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Research Article

The Quaternary Range Dynamics of the Dwarf Lizard, *Parvilacerta parva* (Boulenger, 1887) (Squamata, Lacertidae) in the Anatolian Peninsula

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Abstract

The dwarf lizard, *Parvilacerta parva*, is a characteristic member of the steppe biome in Irano - Anatolian biological hotspot. While this lizard has been included in local faunistic surveys and its morphological variation was addressed, no targeted study has been performed on the ecology and distribution of the species. Here we investigate the range dynamics of dwarf lizards during recent glacial and interglacial periods. We looked at the effects of climatic oscillations on species distribution at Present, Last Glacial Maximum (LGM), and Last Interglacial (LIG) periods using ecological niche modeling (ENM), based on our fieldwork and literature data. The model results suggest that the range of dwarf lizards contracted during the LIG and expanded during the LGM, opposite to the pattern observed in many other temperate reptiles. During the LIG, the distribution of the dwarf lizards had been restricted to the mountainous steppe habitats in Northeastern Anatolia, but during the LGM it expanded to the west by including the new steppe habitats in Sultan, Emir, and Murat mountains and adjacent areas. Climatic factors had a strong influence on shaping the spatiotemporal habitat. The Anatolian Biogeographic Region overlaps with Irano–anatolian biodiversity hotspot, reflecting remarkable species richness in this area. However, faunal elements of the hotspots are under threat due to not only global climate change, but also anthropogenic pressures, such as habitat loss and overgrazing. Our results suggest that the dwarf lizards have potential as indicators for tracking the local effects of global climate change as well as human-induced degradation of the steppe habitat.

Keywords: last glacial maximum, last interglacial, ecological niche modeling, species distribution, Turkey

Introduction

The real accessibility of geographically and climatologically supported organismal information proposes new perceptions into evolutionary processes (Rivera et al., 2021). One of the commonly used approaches to examine these viewpoints is to evaluate species distribution patterns via benefiting from ecological niche modeling (ENM) (Phillips et al., 2006). ENM is deeply associated with georeferenced occurrence data of species (set of geographical coordinates where the species is observed) and environmental data (i.e climatological, and/or topological data) and generates potential geographic distribution predictions for the species of interest (Guisan & Thuiller, 2005). Due to its continuously developing stages, this modeling approach not only gives the current potential distribution of the species but also past and future distribution patterns by using reconstructed climate data projections (IPCC, 2007; Waltari et al., 2007).

One of the undeniable factors to understand biogeography is that modern-day populations and communities have been shaped by the interactions of organisms and their environments in the past (Gherghel, 2021). Besides, it is well known that the climatic oscillations in the Late Pleistocene glacial (Last Glacial Maximum: LGM 21000 years ago) and interglacial periods (the Last Interglacial: LIG ~130000-116000 years ago) have a profound influence on ecosystems in the Northern Hemisphere (Conradi et al., 2020; Perktaş, Gür, Sağlam, et al., 2015; Ülker et al., 2018). The "expansion-contraction" model has been used widely and successfully to explain the change in species distribution during climate fluctuations (Horreo et al., 2018; Provan & Bennett, 2008). According to this model, the climate during the glacial periods was too cold and dry for the survival of most species within their present-day range, so they were retreating to warmer parts of the range at lower latitudes. Thereafter, the species recolonized the new areas at higher elevations with a range expansion during the interglacial periods. However, this model mostly applies to temperate species and is less suitable for those species that have preferences to drier and colder habitats (Gür, 2013).

Studies in the last two decades have uncovered the role of the Anatolian Peninsula as a refugium for several taxa (Gür, 2013; Korkmaz et al., 2014; Kornilios et al., 2012; Perktaş et al., 2015a; Perktaş et al., 2015b; Rokas et al., 2003). Wetter conditions with a higher precipitation rate during the LGM along the western part of the peninsula (Sarıkaya et al., 2008) enabled wider suitable vegetation ranges for the species, which are adapted to the poikilothermic strategy. Multiple studies demonstrated that lizards are particularly good model organisms to examine the evolutionary history dynamics via ENM predictions in terrestrial habitats (Gül et al., 2018; Kurnaz et al., 2016). Because ENM has been widely used to assess a geographic range of species via abiotic environmental conditions (i.e. temperature, precipitation dynamics, and topography) (Kozak et al., 2008). The reason behind this phenomenon was described as the fundamental niche of the species by (Hutchinson, 1957).

The Anatolian Biogeographic Region includes a steppe and steppe forest region of 321754 km2, however, the actual range of the steppe vegetation is limited to 180316 km2 (56% of the potential distribution). The rest of the region (44%) has been transformed into croplands (Ambarlı et al., 2016). The Anatolian steppes host 63% of the herpetofauna diversity in Turkey (Ambarlı et al., 2016). While the complex steppe biome includes a large number of species (Zeng et al., 2014), examining a single representative species can be a practical way for tracing the effects of climate on the Spatio-temporal distribution of the entire ecosystem.

The dwarf lizard, *Parvilacerta parva* (Boulenger, 1887), is a diurnally active species distributed along the steppes and alpine meadows of central and eastern Anatolia and adjacent Armenia. Its chorotype is described as Armeno-Anatolian endemic (Kurnaz, 2020; Sindaco et al., 2000). The geographic distribution of the dwarf lizard has two major climate zones, Central and North-Eastern Anatolia, that are drier and colder than the other zones in Turkey (Beck et al., 2018; Unal et al., 2003). The annual activity period of the dwarf lizards is between mid-April and the end of September, and they hibernate during the winter and very early spring (Arakelyan et al., 2011). This strong dependence on abiotic factors makes the dwarf lizards highly suitable organisms to study via ENM.

Our main aim is to evaluate the effects of climate oscillations on the distribution pattern of the dwarf lizard. We hypothesized that their distribution should have contracted during interglacial climatic conditions (LIG and present) and expanded during drier and colder conditions in LGM. Additionally, we speculate about the role of the Anatolian steppes in the distribution of dwarf lizards throughout the LIG and LGM.

Material and methods

Study area and input data

This study was conducted within 25-460 East Longitude and 34-430 North Latitude, covering the Anatolian Peninsula, the Caucasus Region (since part of the dwarf lizard range in Armenian steppe habitats), and the Levantine Region (where the sister species, *Parvilacerta fraasi*, occurs). A total of 119 occurrence records were gathered from our field observations and the literature records (Atagün, 1984; Baran et al., 1992; Basoğlu & Baran, 1977; Kumlutaş et al., 2004; Mülayim et al., 2001; Peters, 1962) (Supplementary File 1). In cases where the locality information was not directly given in any GPS format, an online geographic system software (i.e. Google Earth Pro) was used to determine the most accurate location. The map of the current distribution for the dwarf lizards is shown in Figure 1. To avoid the spatial sampling biases and misinterpretation of the distribution map, these occurrence records were spatially rarefied by removing at least one locality in each 10 km by using SDM Toolbox 2.0 (Brown, 2014).

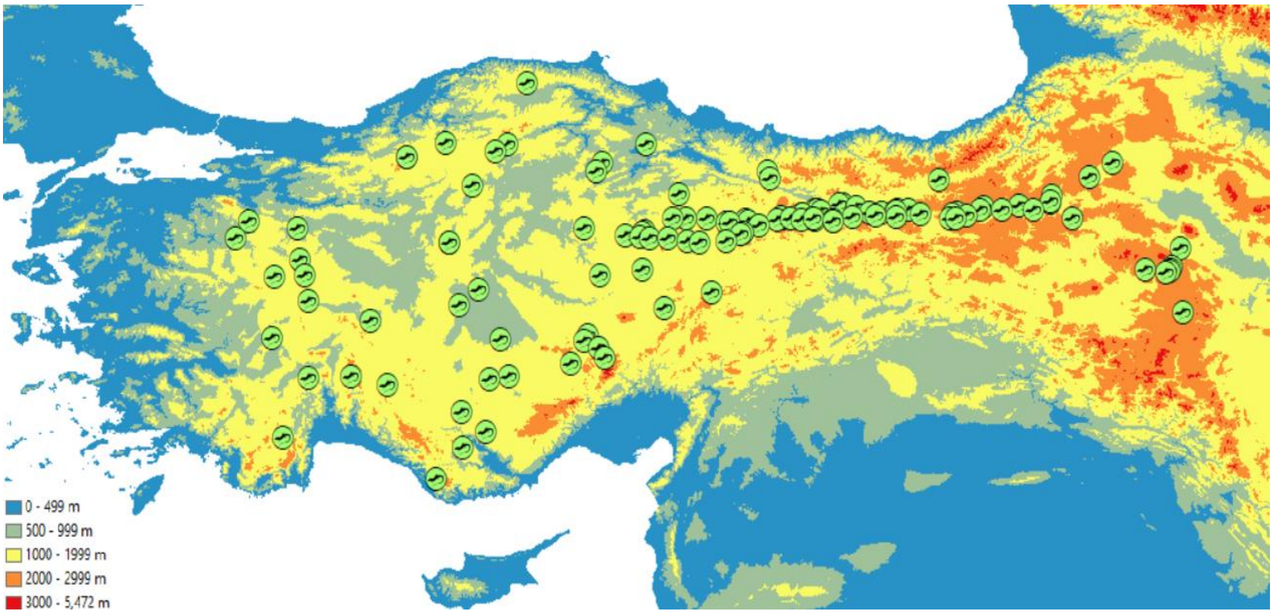

Figure 1. Species occurrence records for the dwarf lizard in Anatolia

Nineteen bioclimatic, and one topographic (elevation) parameter were downloaded from

WorldClim as v.1.4 (Hijmans et al., 2005; www.worldclim.org) in 2.5 Arc Second spatial resolution (~4.63 km at the equator) (Supplementary File 2). In addition, to present climatological parameters, the Model for Interdisciplinary Research on Climate (MIROC) was used for paleoclimatological data on LIG and LGM (Watanabe et al., 2010). The resolution of the LIG climatic data was 30'', therefore we converted these data to a resolution of 2.5' for their compatibility with Present and LGM. All layers were clipped by using ArcGIS 10.6.1 (ESRI) to fit the study area. Correlation coefficients between variables were calculated in R 3.6.3 (R. Core Team, 2018) and highly correlated variable pairs ($r \geq |0.8|$) were excluded from analysis for eliminating the adverse consequences from other parameters (Table 1).

Table 1. Pearson correlation table of variables for the dwarf lizard

	Bio_2	Bio_3	Bio_4	Bio_5	Bio_6	Bio_7	Bio_8	Bio_9	Bio_10	Bio_11	Bio_12	Bio_13	Bio_14	Bio_15	Bio_16	Bio_17	Bio_18	Bio_19	ELEV
Bio_1	-0.06	0.69	-0.67	0.67	0.94	-0.65	-0.20	0.55	0.89	0.96	-0.13	-0.12	-0.37	0.32	-0.09	-0.37	-0.18	0.41	-0.89
Bio_2		**0.34**	**0.27**	**0.48**	**-0.29**	**0.57**	**0.34**	**-0.02**	**0.04**	**-0.18**	**-0.72**	**-0.63**	**-0.63**	**0.19**	**-0.62**	**-0.61**	**-0.45**	**-0.60**	**0.03**
Bio_3			-0.79	0.36	0.72	-0.58	-0.03	0.33	0.41	0.77	-0.30	-0.34	-0.57	0.28	-0.28	-0.53	-0.22	0.20	-0.72
Bio_4				0.02	-0.86	0.94	0.22	-0.31	-0.28	-0.84	-0.18	-0.06	0.17	-0.13	-0.11	0.14	-0.08	-0.57	0.71
Bio_5					0.39	0.12	0.01	0.48	0.87	0.47	-0.52	-0.40	-0.57	0.36	-0.39	-0.58	-0.48	-0.12	-0.50
Bio_6						-0.87	-0.28	0.52	0.71	0.99	0.08	0.03	-0.24	0.25	0.07	-0.23	-0.05	0.58	-0.85
Bio_7							0.31	-0.30	-0.30	-0.82	-0.36	-0.25	-0.05	-0.08	-0.29	-0.07	-0.20	-0.70	0.65
Bio_8								**-0.15**	**-0.19**	**-0.26**	**-0.49**	**-0.46**	**0.06**	**-0.39**	**-0.50**	**0.10**	**0.23**	**-0.67**	**-0.01**
Bio_9									**0.55**	**0.52**	**-0.09**	**-0.10**	**-0.39**	**0.22**	**-0.08**	**-0.40**	**-0.48**	**0.24**	**-0.35**
Bio_10										0.75	-0.24	-0.16	-0.37	0.36	-0.14	-0.39	-0.30	0.23	-0.70
Bio_11											0.00	-0.03	-0.32	0.29	0.01	-0.31	-0.11	0.53	-0.87
Bio_12												0.93	0.48	0.10	0.93	0.47	0.25	0.77	0.21
Bio_13													0.36	0.33	0.99	0.33	0.11	0.77	0.26
Bio_14														-0.66	0.30	0.98	0.80	0.05	0.19
Bio_15														**1.00**	**0.38**	**-0.71**	**-0.65**	**0.48**	**-0.06**
Bio_16																0.27	0.08	0.81	0.23
Bio_17																	0.82	0.02	0.16
Bio_18																		-0.01	-0.14
Bio_19																			-0.25

Ecological Niche Modelling (ENM)

We used the maximum entropy machine learning algorithm (MaxEnt), v 3.4.1 (Phillips et al., 2017) to construct the models under Present conditions and projecting to LIG and LGM. MaxEnt is a useful and widely adopted tool that uses only presence records to get a high model performance even with low occurrence data (Merow et al., 2013). The following settings were applied to the candidate models: the convergence threshold is 0.00001, the maximum number of iterations is 500, the regularization multipliers are 0.1, 0.2, 0.3,...1) , five feature classes (hinge, threshold, product, quadratic, and linear). 20% of occurrence data and 8263 background points were used as test points. To check the importance of variables, the jackknife test was used and ten bootstrap replicates estimated statistical support for the constructed models (Elith et al., 2011). The power of the model was determined by the surface area under the receiver operator (ROC) and the area under the curve (AUC) (Peterson et al., 2008; Phillips et al., 2017). The AUC is a score between 0.5 (no better than random prediction) and 1 (the flawless predicted model).

Results

Pearson correlation coefficients among climatic and topographic layers indicated that four parameters varied 8.5 % to 72.8 % can be taken into account for the species distribution model of dwarf lizards. These were Bio 2 (Mean Diurnal Range), Bio 8 (Mean Temperature of Wettest Quarter), Bio 9 (Mean Temperature of Driest Quarter), and Bio 15 (Precipitation Seasonality). The contributions of the variables are given in Table 2. Based on the results, Bio 9 made the largest contribution to species presence at 72.8 %, and Bio 15 made the lowest contribution at 8.5%. However, the possible effect of Bio 8 was ignored due to its irregular pattern as a climatological parameter. The estimated training AUC value (mean ± SD) from rarefied 103 occurrence points was 0.886 ± 0.027 indicating that the AUC value is sufficiently high to keep in the analysis. Besides, the small SD for the mean AUC indicated that the ENM performance was sufficiently strong in response to variation in the occurrence records for training and test. Lastly, the model constructed from the test occurrence records performed better in each replicate compared to a random prediction ($P < 0.001$).

Table 2. Contribution of variables to model prediction

Variable	**Percent contribution**	**Permutation importance**
Bio_9	72.8	79.6
Bio_2	17.8	15.2
Bio_15	8.5	4.1
Bio_8	0.9	1.2

The logistic outputs of the ENM for three time periods (LIG, LGM, and the present) are shown on Figure 2 a-c. The model prediction for the present period was profoundly consistent with the actual distribution range of the dwarf lizard, also suggesting that the dwarf lizard is almost at equilibrium with the climate (Figure 2 a). This map includes the steppe vegetation and alpine meadows of the Anatolian Peninsula, especially on the central and eastern side, which the species preferably inhabit. However, even though the species range extended to the western part of the Peninsula, the predicted range does not display a continuity pattern like the central and the eastern parts.

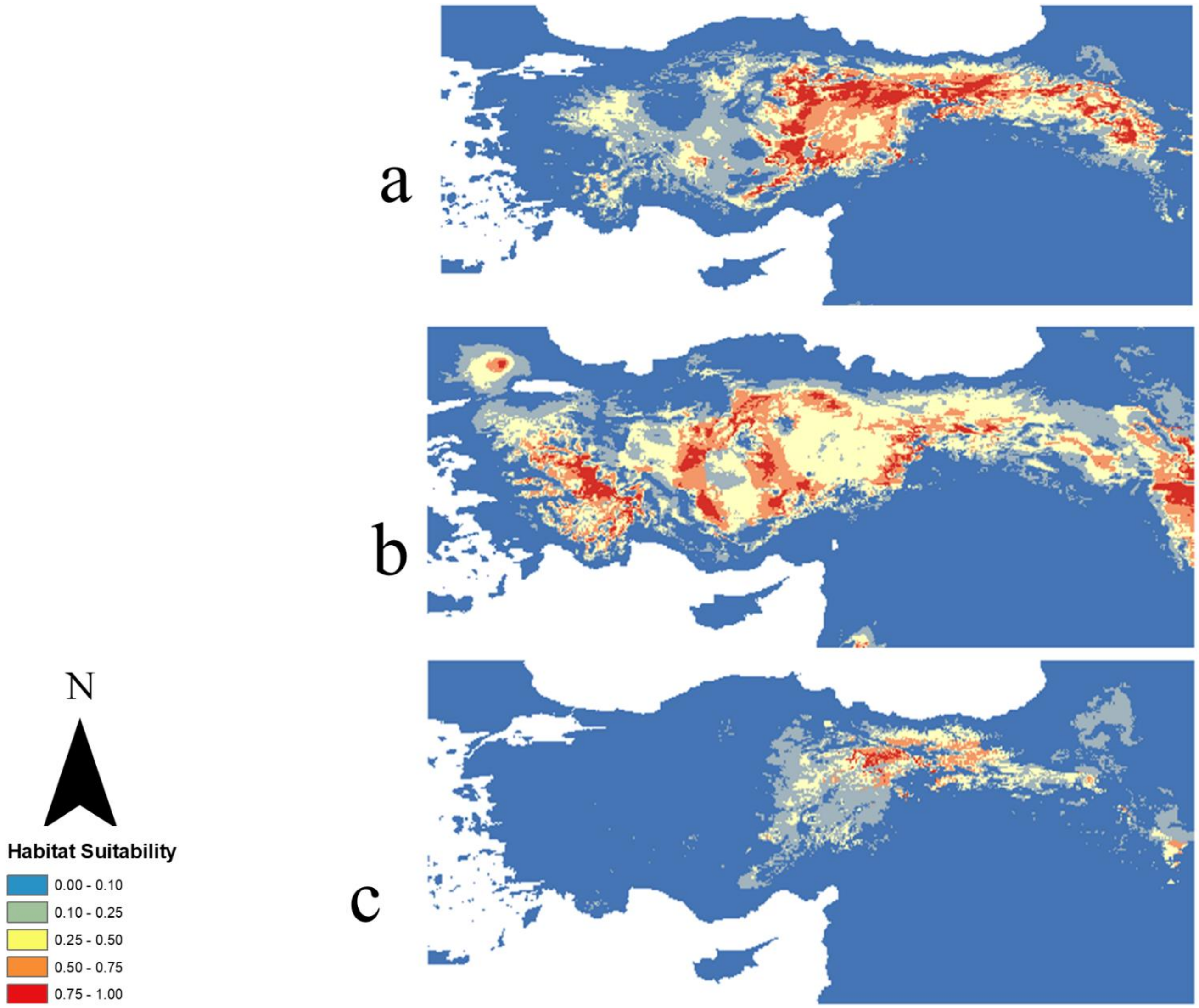

Figure 2. Habitat suitability predictions of the dwarf lizard for a. Present, b. LGM, c. LIG

Discussion

Several biotic and abiotic factors have large effects on the species' distribution (Peterson, 2011). Therefore, to perceive the responses of dwarf lizards to the climatic oscillations through the Late Quaternary glacial-interglacial cycles, we used ENM as a useful tool in analytical biology, to evaluate the range of species and develop hypotheses about their evolutionary history. One of the most useful properties of ENM is that it only requires species occurrences and environmental variables. The Irano - Anatolian biodiversity hotspot is one of the three worldwide hotspots spanning the Anatolian peninsula (Mittermeier et al., 2011). The steppic parts of the Anatolian Biogeographic Region overlap with this hotspot, which hosts one of the seven identified grassland hotspots in the Palearctic Realm (Figure 3) (Dengler et al., 2014). Three factors contribute to the high level of biodiversity in this region: (i) its biological intersection position among Asia, Europe, and Africa continents (Kışlalıoğlu & Berkes, 1987), (ii) land-use history (Ambarlı & Bilgin, 2014), and (iii) wide amplitude of abiotic factors (geology, soil type, climate regimes, etc.) (Şekercioğlu et al., 2011).

The reactions of dwarf lizards to the climate changes through the Late Quaternary epoch are comparable to that in other steppe-dependent species, such as Anatolian ground squirrels (Gür, 2013). The range of dwarf lizards contracted during the interglacial periods and expanded during the glacial periods. In other words, the general pattern of inter-glacial expansion and glacial range contraction of the temperate species ranges (Hewitt, 1999; Hewitt, 2000) does not apply to dwarf lizards. Although the phylogeography of the temperate and cold-adapted species has been comprehensively studied so far, the third group of species, like the dwarf lizard that is adapted to dry and occasionally warm conditions, and occupies steppes and other types of dry meadows, have received less attention (Kajtoch et al., 2016). Distributions of populations of mountainous and boreal taxa were narrower during the inter-glaciations than in glacials, including the Holocene epoch (Schmitt, 2009; Schönswetter et al., 2005; Varga, 2009). Importantly, steppe species are the most threatened organisms and steppes are the most threatened ecosystems in the European continent due to natural (i.e. drying and regional rainfall shifts, enhancing fire risk and restraining the capacity of species to move), and to the human-induced degradation and fractionation of steppes (Cremene et al., 2005; Fekete et al., 2014; Janišová et al., 2011). Further studies in the overlapping areas of the Anatolian Biogeographic Region and the Irano-Anatolian hotspot might also point out that these threats can be valid for these areas.

The fact that the predicted distribution of the dwarf lizards during the present period corresponds closely to its actual range, suggests that dwarf lizards are close to equilibrium with climatological dynamics (Figure 1, 2a). Moreover, this equilibrium also makes the reconstructed past predictions consistent, due to assumptions of species - climate equilibrium and stability of ecological niches over time have been met (Nogués-Bravo, 2009). The bio-climatological envelope that was made by BIOs 2, 8, 9, and 15 that are related to dryland ecosystems has met the expectations for a steppe habitat specialist species that includes the dwarf lizard. The Bio 9 refers to the "mean temperature of the driest quarter", Bio 2 – the "mean diurnal range", and Bio 15 is "precipitation seasonality". These three variables contribute ~ 99.1% to the distribution of the dwarf lizard and have also shaped the ecosystem services of habitats (Chen et al., 2015; Petrosyan et al., 2019). However, the possible effect of Bio 8 "Mean Temperature of Wettest Quarter" (percent contribution: 0.9%, permutation importance: 1.2 %) was ignored due to its odd spatial irregularities within the frame of discontinuities between adjoining pixels within the nonappearance of ecological gradients on the

ground as a climatological parameter (Ashraf et al., 2017; Behroozian et al., 2020).
Anatolian steppes expanded remarkably as a result of cold and dry conditions during the glacial periods (Atalay, 2020). It is most likely that dwarf lizards have followed this habitat expansion. For instance, the steppes in Sultan, Emir, and Murat Mountains may have enabled the lizards to extend their distribution through the LGM (Figure 2b). However, the climatic conditions in the interglacial periods (LIG, present caused the contraction of dwarf lizard populations (Figure 2a, c).

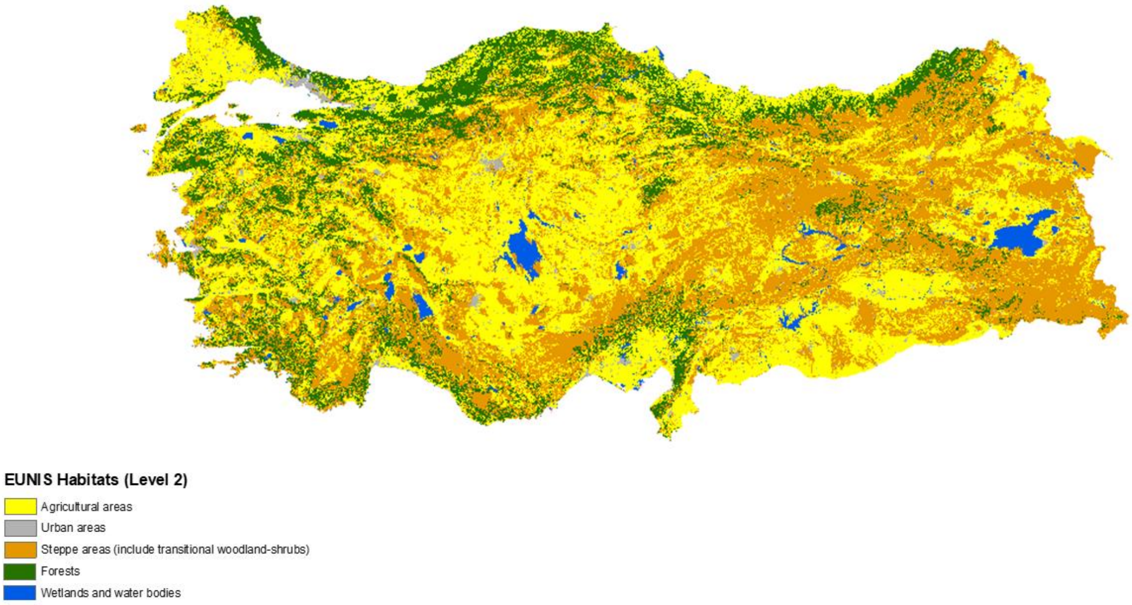

Figure 3. The general land cover types of Turkey (modified from Corine 2018)

Conclusion

Incidentally, as these lizards are currently in the contraction phase, their habitat is further deteriorating due to anthropogenic degradation, such as overgrazing (Fırıncıoğlu et al., 2009). We argue that the dwarf lizard can be considered an indicator species for the Anatolian dry steppe habitat. Further studies on the molecular biogeography of dwarf lizards will help to reveal more details of the history of range dynamics in this lizard species.

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