct comparison and evaluation of niches in the E-space to meet the growing demand for robust approaches that can be used in evolutionary and community contexts (Broennimann et al., 2012). We can employ this technique to determine if two species’ or clades’ ecological niches are equivalent or more similar than would be predicted by chance given a background environment (Broennimann et al., 2012; Brown and Carnaval, 2019; Warren et al., 2021).

Numerous studies have shown that climate niches play a significant role in lineage diversity and speciation (Hua and Wiens, 2013; Lawson and Weir, 2014; Cooney, Seddon and Tobias, 2016; Pitteloud et al., 2017; Castro-Insua et al., 2018; Reis et al., 2018; Vaissi, 2022; Klečková et al., 2023; Vaissi et al., 2023). On the other hand, amphibians are ideal models for investigating how the environment influences lineage diversity because their physiology is strongly influenced by climatic and environmental variables and they have limited dispersal ability (Bovo et al., 2018; Enriquez-Urzelai et al., 2019; Rodríguez-Rodríguez et al., 2020). In this case, we studied the elusive and poorly known Middle Eastern stream salamanders of the relict genus *Paradactylodon*. Three species of *Paradactylodon* (Family: Hynobiidae) are found in the Middle East: *P. mustersi*, *P. persicus*, and *P. gorganensis* (Zhang et al., 2006). *P. mustersi* is endemic to the Hindu Kush mountain range of Afghanistan and is commonly found in fast-flowing melting glacier waters with temperatures ranging from 0°C to 14°C (Ayobi et al., 2022). Iranian *Paradactylodons* are endemic to the Hyrcanian forests of Iran, with *P. persicus* occupying the north and northwest regions and *P. gorganensis* occupying the northeast (Baloutch and Kami, 1995). These species show a degree of climate differentiation in their habitats. Annual precipitation in the Hyrcanian regions decreases from the west (occupied habitat by *P. persicus*) to the east (occupied habitat by *P. gorganensis*) (Karger et al., 2017a, b). The mean annual temperature in the lowland belt is approximately 19.2°C and 5.2°C in the upper-montane region. A recent bioclimatic classification categorizes the eastern and western portions of these forests’ climates as Mediterranean pluviseasonal oceanic.
and temperate oceanic, respectively (Djamali et al., 2011).

The Paradactylodon species diverged from each other by approximately 22.7 and 38.2 MYA (Zhang et al., 2006; Ahmadzadeh et al., 2020), probably as a result of intense orogeny in central Asia (Zhang et al., 2006). The diversification of Iranian Paradactylodon happened earlier than that of Afghani populations, with the diversification of lineages within the Iranian clade occurring in the late Pliocene, at 2.87 MYA (Ahmadzadeh et al., 2020). On the other hand, even though previous studies believed that the Iranian Paradactylodon belonged to two distinct species (Schmidtler and Schmidtler, 1971; Clergue-Gazeau and Thorn, 1978; Kami, 1999; Ebrahimi, Kami and Stöck, 2004; Ahmadzadeh and Kami, 2009; Ahmadzadeh et al., 2011; Frost, 2011), the recent phylogenetic study by Stöck et al. (2019) and Ahmadzadeh et al. (2020) suggested that both species belong to the single species P. persicus, with low genetic divergence and no apparent intraspecific diagnostic characteristics. Our study follows both hypotheses: (1) Paradactylodon has three distinct species, and/or (2) Iranian Paradactylodon populations belong to single species.

Middle Eastern hynobiid salamanders are facing several environmental threats, including deforestation, habitat loss, and changes in land use (Ahmadzadeh and Kami, 2009). Their conservation status is listed as Near Threatened for P. persicus (Papenfuss et al., 2009a), Critically Endangered for P. “gorganensis” (Papenfuss et al., 2009b), and P. mustersi (Papenfuss, Anderson and Kuzmin, 2004). Recent studies have investigated the distribution and conservation status (Ahmadzadeh and Kami, 2009; Ahmadzadeh et al., 2011; Hossenian, 2021; Ayobi et al., 2022), genetic structure, Quaternary distribution dynamics, phylogeny (Yousefi Siahkalroodi, Khederzadeh and Ghadiri Abyaneh, 2015; Ahmadzadeh et al., 2020), skeletochronological evaluation (Zivari and Kami, 2017), reproductive biology, and histology (Rezapour et al., 2009; Heydari Nasrabadi, 2012) of the Paradactylodon species. However, it is unclear, if the climatic niches of Paradactylodon species had an effect on their diversification. For this purpose, we used Ecological niche models to investigate how patterns of diversity in Paradactylodon species are influenced by niche evolution. Identifying the main ecological drivers to species distribution is vital for present conservation efforts as well as a future study into climate change’s impact on biodiversity (Aguirre-Gutiérrez et al., 2015). Therefore, the main goals of this study were to (1) identify the climatic variables that may influence predictions of future habitat losses or gains for Paradactylodon species; (2) determine the proportion of suitable habitats for Paradactylodon species that are expected to lose or gain; and (3) characterize the realized niche differences that promote the evolution of Paradactylodon species by testing the niche conservatism and niche divergence hypotheses. The results of these studies, when combined with the phylogeographic studies (e.g., Zhang et al., 2006; Stöck et al., 2019; Ahmadzadeh et al., 2020), provide a comprehensive and multifaceted picture of niche variation and differentiation, as well as new insights into possible diversification processes within Middle Eastern stream salamanders.

Materials and methods

Study area and species data

The study area covers the entire northern Iran and Afghananist countries inhabited by all Paradactylodon species (fig. 1). We obtained occurrence records from several studies and the Global Biodiversity Information Facility (GBIF), and more details are presented in supplementary table S1). Our analysis proceeded in four classifications: 1. Iranian Paradactylodon is two distinct species (P. persicus and P. gorganensis) following Dubois, Ohler and Pyron (2021). 2. Iranian Paradactylodon is a single species (P. persicus + P. gorganensis) following Dubois, Ohler and Pyron (2021). 3. Paghman Mountain Salamander (P. mustersi) was considered a separate species. 4. We also integrated data sets to figure out the potential distribution of P. persicus + P. gorganensis + P. mustersi. We evaluated records that occurred at a distance greater than
Figure 1. Study area. The occurrence records of *Paradactylodon* species with different colors are shown on the map.

500 m using the R package `spThin` (Aiello-Lammens et al., 2015) to reduce spatial autocorrelation (Boria et al., 2014). Finally, we used 21 presence points for *P. persicus*, 40 for *P. gorganensis*, 12 for *P. mustersi*, and 61 for *P. persicus + P. gorganensis* to build ecological niche models. Species, conservation status, and the number of occurrences included in this study are presented in supplementary table S2. In addition to supplementary table S1, fig. 1 presents the geographic coordinates of occurrences.

**Climatic variables**

We considered climatic factors to explain the realized distributions and niches of *Paradactylodon* species. Climatic variables were obtained from WorldClim version 2.1 database at 30 seconds (1 km²) spatial resolution for recent (1970-2000) and future (2081-2100) climate change projections (https://www.worldclim.org/; Hijmans et al., 2005). In order to avoid a high correlation and redundancy among the predictors, we performed pairwise Pearson correlations, and for $r > 0.75$, the variable with lower biological relevance was excluded. The final dataset included six climatic variables: annual mean temperature (BIO1), mean diurnal range (BIO2), isothermality (BIO3), temperature seasonality (BIO4), annual precipitation (BIO12), and precipitation of the driest month (BIO14).

The MRI-ESM2-0 (Yukimoto et al., 2019) and GISS-E2-1-G (Kelley et al., 2020) global climate models from the Meteorological Research Institute and Goddard Institute for Space Studies were averaged to provide future data. These models are relatively good performances among the 32 Eurasian models, considering reproducing the correct sign of the land surface air temperature trends as well as reproducing the trend magnitude (Sun et al., 2022). Based on the analysis of the lowest and highest limits of the shared socioeconomic pathways (sps), from Phase 6 of the Coupled Model Intercomparison Project (CMIP6), future conditions were predicted for 126 (lowest emissions, smallest temperature increase) and 585 (highest emissions, largest temperature increase) (Eyring et al., 2016).

**Species distribution modeling**

There are many techniques employed currently for distribution modeling, each with a unique model selection strategy, definition of fitted functions and interactions, ability to manage imperfect detection and sampling biases, etc. (Franklin, 2010; Peterson et al., 2011; Guisan, Thuiller and Zimmermann, 2017). It is known that different species distribution modeling techniques produce various prediction results (Hao et al., 2019). Additionally, the method of modeling used can have a considerable impact on the model’s predictive performance (Hao et al., 2019). However, no one method consistently outperforms others in terms of performance across species, regions, and applications (Segurado and Araujo, 2004; Elith et al., 2006; Pearson et al., 2006). Due to this, combining the prediction results from numerous models into an “ensemble” is thought of as a solution to this challenge (Araújo and New, 2007). Therefore, in this study, an ensemble of ten species distribution models was simulated using the “biomod2” package (v 4.2-3) (Thuiller et al., 2023) in R (v 4.2.0), following the default settings provided by Guisan, Thuiller and Zimmermann (2018) in the geographic (G)-space. These algorithms were two regression methods (GLM and MARS), five machine-learning or complex methods (ANN, GAM, GBM, MaxEnt, and RF), two classification methods (CTA and FDA), and finally a range envelope (SRE). Supplementary table S3 contains a description of each algorithm, along with its name, abbreviation, required data, advantages, limitations, and individual model options.
Absence and presence datasets are necessary for most of these modeling techniques (supplementary table S3), but finding actual absence data can be difficult. Therefore, we produced 500 random pseudo-absences within the study area, following Wisz and Guisan (2009), Barbet-Massin et al. (2012), and Guisan, Thuiller and Zimmermann (2018). The procedure was repeated three times to correct the potential bias of the sample because the generation of pseudo-absences is a stochastic process due to the random selection of pseudo-absences (Allouche, Tsoar and Kadmon, 2006). The models are calibrated on 80% of the data (the training set) and evaluated on the remaining 20% (the validation set). The procedure is repeated 10 times. The average of climatic variables was evaluated for the models. A higher average represents the importance of the variable (Guisan, Thuiller and Zimmermann, 2018). Performance of ensemble models was evaluated using the multi-metric approach to determine the variability among estimates, the True Skill Statistics (TSS), Area Under Curve-Receiver Operating Characteristics Statistics (AUC), Cohen’s Kappa (KAPPA), and Continuous Boyce Index (CBI) (Cohen, 1960; Hanley and McNeil, 1982; Fielding and Bell, 1997; Boyce et al., 2002; Allouche, Tsoar and Kadmon, 2006; Hirzel et al., 2006). The TSS and KAPPA values range from −1 to +1, with 1 representing perfect agreement and 0.60 to 0.90 representing fair to good model performance, respectively (Allouche, Tsoar and Kadmon, 2006). AUC values between 0.60 and 0.90 are considered average; 0.60 and lower are considered poor; and 0.90 and greater are considered good (Phillips, Anderson and Schapire, 2006). Finally, the CBI varies from −1 to 1, where −1 is an inverse model, 0 is a random model, and 1 is a perfect model (Boyce et al., 2002; Hirzel et al., 2006).

The BIMOD_EnsembleModelling() function is used to create ensemble models. To reduce the number of outputs, we take into account two “ensembling” options: committee averaging and weighted mean (Guisan, Thuiller and Zimmermann, 2018). We combine all models, algorithms, pseudo-absences sampling, and cross-validation runs to produce our ensembles of models (Guisan, Thuiller and Zimmermann, 2018). For the creation of committees and defining weights, TSS was used as an evaluation reference. This means only models with a TSS ≥ 0.8 are used to create the final ensemble (Guisan, Thuiller and Zimmermann, 2018).

Species range change

We assessed and illustrated future range changes for each species using the BIOMOD_RangeSize() function in the biomod2 package (Thuiller et al., 2023). Two outputs are produced by this function: a table that contains summary details about how a species’ range has changed and a spatial map that shows areas where a species may gain or lose suitable habitat. Both output configurations provide more details on four absolute metrics: “Loss” indicates the number of pixels that the studied species is predicted to lose as a result of climate change; “Absent” indicates the number of pixels that the studied species is not currently occupying but are predicted to be unsuitable under climate change; “Stable” indicates the number of pixels that the studied species is predicted to occupy both currently and in the future; and “Gain” indicates the number of pixels that the studied species does not currently occupy but is expected to occupy in the future. Finally, three additional relative metrics were derived from these four metrics, including “percent loss”, which corresponds to the percentage of currently occupied sites to be lost and is calculated as “loss / (loss + stable)”; “percent gain”, which corresponds to the percentage of new sites given the size of the species’ current distribution; and “range change”, which represents the overall result and is predictive and is equal to “percent gain − percent loss” (Guisan, Thuiller and Zimmermann, 2018).

Niche analyses

The ordination technique approach was applied to perform niche overlap analyses, either between pairs of the P. persicus and P. gorganensis, P. persicus and P. mustersi, P. gorganensis and P. mustersi, and P. persicus + P. gorganensis and P. mustersi. The PCA-environment (PCA-env) framework and ordination technique were used to evaluate the E-space. Climate variables are changed into spaces with two dimensions and two principal components. The minimum and maximum PCA values in the background are used to define grid cells with diameters of 100 × 100 and to project the two-dimensional environmental space. Each species’ smoothed density of occurrences in each grid cell is calculated using a kernel density function (Broennimann et al., 2012). The overlap between niches was calculated using Schoener’s D and Bellinger’s I metrics, which range from 0 (no overlap) to 1 (complete overlap).

The niche equivalency test and niche similarity test with a 95% confidence interval were used to test the null hypothesis that Paradactylodon species had equivalent and similar niches. The niche conservatism and niche divergence hypotheses are frequently addressed using these two statistical tests (Glennon, Ritchie and Segraves, 2014). The niche equivalency test compares two niches to determine whether they are equivalent by randomly permuting occurrences between ranges. The niche similarity test examines if the species’ niches are more or less similar than would be expected by chance using random shifts of niches within accessible conditions in the study region (Warren, Glor and Turelli, 2008; Broennimann et al., 2012; Di Cola et al., 2017). By using the “alternative” option at ecospat, we investigated niche conservatism (alternative = greater, i.e., the niche overlap is more equivalent/similar than random) and niche divergence (alternative = lower, i.e., the niche overlap is less equivalent/similar than random) (Broennimann et al., 2012; Di Cola et al., 2017). We ran 1000 permutations to evaluate each hypothesis. All analyses were carried out using the ecospat package in the R program (v. 4.2.0) (Broennimann et al., 2023).
Table 1. Mean of variable importance (%) by the ten algorithms for the *Paradactylodon* species.

<table>
<thead>
<tr>
<th>Species</th>
<th>BIO1</th>
<th>BIO2</th>
<th>BIO3</th>
<th>BIO4</th>
<th>BIO12</th>
<th>BIO14</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. persicus</em></td>
<td>19.78</td>
<td>23.79</td>
<td>12.91</td>
<td>15.54</td>
<td>12.40</td>
<td>15.55</td>
</tr>
<tr>
<td><em>P. gorganensis</em></td>
<td>7.00</td>
<td>46.53</td>
<td>17.50</td>
<td>8.71</td>
<td>13.64</td>
<td>6.58</td>
</tr>
<tr>
<td><em>P. mustersi</em></td>
<td>29.80</td>
<td>10.14</td>
<td>12.13</td>
<td>9.35</td>
<td>24.60</td>
<td>13.95</td>
</tr>
<tr>
<td><em>P. persicus</em> + <em>P. gorganensis</em></td>
<td>12.02</td>
<td>41.40</td>
<td>16.49</td>
<td>12.50</td>
<td>10.43</td>
<td>7.14</td>
</tr>
<tr>
<td><em>P. persicus</em> + <em>P. gorganensis</em> + <em>P. mustersi</em></td>
<td>14.49</td>
<td>33.81</td>
<td>16.89</td>
<td>17.55</td>
<td>7.91</td>
<td>9.31</td>
</tr>
</tbody>
</table>

Annual Mean Temperature (BIO1); Mean Diurnal Range (BIO2); Isothermality (BIO3); Temperature Seasonality (BIO4); Annual Precipitation (BIO12); and Precipitation of Driest Month (BIO14).

Figure 2. Recent (A: 1970-2000) and future (2081-2100) habitat suitability of *Paradactylodon* species based on the consensus model under optimistic (B: ssp126) and pessimistic (C: ssp585) scenarios.

Results

Species distribution modeling

Ensemble models showed high TSS, AUC, KAPPA, and CBI values, indicating good performance (supplementary table S2). Mean diurnal range for *P. persicus*, *P. gorganensis*, and *P. persicus* + *P. gorganensis* and annual mean temperature for *P. mustersi* were found to be the most significant factors influencing the distribution range (table 1). The habitat suitability map for recent climate conditions indicates that Hyrcanian forests and central-eastern Afghan areas have highly suitable habitats for *Paradactylodon* species (fig. 2A). In the face of future climate change, the majority of the distribution...
of *P. persicus* + *P. gorganensis* + *P. mustersi* may be lost (76.98% on ssp126, and 79.87% on ssp585), while predicted habitat gains are 11.90% and 17.82% (fig. 2 and supplementary fig. S1). The detailed responses of each species to climate change are as follows:

**P. persicus**: Mean diurnal range (23.79%) and annual mean temperature (19.78%) are the two most important variables affecting the *P. persicus* distribution, respectively (table 1). The habitat suitability map under recent climate conditions indicates that the Hyrcanian forests, especially the western parts, have high habitat suitability (supplementary fig. S2). In the face of future climate change, the majority of the distribution of *P. persicus* may be lost (93.52% on ssp126, and 97.68% on ssp585), while predicted habitat gains are just 1.1% and 2.70% (table 2, supplementary fig. S6).

**P. gorganensis**: Mean diurnal range (46.53%) and isothermality (17.50%) are the two most important variables affecting the *P. gorganensis* distribution, respectively (table 1). The habitat suitability map under recent climate conditions indicates that the eastern parts of Hyrcanian forests have high habitat suitability (supplementary fig. S3). In the face of future climate change, the majority of the distribution of *P. gorganensis* may be lost (73.47% on ssp126, and 92.93% on ssp585), while predicted habitat gains are just 1.17% and 1.67% (table 2, supplementary fig. S7).

**P. mustersi**: Annual mean temperature (29.80%) and annual precipitation (24.60%) are the two most important variables affecting the *P. mustersi* distribution, respectively (table 1). The habitat suitability map under recent climate conditions indicates that the central areas to the east of Afghanistan have high habitat suitability (supplementary fig. S4). In the face of future climate change, the majority of the distribution of *P. mustersi* may be lost (86.60% on ssp126, and 92.44% on ssp585), while predicted habitat gains are 56.88% and 56.88% (table 2, supplementary fig. S8).

**P. persicus** + **P. gorganensis**: Mean diurnal range (41.40%) and isothermality (16.49%) are the two most important variables affecting the *P. persicus* + *P. gorganensis* distribution, respectively (table 1). The habitat suitability map under recent climate conditions indicates that the Hyrcanian forests have high habitat suitability for *P. persicus* + *P. gorganensis* (supplementary fig. S5). In the face of future climate change, the majority of the distribution of *P. persicus* + *P. gorganensis* may be lost (86.60% on ssp126, and 92.44% on ssp585), while predicted habitat gains are just 1.08% and 2.80% (table 2, supplementary fig. S9).

### Niche analyses

The first two components of the PC explained 80.52%, 82.04%, 75.13%, and 70.74% of the total variance when comparing the climatic data of *P. persicus* and *P. gorganensis*, *P. persicus* and *P. mustersi*, *P. gorganensis* and *P. mustersi*, and *P. persicus* + *P. gorganensis* and *P. mustersi* (table 3, supplementary fig. S10). *P. persicus* and *P. gorganensis* (*D* = 0.23, *I* = 0.41) overlapped moderately, while *P. persicus* and *P. mustersi* (*D* = 0.05, *I* = 0.06), *P. gorganensis*

### Table 2. Species range change (SRC) of *Paradactylodon* species in recently suitable habitats (gain/loss) by 2081-2100 under optimistic (ssp126) and pessimistic (ssp585) scenarios.

<table>
<thead>
<tr>
<th>Species</th>
<th>ssp126</th>
<th></th>
<th></th>
<th>ssp585</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Lost (%)</td>
<td>Gain (%)</td>
<td>SRC</td>
<td>Lost (%)</td>
<td>Gain (%)</td>
<td>SRC</td>
</tr>
<tr>
<td><em>P. persicus</em></td>
<td>93.52</td>
<td>1.11</td>
<td>-92.41</td>
<td>97.68</td>
<td>2.70</td>
<td>-94.98</td>
</tr>
<tr>
<td><em>P. gorganensis</em></td>
<td>73.47</td>
<td>1.17</td>
<td>-72.29</td>
<td>92.93</td>
<td>1.67</td>
<td>-91.26</td>
</tr>
<tr>
<td><em>P. mustersi</em></td>
<td>80.36</td>
<td>56.88</td>
<td>-23.48</td>
<td>80.23</td>
<td>51.96</td>
<td>-28.26</td>
</tr>
<tr>
<td><em>P. persicus</em> + <em>P. gorganensis</em></td>
<td>86.60</td>
<td>1.08</td>
<td>-85.51</td>
<td>92.44</td>
<td>2.80</td>
<td>-89.63</td>
</tr>
<tr>
<td><em>P. persicus</em> + <em>P. gorganensis</em> + <em>P. mustersi</em></td>
<td>76.98</td>
<td>11.90</td>
<td>-65.07</td>
<td>79.87</td>
<td>17.82</td>
<td>-62.05</td>
</tr>
</tbody>
</table>

The habitat suitability map under recent climate conditions indicates that the central areas to the east of Afghanistan have high habitat suitability (supplementary fig. S4). In the face of future climate change, the majority of the distribution of *P. mustersi* may be lost (80.36% on ssp126, and 80.23% on ssp585), while predicted habitat gains are 56.88% and 56.88% (table 2, supplementary fig. S8).
and *P. mustersi* (*D* = 0, *I* = −2.22), and *P. persicus* + *P. gorganensis* and *P. mustersi* (*D* = 0.04, *I* = 0.09) had a low or zero niche overlap (table 3, fig. 3).

The niche equivalency and similarity tests are summarized in table 3. In the niche equivalency test, *P. persicus* vs. *P. gorganensis* (*P* = 0.001), *P. gorganensis* vs. *P. persicus* (*P* = 0.001), *P. persicus* vs *P. mustersi* (*P* = 0.01), and *P. mustersi* vs. *P. persicus* (*P* = 0.01) supported the ND hypothesis (table 3). The similarity test resulted in a *P* > 0.05 rejecting the niche divergence hypothesis for any species. However, *P. persicus* vs. *P. gorganensis*, *P. mustersi* vs. *P. persicus*, and *P. persicus* + *P. gorganensis* vs. *P. mustersi* revealed significant results in the niche similarity test for the niche conservatism hypothesis (table 3).

**Discussion**

Ecological niche models and multivariate niche analyses were used to determine environmental variations between *Paradactyloleon* species in the Hyrcanian forests of Iran and central-eastern Afghan areas through the Hindu Kush mountain range. The hypothesis was whether *Paradactyloleon* lineages maintained similar niches after separation, which may provide new insight into the evolution of Middle Eastern hynobiid salamanders. Hence, we investigated the relationship between niche conservatism and niche divergence, and lineage diversification. According to the study’s findings, climatic niche divergence and conservatism (table 3) may have contributed to the evolution of the *Paradactyloleon* species. Further, the comparison of ecological niches in this study contributes to a better understanding of how species diversification occurs in Hyrcanian forests, which is in line with Vaissi and Rezaei’s, (2022) study. In detail, Amiri et al. (2021) reported that the Hyrcanian wood frog, *Rana pseudodalmatina*, is divided into two western and eastern regional clades within the Hyrcanian forest. Later findings by Vaissi and Rezaei (2022) support the idea that these clades...
regional clades are restricted by a particular set of climatic and macroenvironmental factors and have experienced significant niche divergence.

The primary focus of this study was on climate-related factors that can restrict Paradactylodon’s distribution. In this regard, ecological niche models based on the ensemble of ten species distribution models were performed separately for *P. persicus*, *P. gorganensis*, *P. mustersi*, *P. persicus* + *P. gorganensis*, and *P. persicus* + *P. gorganensis* + *P. mustersi*. Results indicated that climatic factors, especially temperature affects the distribution of Paradactylodon species. Accordingly, the mean diurnal range (mean of monthly (max temp - min temp)) is the most significant factor affecting the distribution of *P. persicus*; and *P. gorganensis*; and annual mean temperature is the most significant factor influencing *P. mustersi* (table 1). The findings clearly show that Hyrcanian forests are not suitable for *P. mustersi* (supplementary fig. S4). Iranian Paradactylodon also showed similar results, indicating that the central-eastern Afghan areas are not a suitable habitat for them in terms of climate (supplementary figs. S2-S3). The highest suitability for *P. persicus* is in the western parts of the Hyrcanian forests, and the highest suitability for *P. gorganensis* is through the eastern Hyrcanian forests, even with some overlap in G-space (supplementary figs. S2-S3). In other words, extreme eastern and western habitats are more suitable than central habitats for Iranian Paradactylodon.

The species distribution analyses conducted by Ahmadzadeh et al. (2020) showed that climate oscillations during the Pleistocene significantly reduced the Iranian Paradactylodon’s suitable habitat, forcing it to move to lower altitudes. Based on these results (Ahmadzadeh et al., 2020), it appears that the Iranian Paradactylodon was endemic to the Hyrcanian region both during the Last Glacial Maximum (LGM: 21 ky BP) and mid-Holocene (6 ky BP). In this study, we modeled the distributions of Paradactylodon species to evaluate how they...
will respond to future climate change and identify potential climate refugia in the future. In our study, *Paradactyloodon* species showed a high vulnerability to climate change by 2081-2100, with a nearly total loss of their distribution patterns (figs. 2, supplementary figs. S2-S4). The species’ range shift also shows how future climate change will affect most of the range’s margins, particularly at lower altitudes (supplementary fig. S1 and figs. S6-S9). In the future, *Paradactyloodon* species’ ranges may become more fragmented than they were recently. Ensemble models suggest that the central-eastern regions of Afghanistan, a strip from the west at higher altitudes, and a small region from the east of the Hycranian forests may act as a climate refugium for *Paradactyloodon* species (fig. 2, supplementary fig. S1). During the glacial period, these regions acted as refuges for many species, and populations expanded there afterward (e.g., Ahmadzadeh et al., 2013, 2020; Wielstra et al., 2013; Parvizi et al., 2018; Amiri et al., 2021). Additionally, Shirabad Cave, located 70 kilometers to the east of Gorgan at 36° 57′ N, 55° 03′ E, is the primary location of the Gorgan mountain salamander (Kami, 2004). Caves have stable microclimates and may act as microrefugia for species that can utilize both surface (troglophiles) and cave environments (Bryson et al., 2014). As a result, it is crucial to consider future climate change as a potential threat to this species and to establish effective conservation efforts.

The climate niche appears to be the main driver of amphibian diversification (Knouft et al., 2006; Kozak and Wiens, 2006, 2007, 2010; Alexander Pyron and Burbrink, 2009; Hua and Wiens, 2010; Hoskin et al., 2011; Cadena et al., 2012; Smith et al., 2014). We found evidence for niche differentiation by comparing niches in the E-space (table 3). As a result, niche overlap data showed some overlap between *P. persicus* and *P. gorganensis*, and the equivalence test’s niche divergence hypothesis supported that species inhabit different environmental niche spaces (table 3). According to Schoener’s D and Hellinger’s I results, there was little niche overlap between Iranian *Paradactyloodon* and Paghman Mountain Salamander (table 3). The niche equivalency statistic for *P. persicus* vs. *P. mustersi* in the niche divergence test was significant, but it was not significant for *P. gorganensis* vs. *P. mustersi* and *P. persicus* + *P. gorganensis* vs. *P. mustersi*. On the other hand, the niche similarity test for the niche conservatism hypothesis showed significant effects for *P. persicus* vs. *P. gorganensis*, *P. mustersi* vs. *P. persicus*, and *P. persicus* + *P. gorganensis* vs. *P. mustersi*. In addition, the PCA-env results in E-space suggest that the *Paradactyloodon* species inhabit regions with significant climate changes. These results suggest that Iranian *Paradactyloodon*’s evolution within the eastern and western portions of the Hycranian forests may be accelerated by niche divergence. Therefore, following Dubois, Ohler and Pyron (2021), this study suggests that *Paradactyloodon* populations from eastern Hycranian forests that were previously identified as *P. gorganensis* but later synonymized (see Ahmadzadeh et al., 2020) are a valid subspecies, *P. p. gorganensis*. These results show that ecological diversity within a lineage is not a monotonous process but is rather influenced by the environment’s complexity, climatic stability, and species adaptability (McCormack, Zellmer and Knowles, 2010; Wooten and Gibbs, 2011; Hernandez, Escoriza and Hou, 2018).

Finally, this study suggests that these endemic salamanders, especially *P. persicus*, may be the most threatened species in Central Asia in the future and need more urgent conservation efforts. We also demonstrated how integrating data from various sources, such as ecological and historical biogeography, phylogeographic and phylogenetic approaches, can support our understanding of how species evolve and exist in their environments. Additionally, our findings confirm previous studies on mammals (e.g., Olalla-Tárraga et al., 2011; Loera, Sosa and Ickert-Bond, 2012; Castro-Insua et al. 2018), birds (e.g., Cox et al., 2014; Tirozzi et.
al., 2022), reptilians (e.g., Jezkova and Wiens, 2018; Enriquez-Urzela et al., 2022), amphibians (e.g., Hu et al., 2016; Hernandez, Escoriza and Hou, 2018; Vaissi, 2022; Vaissi and Rezaei, 2022), fish (e.g., Cumuler and Tobler, 2016; Calixto-Rojas et al., 2021), and insects (e.g., Volf et al., 2018; Hiller et al., 2019; Klečková et al., 2023) by highlighting the significance of taxonomic scale when concluding conservatism and divergence in niche evolution (Kozak and Wiens, 2006; Warren, Glor and Turelli, 2008). However, it is important to note that other factors, such as topography and vegetation cover concerning microclimate conditions, also explain the presence of terrestrial urodeles in specific habitats (Parker, 1991; Kluber, Olson and Puettmann, 2009; Hernandez, Escoriza and Hou, 2017). On the other hand, pathogens, competitors, and predators play an important role in limiting the range of species (Gaston, 2003; Gotelli, Graves and Rahbek, 2010; Sun, Bates and Dulvy, 2011). Therefore, more research in these areas is required.

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References


