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Ecological niche differentiation among three subspecies of the vulnerable Russian tortoise *Testudo horsfieldii* through its distribution range

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T. h. horsfieldii, T. h. rustamovi and *T. h. kazakhstanica* – are all allopatric. In the present study, the ecological niche divergences among three subspecies were evaluated using a bioclimatic dataset. Suitable habitat predictions and niche similarity tests indicated that the three subspecies have significantly different ecological niches. Temperature is an important factor for the presence of a subspecies, but the threshold is different for each subspecies. Temperature appears to limit the range for the northern subspecies *T. h. kazakhstanica*, but not for the two southern subspecies *T. h. rustamovi* and *T. h. horsfieldii*, which have relatively wide ranges in Central and Southwest Asia. Local adaptations to distinct climates and the microevolution process may have played important roles in this differentiation. It is recommended to evaluate these subspecies using molecular markers, in order to estimate the demographic relationships amongst them and to make taxonomic decisions.

Key words: Asia, Testudinidae, ecological species concept, local adaptation, microevolution.

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Any species lives, feeds and reproduces within its own geographic range. Organisms adapt to the specific conditions that exist in different environments, such as the competition, vegetation, altitude, temperature and precipitation (Agapow *et al.* 2004; King *et al.* 2021; Polechová & Storch 2008). Together, these factors can form the structure of the ecological niche of a given species. A species also can have dispersed populations and, in some cases, include several allopatric subspecies (Morán-Ordóñez *et al.* 2017). From the point of view of all species concepts, allopatric subspecies are known to be very prone to the divergence and separation of their ecological niches, due to local adaptations to the environmental conditions (King *et al.* 2021). Among the factors involved in ecological divergence, abiotic factors such as the temperature and moisture levels have the greatest impact on the local adaptation of populations (Bayat *et al.* 2021; González-Salazar *et al.* 2013). Reptiles are highly dependent on temperature for their activity levels, reproductive cycles and body metabolism, so this is considered a vital factor influencing their distribution range (Bogert 1949; Kearney *et al.* 2009; Moreira *et al.* 2018).

Ecological niche modelling (ENM), a technique that predicts ecological niches, is used in many different studies such as conservation biology, responses to climate change, palaeodistribution patterns and taxonomic delimitations among species (Peterson & Soberón 2012; Warren & Seifert 2011). One of the applications of ENM is to specify the boundaries of ecological niches using only abiotic factors for different species (Jiménez & Soberón 2022). Within species complexes, it has been hypothesised that populations occur in similar microhabitat conditions (Wiens *et al.* 2010; Wiens & Graham 2005). However, ecological niche differentiation is an important part of evolutionary history and may reinforce local adaptations, especially among allopatric populations (Schluter 2001; Turelli *et al.* 2001).

Testudines are known as a reclusive group of reptiles that are difficult to detect, and it is therefore difficult to collect ecological data (Zug *et al.* 2001). Within Iran, there are 5 species of freshwater turtle, 5 species of sea turtle and 2 species of tortoise, all of which are considered as threatened (Safaei-Mahroo *et al.* 2015). *Testudo horsfieldii* (Russian tortoise) has three subspecies in the study area, including *T. h. horsfieldii* that is distributed in Eastern Iran, Western Afghanistan and Pakistan; *T. h. kazakhstanica* that is distributed in Kazakhstan and Uzbekistan; and *T. h. rustamovi* that is distributed in Southern Turkmenistan and Northeastern Iran (Bonnet *et al.* 2001; Kami 1999; Rezazadeh *et al.* 2014). These three subspecies of *T. horsfieldii* are allopatric and occur in different habitats across the distribution range (Fritz *et al.* 2009). This tortoise is a species that prefer mosaic habitats, such as open vegetation surrounded by shrubs. This type of habitat is ideal for the developmental stages and reproduction of the tortoise (Fernández-Chacón *et al.* 2011). Anthropogenic effects resulting in changes of microclimate elements of the habitat are the main threats to the future of *Testudo horsfieldii*. In this study, I model the ecological niches of these three subspecies using ecological niche modelling, in order to calculate differences between the niches.

Materials and Methods

Occurrence records and environmental data

Occurrence records of the three subspecies were obtained from direct fieldwork and literature searches (Fritz *et al.* 2009; Kami 1999). In total, 63 presence records were gathered and georeferenced, as follows: 12 records for *T. h. horsfieldii*; 37 records for *T. h. kazakhstanica*; and 14 records for *T. h. rustamovi* (Supplementary Material SM.01.). Nineteen bioclimatic variables (Table 1) were downloaded under current climate conditions (1950-2010) from the WorldClim website (Hijmans *et al.* 2005) (www.worldclim.org) in a 30 arc-second (approximately 1 km^2) resolution (Appendix 1). The layers were cropped using ArGIS (ESRI) for the study area including the countries of Iran, Afghanistan, Pakistan, Turkmenistan, Uzbekistan, Kazakhstan, Tajikistan and Kyrgyzstan in Asia (Fig. 1). The bioclimate layers and occurrence records were employed in openModeller v. 1.0.7 (de Souza Muñoz *et al.* 2011) to obtain the point values for each variable independently, and were then imported to SPSS 16.0 to calculate the bivariate Pearson correlation coefficient and select the correlated variables. Pairs of variables with a higher correlation than 0.75 were not considered for the analyses, which meant that the below layers were chosen for the analyses (Dormann *et al.* 2013; SM.02.): *T. h. horsfieldii*: BIO 2, 3, 4, 5, 7, 8, 14; *T. h. kazakhstanica*: BIO 1, 2, 3, 4, 8, 9, 11, 13, 14, 15, 17, 19; and *T. h. rustamovi*: BIO 3, 4, 5, 7, 8, 9, 10, 13, 15, 18, 19 (Table 1).

Table 1

Description of variables used in the MaxEnt model for the *Testudo horsfieldii* subspecies ENMs

BIO1	Annual Mean Temperature
BIO2	Mean Diurnal Range [Mean of Monthly (Max Temp – Min Temp)]
BIO3	Isothermality
BIO4	Temperature Seasonality
BIO5	Maximum Temperature of the Warmest Month
BIO6	Minimum Temperature of the Coldest Month
BIO7	Temperature Annual Range
BIO8	Mean Temperature of the Wettest Quarter
BIO9	Mean Temperature of the Driest Quarter
BIO10	Mean Temperature of the Warmest Quarter
BIO11	Mean Temperature of the Coldest Quarter
BIO12	Annual Precipitation
BIO13	Precipitation in the Wettest Month
BIO14	Precipitation in the Driest Month
BIO15	Precipitation Seasonality
BIO16	Precipitation in the Wettest Quarter
BIO18	Precipitation in the Warmest Quarter
BIO19	Precipitation in the Coldest Quarter

Habitat suitability prediction

Ecological niche modelling analyses were run using Maxent 3.3.3e (Phillips *et al.* 2006; Phillips *et al.* 2017) to predict the bioclimate suitability for each subspecies independently. The maximum entropy (Maxent) algorithm used the bioclimatic layers and presence points to predict the areas with a suitable habitat (Elith *et al.* 2011). Models were built using 75% of the data, while the remaining 25% was considered as test data and was used to train the model. The model accuracy was evaluated by area under the curve (AUC) tests, with anything above 0.95

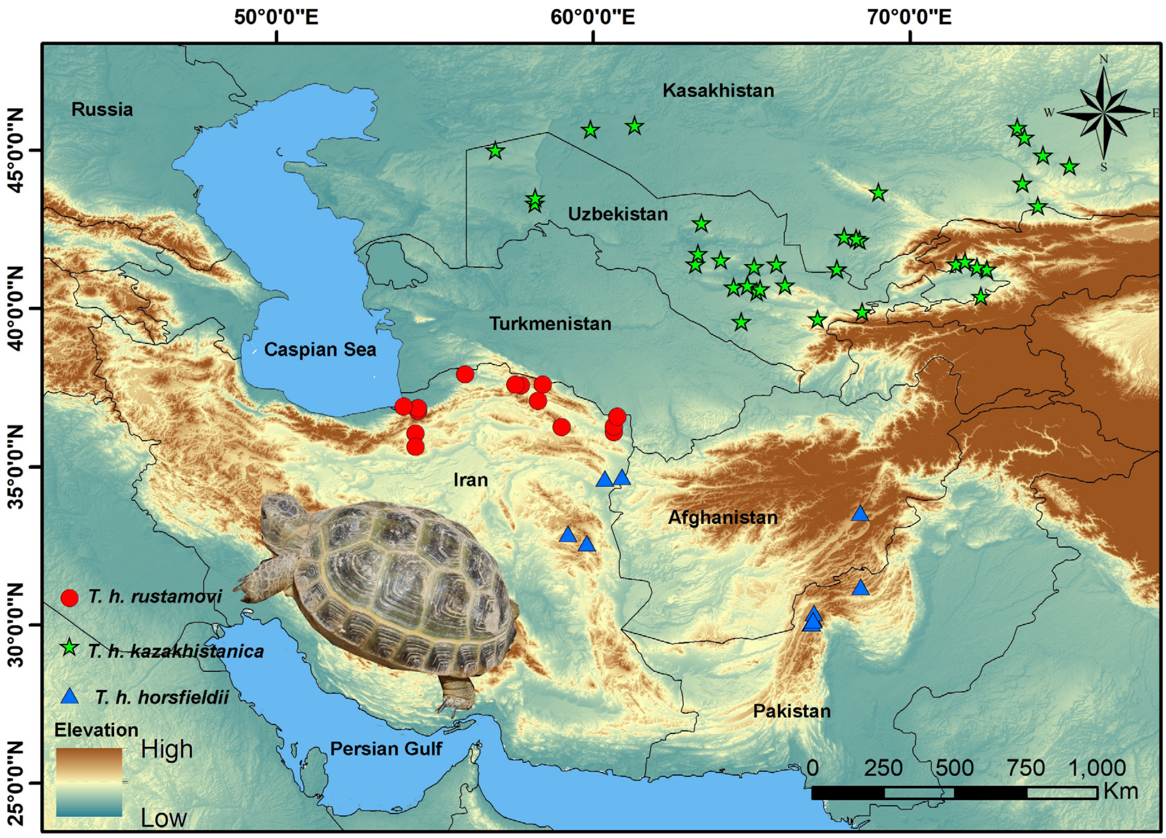

Fig. 1. Distribution of occurrence records of the subspecies of *Testudo horsfieldii* in Central and Southwest Asia.

determined to be a robust estimate of predictability. Ecological niche divergence was tested among the subspecies using ENMTools 1.3 (Warren *et al*. 2010). The software calculated the niche overlap and dose niche identity test based on two indices; Schoener's *D* (Warren *et al*. 2008) and Hellinger's-based *I* (Schoener 1968). Schoener's *D* calculates the suitable range for a given species based on the probability distributions for inhabiting particular regions (cells in the raster grid), calculating the niche overlap based upon the species abundance in those locations; while Hellinger's-based *I* is based purely on probability distributions, without the assumptions of Schoener's *D* (Warren *et al*. 2010).

Point-based analysis

The data for each pixel was obtained using openModeller v. 1.0.7 for all 19 bioclimatic layers and was imported into SPSS 16.0 for the statistical analyses. Differentiations of bioclimate variables between the three subspecies of *Testudo horsfieldii* were evaluated using an Analysis of Variance (ANOVA) to detect the significantly different bioclimate variables ($p < 0.05$). A principal component analysis (PCA) and discriminate function analysis (DFA) were run to examine the niche differences between subspecies.

Results

Ecological Niche Models (ENMs)

All of the ENMs confirmed that the subspecies do not largely overlap in their distribution, except for small areas with a lower suitable habitat (Fig. 2). The AUC values of the ENMs indicated that the models were predicted with a high accuracy (0.937 ± 0.007 for *T. h. horsfieldii*; 0.944 ± 0.010 for *T. h. kazakhstanica*; 0.896 ± 0.064 for *T. h. rustamovi*). The ENM predicted that *T. h. kazakhstanica* is restricted by some bioclimatic conditions such as temperature; according to the results, it mostly prefers a temperature between 20 and 30℃. The subspecies distribution is also restricted by the Kopet Dagh Mountain in the southern part of its distribution, so it cannot disperse southward to Iran (Escoriza & Hassine 2022). By contrast, the predicted suitable habitat for *T. h. horsfieldii* and *T. h. rustamovi* was larger (Fig. 2). The models indicated that the *T. h. horsfieldii* and *T. h. rustamovi* distribution is highly dependent on isothermality (variable BIO3), while *T. h. kazakhstanica* appears to be dependent on the mean temperature of the driest quarter (BIO9) (Table 2).

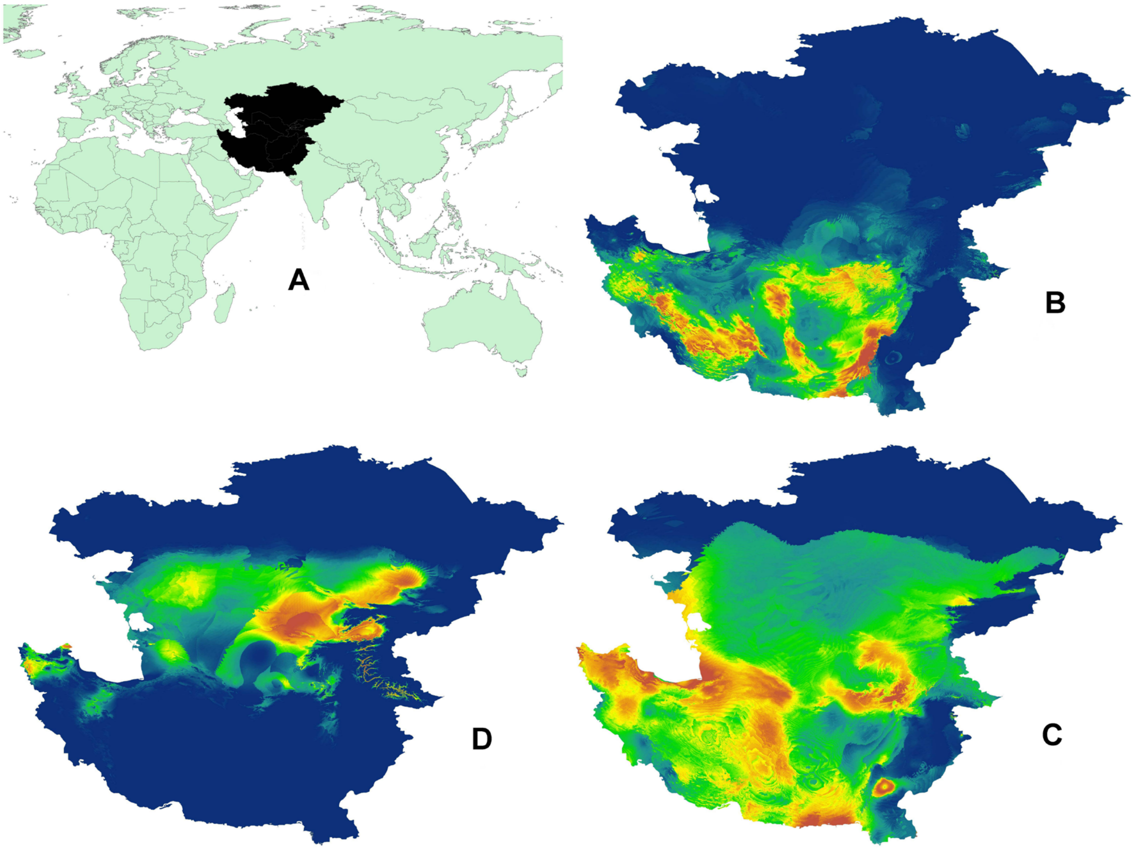

Fig. 2. Habitat suitability predictions for the three subspecies of *T. horsfieldii*. A warmer colour refers to the highly suitable regions. A – Map of the world with the black part referring to the study region; B – *T. h. horsfieldii*; C – *T. h. rustamovi*; D) *T. h. kazakhstanica*.

Table 2

Bioclimate variable contribution percent in the ecological niche modelling of *Testudo horsfieldii*. Bold values refer to the variables with the largest contribution for each subspecies in the ENMs

Variable	*T. h. horsfieldii*	*T. h. kazakhstanica*	*T. h. rustamovi*
BIO3	**59.2**	10.2	**28.8**
BIO8	23.7	5.2	2.1
BIO14	6.3	8.9	0
BIO2	2.8	15.1	0
BIO7	2.5	0.3	9.5
BIO5	2.4	0	1.8
BIO4	1.4	5.3	20.9
BIO17	0.7	4.3	0
BIO15	0.3	6.1	11.3
BIO19	0.2	1.7	4.1
BIO18	0.2	1.3	9.2
BIO13	0.2	3.6	4.5
BIO16	0.1	0.8	0
BIO9	0	**23.4**	0
BIO6	0	0.3	0
BIO12	0	1.5	0.7
BIO11	0	7.4	0
BIO10	0	0.3	3
BIO1	0	4.5	0

Niche similarity test

The niche overlap was calculated by ENMTools 1.3 (Warren *et al.* 2010), which found the lowest niche overlap between *T. h. kazakhstanica* and *T. h. horsfieldii* (Hellinger's-based $I = 0.327$ and Schoener's $D = 0.110$), and the most similar overlap between *T. h. rustamovi* and *T. h. horsfieldii* (Hellinger's-based $I = 0.830$ and Schoener's $D = 0.557$). The two subspecies *T. h. rustamovi* and *T. h. kazakhstanica* (Hellinger's-based $I = 0.646$ and Schoener's $D = 0.365$) showed a similarity between the lowest and highest values (0.110<0.365<0.557). The ENMs between the three subspecies also indicated that the estimated niche models were distinct from the true calculated niche models (Fig. 3; Table 3).

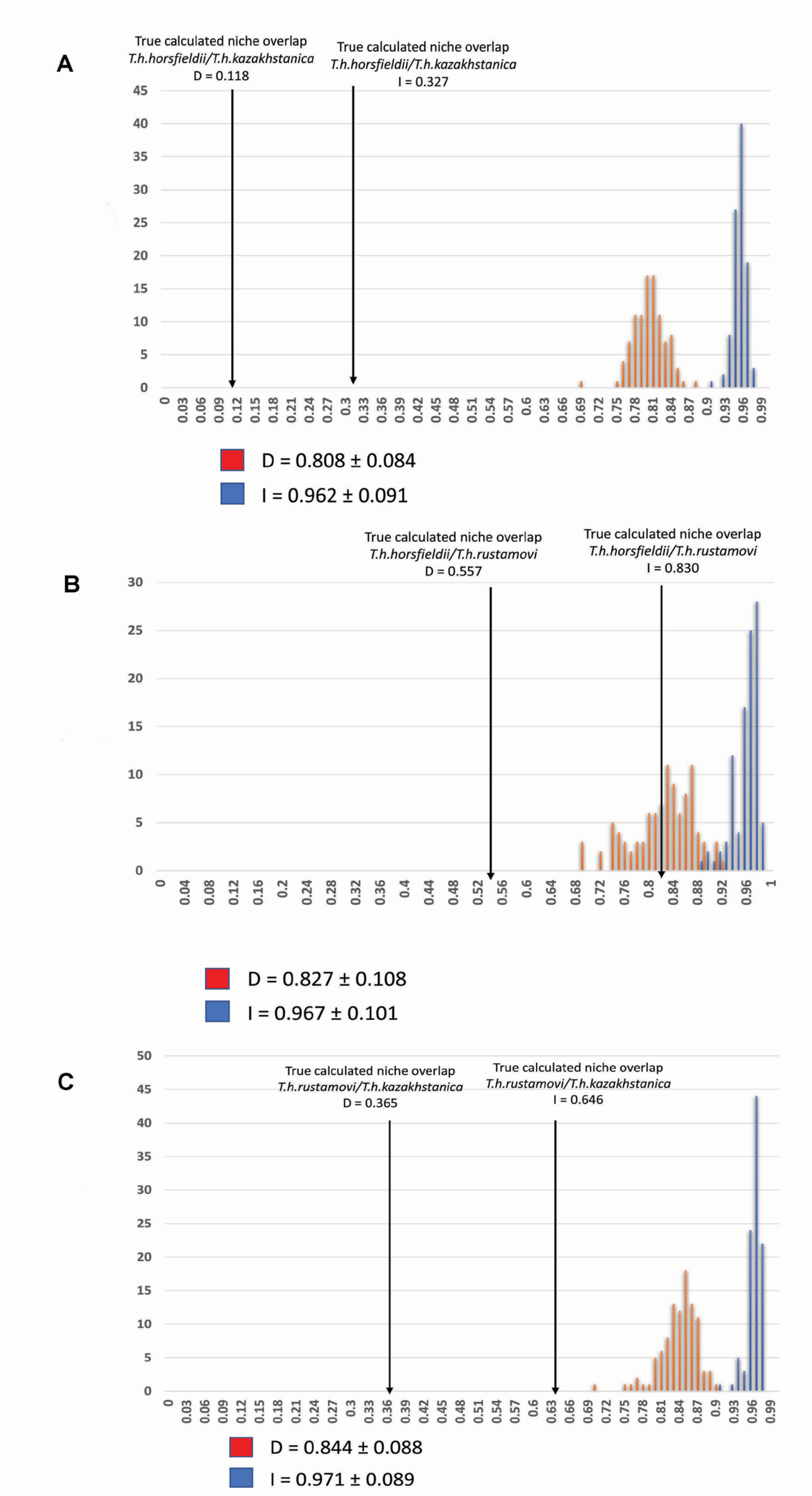

Fig. 3. Results of the identity test. Black arrows refer to the actual niche overlap, as calculated by ENMTools (*D* and *I*). A – *T. h. horsfieldii* and *T. h. kazakhstanica*; B – *T. h. horsfieldii* and *T. h. rustamovi*; C – *T. h. rustamovi* and *T. h. horsfieldii*. The x-axis indicates the values of *D* and *I*, whereas the y-axis refers to the number of randomisations.

Table 3

Pairwise identity test results between subspecies of *Testudo horsfieldii* for both the Hellinger's-based *I* and Schoener's *D* indices. In all of the tests, H_1 is out of the range of H_0, so it can confirm the significant differentiation between those subspecies

Taxon	D_{H0} (mean ± SD)	D_{H1}	I_{H0} (mean ± SD)	I_{H1}
T. h. horsfieldii and *T. h. kazakhstanica*	0.808 ± 0.084	0.118	0.962 ± 0.091	0.327
T. h. horsfieldii and *T. h. rustamovi*	0.827 ± 0.108	0.557	0.967 ± 0.101	0.830
T. h. kazakhstanica and *T. h. rustamovi*	0.844 ± 0.088	0.365	0.971 ± 0.089	0.646

Point-based analysis

Pixel values for each subspecies were obtained and, when the Analysis of Variance (ANOVA) was performed, it was found that 14 variables were significant among them (BIO1, 2, 3, 4, 6, 7, 8, 9, 11, 13, 14, 15, 16, 19) (Table 4). The PCA analysis was run and the first three principal components (PC) explained 90% of the variation, with the following order: 52%, 24% and 13% of all variation, respectively. Three- and two-dimensions plots of the PCA showed the variability among the subspecies (Fig. 4, 5). A discriminant analysis separated the three subspecies further (Fig. 6). Wilks' Lambda for the analysis was obtained as 0.008 ($p \geq 0.05$) and indicated a significant value.

Discussion

The ecological niche modelling (ENM) among the three threatened subspecies of *Testudo horsfieldii* indicates possible niche differentiation between them. The flat, dry and moderate climate regions in central Asia (steppe desert) are primarily occupied by *T. h. kazakhstanica*; whereas the other two subspecies, *T. h. rustamovi* and *T. h. horsfieldii*, are generally more widespread and are found in the foothills of the dry, hot shrubland of eastern Iran, Afghanistan and Pakistan (Kami 1999). Isothermality (BIO3) and the mean temperature of the driest quarter (BIO9) made the largest contribution in the predicted models for these subspecies (*T. h. rustamovi* and *T. h. horsfieldii* and *T. h. kazakhstanica,* respectively). Based on

Table 4

ANOVA result of bioclimate layers among three subspecies. Bold values refer to the significant variables

	Sum of Squares	df	Mean Square	F	Sig.
BIO1	5220.281	2	2610.140	3.868	**0.026**
BIO10	1173.950	2	586.975	1.141	0.327
BIO11	36733.253	2	18366.627	14.790	**0.000**
BIO12	30934.898	2	15467.449	1.985	0.146
BIO13	3672.424	2	1836.212	9.180	**0.000**
BIO14	57.532	2	28.766	3.854	**0.027**
BIO15	6678.230	2	3339.115	18.728	**0.000**
BIO16	18446.402	2	9223.201	6.461	**0.003**
BIO17	350.814	2	175.407	1.735	0.185
BIO18	10.000	2	5.000	.022	0.978
BIO19	11941.837	2	5970.919	6.618	**0.003**
BIO2	8936.822	2	4468.411	59.381	**0.000**
BIO3	1412.361	2	706.181	105.529	**0.000**
BIO4	7.811E7	2	3.905E7	43.658	**0.000**
BIO5	1603.565	2	801.782	1.491	0.234
BIO6	23576.161	2	11788.080	8.287	**0.001**
BIO7	37476.959	2	18738.479	25.025	**0.000**
BIO8	10418.979	2	5209.489	18.185	**0.000**
BIO9	11845.627	2	5922.814	6.677	**0.002**

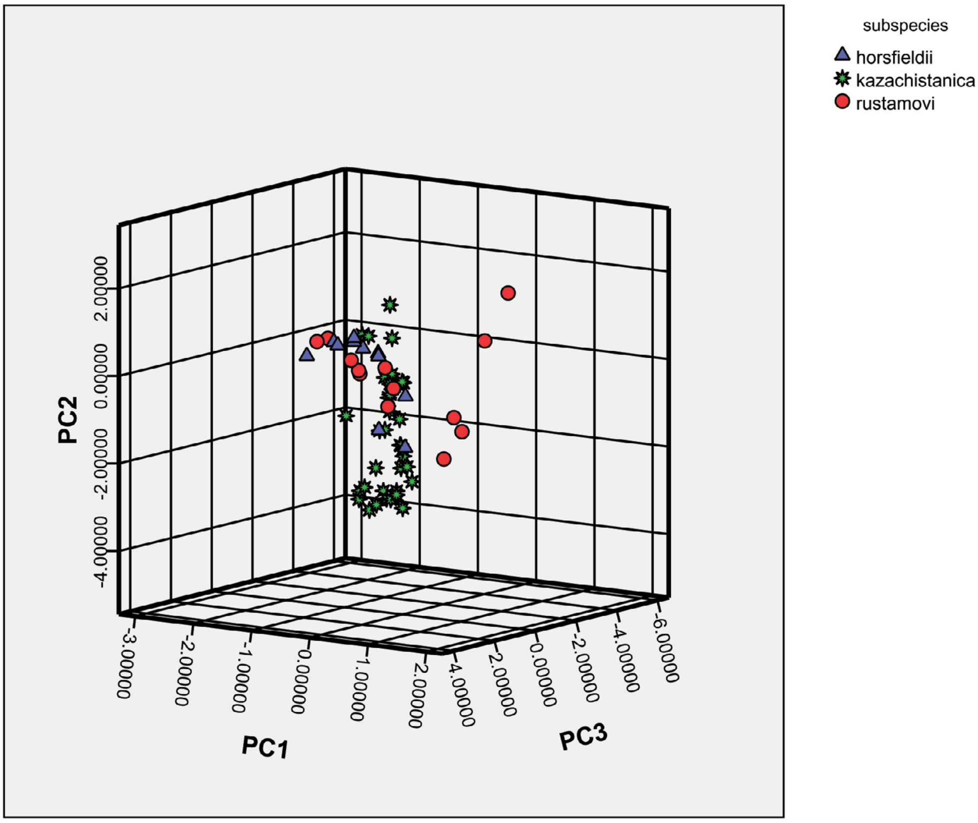

Fig. 4. Principal component analysis (PCA) of niche variation among the three subspecies of *Testudo horsfieldii* as a three-dimensional axis.

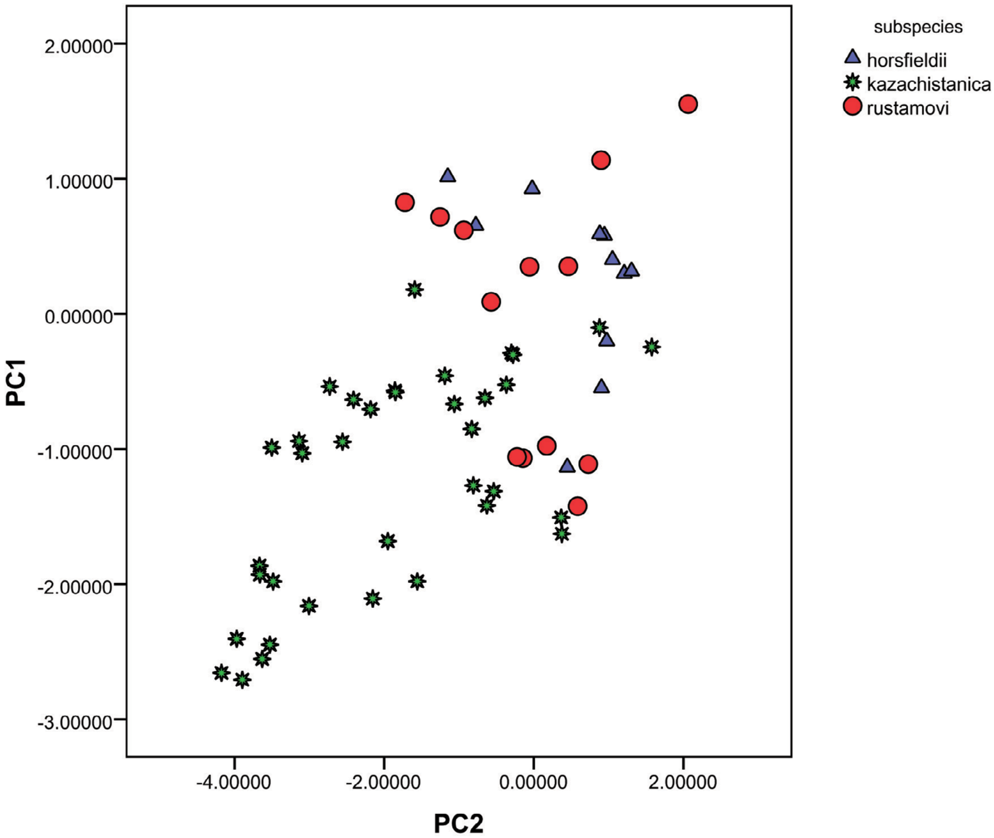

Fig. 5. Principal component analysis (PCA) of PC1 versus PC2, to illustrate the niche variation the three subspecies of *Testudo horsfieldii.*

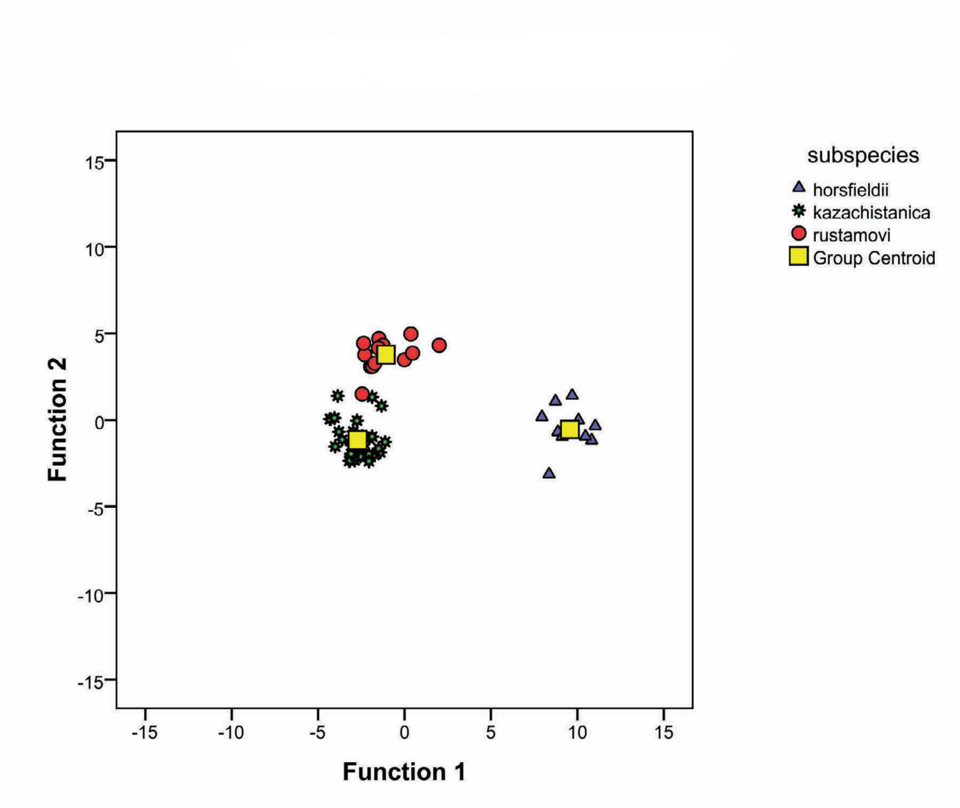

Fig. 6. Canonical Discriminant Functions (1 vs 2) of niche differentiation among the three subspecies of *Testudo horsfieldii*.

BIO9 (Mean Temperature of the Driest Quarter), the most suitable temperature for the subspecies is 25℃, which means temperatures lower and higher than this average value are not favourable for *T. h. kazakhstanica* through the distribution range, because the average temperature can determine the type of vegetation cover and the temperature tolerance will change accordingly. Isothermality appears to be an effective variable for predicting the suitability for both *T. h. horsfieldii* and *T. h. rustamovi*, but the range is wider for *T. h. rustamovi* (from 18% to 50%). The BIO3 range for *T. h. horsfieldii* is 27% to 50%, which means that the diurnal temperature range is higher in northeast Iran than in South Afghanistan and West Pakistan. Furthermore, the niche identity tests among the three subspecies indicated a degree of differentiation between *T. h. horsfieldii* and *T. h. rustamovi*. In addition, the range restricted *T. h. kazakhstanica*. This is the first study to confirm an ecological distinction between these subspecies.

In this study, I statistically evaluated the niche differentiation among *T. h. horsfieldii, T. h. rustamovi* and *T. h. kazakhstanica* using bioclimatic layers. I found a niche differentiation between the distribution range restriction in *T. h. kazakhstanica* and the other two more wide-ranging subspecies. The geographic distribution of each subspecies has an effect on the bioclimatic variability among all the subspecies (Hoskin *et al*. 2005; Stephens & Wiens 2003). Given the specific environmental conditions in each region of their respective distribution, it will be worthwhile to examine the local adaptations within populations in the future (Keller & Seehausen 2012; Wiens 2004).

Finally, in this study, niche differentiation among the three subspecies of *Testudo horsfieldii* was evaluated using bioclimatic layers, with the results indicating that they show some variation. I can therefore suggest that a molecular study needs to be conducted among these subspecies, to reconfirm the hypotheses discussed above and clarify the taxonomic analysis, in order to ensure the conservation of these three subspecies.

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Author Contributions

Research concept and design, Collection and/or assembly of data, Data analysis and interpretation, Writing the article, Critical revision of the article, Final approval of article – S.S. Hosseinian Yousefkhani.

Conflict of Interest

The author declares no conflict of interest.

Supplementary Material

Supplementary Materials to this article can be found online at:
http://www.isez.pan.krakow.pl/en/folia-biologica.html

Supplementary files:

SM.01. Geographic locations of three subspecies in this study.

SM.02. Results of bioclimatic factors' analysis.

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